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## Pro-social Behavior

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## Definition

*Pro-social behavior* is any voluntary action or set of actions performed by an individual that serves to benefit another individual or individuals, whether that action has a direct or indirect benefit to the actor.

## Introduction

Pro-social behavior, or behavior that benefits another individual, is of interest to researchers studying both humans and other animals. Perhaps because it is of widespread interest, there are a variety of different usages across disciplines. For our purposes, pro-social behavior encompasses all acts that benefit another individual, including altruism and reciprocity (the former being differentiated by a cost to the actor and the latter by the alternation of benefits between the individuals involved; see entries in this encyclopedia for more detail). Importantly, pro-social behavior does not necessarily imply pro-social *intent*; animals may act in a way that is functionally pro-social without any intention of doing so (see discussion of function versus mechanism, below). For instance, an individual may provide a benefit to another as a side effect of an action that benefits himself or herself, and there is no assumption that animals understand their actions as pro-social. Thus, it is more appropriate to discuss whether an animal engages in pro-social behavior, which is agnostic to intent, rather than whether they behave pro-socially, which is often assumed to imply active intent on the part of the actor.

The hypothesized function of pro-social behavior is to strengthen affiliative bonds, which are critical for group-living species that must work together in at least some contexts. Pro-social behavior includes behaviors such as grooming, support, or food sharing that are widespread across species, as well as behaviors seen in a more limited number of species, such as alarm calls given to alert conspecifics to a predator's presence. Despite the hypothesized importance of pro-social behavior, it has proven remarkably difficult to demonstrate this behavior in experimental contexts. This could be because pro-social behavior is rare, of course, but this runs counter to evidence from the field, which in some species indicates fairly frequent pro-social behavior

across a variety of contexts. Some authors have argued that this apparent contradiction is more likely due to subjects not understanding the purpose or mechanics of the tasks designed to elicit pro-social behavior than to pro-social behavior being rare in reality. Moreover, despite their challenges, due to the ability to manipulate factors one by one, experiments are key for understanding the contexts in which pro-social behavior occurs and determining what, if anything, subjects understand about their behavior.

Because of the breadth of potentially pro-social behaviors, for this entry we narrow to focus to a recent body of work considering the degree to which animals make decisions that benefit others. Although such decisions typically involve a small cost (the opportunity cost of making the decision), in order to maximize the chances of finding pro-social behavior, most do not entail any other costs to the actor making the choice and are therefore not altruistic. Moreover, most experiments explicitly avoid the possibility of reciprocity. Nonetheless, such work is important to consider within the contexts of both altruism and reciprocity, which we do briefly at the end of this entry. Finally, unless otherwise specified, we throughout refer to pro-social behavior in the functional sense of behavior that provides a benefit to another but remains agnostic as to the intent of the actors.

## Pro-social Behavior in Naturalistic Settings

Although recent work has focused on experimental contexts designed to understand the mechanisms underpinning pro-social behavior, original work on the topic derives from field observations or from observations made in naturalistic captive populations. Perhaps the most commonly reported pro-social behavior is grooming. Although grooming serves a biological function (i.e., removing parasites, which helps maintain health), many animals, including primates, engage in far more grooming than is necessary for health purposes and subjectively appear to enjoy being groomed. In addition, endocrine changes have been observed in conjunction with social grooming, indicating

that social grooming has a physiological effect. As mentioned above, there is evidence that grooming strengthens social bonds, which can be critical for fitness. Recent work in baboons shows that females with more friends both live longer and have more surviving offspring than those with fewer friends (Silk et al. 2003). Grooming is not particularly costly nor is it zero sum (i.e., grooming one animal does not remove the possibility of grooming another, the way that food shared with one individual cannot then be shared with another), which may contribute to why it is such a widespread pro-social behavior.

Food sharing, a costlier pro-social behavior, has been seen in several primate species; however, food sharing occurs in much more limited contexts than grooming. For example, chimpanzee food sharing is generally limited to sharing with infants, excepting situations in which individuals work together to acquire food. Chimpanzees show coordinated hunting, or at least simultaneous hunting with allies, and often share the spoils of a hunt with others that participated in the hunt, even those that are not related to them (Boesch and Boesch 1989). Importantly, forest-dwelling chimpanzee populations, such as those in the Taï forest in the Ivory Coast, where tree cover is contiguous, are much more likely to meat-share than populations that live in more open grounds, such as the Gombe populations. This is presumably because the smaller, lighter monkeys they hunt can more easily escape in contiguous forest, where they can more easily run between trees than the heavier chimpanzees, than in isolated trees, where they can be treed by individual chimpanzees. This may make coordination more essential, and meat-sharing based on hunt participation has been suggested to be a key feature in maintaining cooperative hunts. While other species engage in cooperative hunting and prey-sharing based on hunt participation (i.e., lions), this type of active meat-sharing post-hunt is more rare.

Food sharing in the form of allonursing is also seen in some species. Although uncommon, it does occur in primates; golden snub-nosed monkey and capuchin monkey females have been reported to nurse each other's offspring. Allonursing has been most often observed in

species that typically reproduce in litters, such as rodent and canid species. This is hypothesized to be because a mother nursing a litter is already expending a lot of energy producing a large amount of milk, so it may be that nursing additional young incurs a low additional cost relative to the overall cost already incurred (MacLeod and Lukas 2014). However, allonursing in these primates, who produce only a single offspring at a time, is more costly. It is possible that this occurs in species in which females form very long-term relationships, changing the cost-benefit ratio, similar to what is seen with cooperative breeding.

Perhaps the most costly pro-social behavior seen in natural contexts is adoption of non-offspring, which incurs an individual cost of energy, time, and a potential loss of reproductive fitness. Both male and female wild chimpanzees have been observed adopting non-kin orphaned infants in their group upon the death of the infant's biological mother (i.e., Boesch et al. 2010). Such adoptions generally involve multiple pro-social behaviors; for example, male adopters have been observed sharing food with their adoptees, as well as providing support in aggressive conflicts with other group members, and female adopters may allonurse. Although most (but not all) cases of primate adoption occur on the death of the mother, other mammals adopt non-kin offspring following separation from their own infants (i.e., northern elephant seals). Such adoption is unlikely to be due to a lack of recognition, because playback experiments have shown that elephant seal mothers can acoustically distinguish their pups from unknown pups, suggesting that they are actively accepting non-kin offspring.

Of course, adoption may sometimes benefit the adopters, emphasizing the fact that lines can blur between pro-social and self-beneficial behavior. Brood size in the lesser snow goose can fluctuate post-hatch and past the stage where goslings would be expected to recognize their parent, including *increasing* brood sizes, which suggests emigration of new chicks (Williams 1994). These increases in brood size appear to increase the "social rank" and viability of the group as a whole and appear to have little extra cost to the parent of the brood. Such alloparenting occurs in

other birds, and aside from the social rank hypothesis, others have suggested that tolerance of added non-kin to a brood may also increase the reproductive fitness of the parent by providing their biological offspring with proximate non-kin that become potential mates.

Finally, there are numerous anecdotes about pro-social behavior, particularly in species such as primates, dolphins, elephants, and dogs. This list, not surprisingly, correlates with species that are both most often observed and are among the largest brained species; it is likely that similar behaviors observed in a species with a smaller brain would be interpreted very differently. Aside from this reporting bias, anecdotes are not typically used in animal behavior because of the risks of false positives (i.e., one pro-social-looking behavior is reported and thousands of cases in which the animals are not pro-social are not) and the risk of over-interpreting the animals' actions, not to mention it is impossible to determine the subjects' motivations. In many cases, purported pro-social behavior could be explained in another way, and the two interpretations cannot be disambiguated. For instance, in a famous case in which a gorilla female carried a young human child who fell into the exhibit to the keepers waiting at the enclosure's door, there was a debate over whether her behavior represented a recognition of the young boy's predicament and an idea for how to solve it or whether she was following the behavior pattern she had been rewarded for previously by the keepers.

Despite these challenges, however, anecdotes can provide key insight into rarer forms of pro-social behavior. Although they cannot replace careful experiments, they can provide suggestions as to what is worth considering. For instance, there are numerous anecdotes of apes helping others who need assistance with no apparent gain on their part. This includes reports of acquiring hard-to-reach foods for older individuals or rescuing youngsters from the moat. There is some evidence of cross-species pro-social concern, such as a female bonobo who found a stunned, but otherwise unharmed, bird on the ground in her enclosure, carried it high into a tree, and, attempting to orient its wings correctly, set it

loose into the air (de Waal 2009). While we can debate the weight we should put on these anecdotes, one can test them by developing experiments that replicate some aspect of the context. Indeed, given the preponderance of cooperative or pro-social interactions now documented in the literature, including across different species, anecdotes like this are useful for developing new lines of inquiry.

## Experimental Evidence of Pro-social Behavior

Despite the substantial body of field literature implying pro-social behavior, most of this fieldwork is observational, limiting our ability to determine subjects' motivations and the underlying mechanisms. As a result, recent work has moved to the lab, where conditions can be tightly controlled. Somewhat surprisingly, however, finding evidence of pro-social behavior in experimental tests has proven to be difficult. While this could indicate that the supposedly pro-social behavior witnessed in observational contexts has other explanations, it is also possible that the subjects either failed to understand the purpose or mechanisms of the tasks (i.e., did not understand the contingencies of an apparatus), or that the experiments did not involve a context that would typically elicit pro-social responses. The majority of the work in this area has been in primates, although it will be important to see how other species respond as well.

The most commonly used paradigm is the *pro-social choice task*. The basic task involves giving the subject a choice between an option that rewards both subject and a conspecific (the "pro-social" option) and an option that rewards only the subject. Subjects are said to behave pro-socially if they choose the pro-social option more frequently when in the presence of a conspecific – that is, when there is someone to benefit – than when alone (called the partner absent condition). This partner absent control is critical for useful interpretation of results, because without it, it is difficult to assess if subjects are making choices based on some criterion irrelevant

for pro-social choice (for instance, the total amount of food that is present or a mistaken belief that they will be able to access the food). A benefit of this task is that, aside from testing pro-social behavior, it is easy to include variations that alter the benefit to the actor or the action required to benefit the recipient (effectively changing the "cost").

This task has been used in a variety of species that have shown naturally occurring pro-social behavior, but nonetheless, results are quite mixed. The history of pro-social studies in chimpanzees nicely illustrates the challenges of designing a task for complex social behaviors. Early studies in chimpanzees, all based on the pro-social choice design, yielded no evidence of pro-social decision-making. In one early task, chimpanzee subjects were given a choice between two platforms, each of which contained a reward for the subject and one of which also contained a reward for the conspecific (if present). Rewards were obtained by pulling in a "sweeper" that brought the foods within reach. Chimpanzees were no more likely to choose the option that delivered food to both themselves and their partner when the partner was present than when they were absent, which they hypothesized meant that the chimpanzees were not choosing to be pro-social (Silk et al. 2005). Another study, completed independently but at the same time, used a slightly different design and found the same results (Jensen et al. 2006). In addition to the pro-social option, this latter study included both an altruism condition (subjects could reward partners, but not themselves) and a spite condition (subjects could actively block partners from receiving food), yet the chimpanzees never responded in a way that indicated that they were sensitive to anything but their own outcomes. This study also included an additional control that was not possible in the first study but that suggested that the subjects understood which foods were available in the different conditions.

One hypothesis for why the chimpanzees were not pro-social was that they were so focused on their own rewards that they failed to pay any attention to their partners. This could have explained their apparent understanding of the

task, yet their failure to behave pro-socially. Thus, in a subsequent design, chimpanzees were given the option to acquire their own reward followed by their partner's. The prediction was that if the challenge for the chimpanzees was that they were too focused on their own outcomes to pay attention to their partner's needs, this would allow them to do so. Nonetheless, subjects again failed to choose the option that helped their partner at any higher rate when their partner was present than absent (although they always obtained their own food; Vonk et al. 2008). Another hypothesis was that the chimpanzees may not have behaved differently because there was no reason to do so; after all, one key hypothesis for the evolution of helping behavior is reciprocity, and in these studies the partner was never in a position to reciprocate. To test whether reciprocity played a role, pairs received the same pro-social choice task as in Silk et al. (2005) but alternated access to the apparatus on a trial-by-trial basis. The prediction was that they would behave more pro-socially in this reciprocal condition, but yet again, they did not make pro-social choices (Brosnan et al. 2009).

Another possibility was that chimpanzees were simply not pro-social in such tasks. To address this, experimenters tested bonobos, a great ape species that is closely related to chimpanzees but is considered a more peaceful and affiliative species than chimpanzees (who are generally considered more competitive). Therefore, the expectation might be that bonobo subjects are more likely to act pro-socially. However, bonobos were not more likely to choose pro-socially in an analogue of the pro-social choice task (Tan et al. 2015), and evidence for food sharing differences between chimpanzees and bonobos has been inconsistent. This supports the hypothesis that it may be something about the task that is challenging, and indeed, even human children have failed to exhibit pro-sociality in the no-cost primate version of the task due to the attentional demands required, so the failure of other primates to do so is not necessarily surprising.

Of course, all of the above studies shared in common a reliance on food sharing as the expression of pro-social choice, and in most cases in the wild, pro-social behavior is elicited in non-food contexts, such as providing grooming or support. Thus, experimenters also began testing pro-social behavior in a more naturalistic way using a helping task, in which the subject gives aid to another individual to help the recipient achieve some goal or reward. As many primates have been observed helping in-group conspecifics in the wild, it may also be more ecologically relevant. In a series of early tests, a small sample of young chimpanzees helped both a human experimenter and each other acquire out of reach objects, even if doing so required extra effort (Warneken and Tomasello 2006), although they failed to do the same when the experimenter's goal was less obvious (as in avoiding a physical barrier). Subsequent studies by this group indicated that chimpanzees were sensitive to whether assistance was actually needed by a conspecific. Further, in a flexible helping task, chimpanzees were able to assess what tool would best benefit a conspecific, and spontaneously provided that tool (Yamamoto et al. 2009).

Because of the success of the helping tasks, researchers again questioned why chimpanzees – who do share food in at least some contexts – were not doing so in the pro-social choice tasks. New methods focused on altering the methods of the task to be more relevant to the chimpanzees. For example, one possibility was that the barpull task was too complicated, and indeed, when subjects chose between two tokens (rather than pulling in one of two options), they more often chose the pro-social option (Horner et al. 2011). This study was criticized for not including a partner absent condition, and this result failed to be replicated in subsequent study (Amici et al. 2014); however, a key point was that in this task, the food rewards were not visible to the subject throughout a trial. In helping tasks, too, the occlusion of the recipient food reward or using symbols to represent food quantities was more likely to produce pro-social results. These results indicated that the presence or absence of visible food could be a crucial task feature in both the pro-social and the helping tasks.

Two more recent studies strongly suggest that the chimpanzees either did not understand or were

not motivated by the pro-social choice task in its original form. In the first, the researchers replicated the original Silk et al. (2005) pro-social task with the same subjects and apparatus, with one tweak; after subjects had experience as the actor making the choice, they were given experience as the *recipient* to another chimpanzee who had been trained to always make the pro-social choice. Following this, the subject was put back with their original partner and given another pro-social choice test. Initially, no subject showed evidence of pro-social behavior but, after experience as the recipient, they began to choose the pro-social option more frequently when with their partner, indicating that they may have learned something about either the goals of the task or the experience of their partner (these are not mutually exclusive; Claidiere et al. 2015). In the second study, chimpanzee subjects only got the option to make a pro-social choice after their partner (who would be the recipient of a pro-social choice) gave up food in order to unlock the apparatus. Subjects were far more pro-social subsequent to this than in control conditions in which the partner's initial unlocking was unnecessary, or a human experimenter unlocked the apparatus (Schmelz et al. 2017). Indeed, they even chose the pro-social option when the partner got more than they did, to a limit. This indicates that chimpanzees may only be motivated to provide pro-social rewards when there is a reason to do so, something that was not present in earlier studies.

Other species have showed far more evidence of pro-social behavior even with the original pro-social choice task, although there remains variability. Capuchin monkeys, a species that, like chimpanzees, are highly cooperative and has a large brain-to-body ratio (a purported measure of cognitive ability), made other-regarding choices on both a version of the pro-social choice task (Lakshminarayanan and Santos 2008) and the token-based task (de Waal et al. 2008), as well as the helping task (Drayton and Santos 2014). As in the chimpanzees, however, the response is not consistent. Capuchins in another study were only pro-social when the disparity between their reward and their conspecific's was relatively low (Brosnan et al. 2010), and the same monkeys who succeed on the token-based task showed no evidence of pro-social behavior on several alternatives, such as a touch screen version of the task or an alternate helping task in which they could provide rewards to a conspecific partner. In addition, the abovementioned replication of both the pro-social choice tasks and the token study not only found no evidence of pro-social behavior in chimpanzees, but no evidence in either capuchins or spider monkeys, either (Amici et al. 2014). It's not clear why capuchins would make pro-social decisions in more contexts than did chimpanzees, but it may relate to either their social system or a different interpretation of the experimental context.

Finally, some of the best evidence of pro-social behavior in the primates comes from callitrichids, a cooperatively breeding species of New World monkey. In cooperatively breeding species, many individuals in a group help to raise offspring within the group, and both parents provide equal amounts of investment in offspring rearing. One hypothesis in the literature is that a cooperative breeding system may encourage pro-social decision-making, due to this interdependence. Consistent with this, common marmosets given the choice to donate to an unrelated recipient are more likely to behave pro-socially to a bonded pair-mate than to an empty cage; interestingly, only male and female "breeder" individuals showed this pattern, while female "helper" marmosets were no more likely to choose pro-socially than without a recipient present (Burkart et al. 2007). However, this pattern isn't always consistent; marmosets are *less* likely to donate altruistically to a groupmate than to a stranger, although when given oxytocin, a hormone related to bonding, marmosets now prefer to behave pro-socially toward a familiar pair-mate rather than a conspecific stranger (Mustoe et al. 2015; see discussion of the endocrinology of pro-social behavior below). This hypothesis is supported outside the primate literature as well. Although not all corvids make pro-social choices, cooperative breeding azure-winged magpies do (Horn et al. 2016).

Some of the best evidence of pro-social behavior comes from rodents. Rats will spontaneously free a trapped cagemate, even before they open

container of chocolate, and often even shared the chocolate with the freed cagemate. Rats also provide evidence as to what factors influence pro-social behavior. For instance, rats help familiar cagemates and strangers of familiar strains more than conspecifics of unfamiliar strains (Bartal et al. 2014). One key distinction between the rodent tasks and the version presented to other species is that the rodent tasks all feature a salient negative stimulus, in the form of a distressed conspecific, whereas the pro-social choice task both has less emotional valence and involves providing a positive benefit rather than taking away a stressor. It may be that pro-social behavior is simply more likely in such negative, high valence contexts, although rats appear to be pro-social in more positively valenced contexts as well. In addition, the partner's distress may be an aversive stimulus, which may increase the chances of subjects acting to help (this has been ruled out in several tasks). Overall, this series of studies reiterates the importance of context and the subjects' understanding and interpretation of the paradigm in studying pro-social behavior.

## Factors Influencing Pro-social Behavior

In order to understand when and under what conditions pro-social behavior occurs, and to understand its evolution, it is important to understand the social and contextual factors that affect pro-social behavior.

### Dominance
Because pro-social behavior involves an interaction between two or more individuals, it's unsurprising that these behaviors would be influenced by the social relationship. Indeed, as dominants typically obtain more resources, and lower-cost services such as grooming are typically directed up the hierarchy, a reasonable hypothesis is that dominant individuals would receive more benefits from lower-ranking individuals than the reverse. However, in a modified pro-social task, dominant rhesus macaques were more likely to deliver the food to a subordinate monkey than vice versa (Massen et al. 2010). The authors hypothesize

that dominants were using generosity to maintain alliances with subordinates and preserve their status, a result supported in other primate species dominant chimpanzees are more often involved in food transfer than more subordinate individuals. Observations of avian species, such as rooks, indicates that seemingly altruistic food sharing may be used as a costly symbol by dominants that wish to broadcast their high-ranking status.

### Existing Social Bonds
There is a large body of evidence suggesting that individuals act more pro-socially toward a recipient with whom they have an existing affiliative relationship. This intuitively makes sense; an existing affiliative relationship by definition indicates recurring interactions with the same individual, presumably increasing the benefit of pro-social behavior for the actor (or the cost of failing to be nice). Indeed, capuchin monkeys are more likely to choose a pro-social option when paired with a close social partner (de Waal et al. 2008), and, as discussed above, rats help members of familiar strains, but not unfamiliar ones. Similarly, female mice (but not male mice) will approach a trapped and suffering same-sex familiar conspecific to initiate social contact, and they do so significantly more than they approach an unfamiliar conspecific in the same situation (Langford et al. 2010). This isn't always the case. Black-tufted marmosets were less inclined to share with groupmates than they were with strangers (Mustoe et al. 2015). The authors posit, however, that this is because in this cooperatively breeding species, a stranger is a potential new group member and thus may be a high priority for establishing social bonds.

### Communicated Intent
It has also been hypothesized that pro-social behavior should be influenced by the partner's need and that, in particular, pro-social behavior may be more common when the recipient has expressed need. There has been virtually no evidence for this in primates; however, in corvids, a recipient's approach to a reward area increased the likelihood that an actor would choose to reward both them self and the recipient rather

than just themself. However, the researchers that conducted the study posit that this effect was due to the attention directing to the reward rather than to the recipient's inherent desire for the reward (Schwab et al. 2012). Indeed, despite these being species with complex communicative repertories, it is unclear whether the recipients even indicate desire in this way.

## Hormonal Influences

Differences in endogenous (i.e., naturally occurring) hormones may influence the likelihood of an actor behaving pro-socially. Perhaps the most researched is oxytocin, a neuropeptide hormone that has a variety of effects on social bonding in mammals, often in mother-infant interactions or sexual behaviors. Evidence from multiple primate species supports an association between urinary oxytocin levels and rates of affiliative behaviors and strength of social relationships among individuals (Crockford et al. 2013). Supporting the hypothesis that oxytocin plays a causal role in pro-social behavior, oxytocin treatment appeared to shift the preferences to behave pro-socially to an in-group member in marmosets, a cooperative breeding species (Mustoe et al. 2015). However, there has been very little evidence of oxytocin influencing pro-social or cooperative behavior in other studies, suggesting that while endogenous oxytocin rates may vary with pro-social behavior, there is not a causal link such that increasing oxytocin increases pro-social behavior or, if there is, it is quite a bit more complicated. For instance, oxytocin interacts with another hormone, cortisol, to produce an anxiolytic effects in humans and, it is hypothesized, other species. Such a physiological interaction might inform the emergence of social contact behaviors in response to a conspecific's pain, as observed in mice. The differing levels of these endogenous hormones and their interaction are all factors that play a key role in determining an individual's behavior in a given context, especially in species that exhibit complex social cognition, and more research in this area is clearly warranted.

## Cognitive Factors

There has been some debate about which socio-cognitive abilities are necessary for pro-social behavior to emerge. On the one hand, functional pro-social behavior may be based on positive social reinforcement of certain types of behavior, which requires little in the way of cognition. On the other hand, understanding others' needs or the effect of one's behaviors on others could lead to more complex or directed forms of pro-social behavior. Theory of mind, or the ability to attribute mental states to or take the perspective of others, would allow individuals to make inferences about another's needs or desires using those behavior cues and has been hypothesized to be integral to altruism and helping behavior. For instance, subjects could predict what a conspecific might want, which would be useful in tailoring specific pro-social behaviors (Barnes et al. 2008). However, there is not a lot of evidence for perspective taking in other species, which may indicate that it is not an essential component of pro-social behavior, however useful it might be. Indeed, many species that display pro-social behaviors both in experimental paradigms and in wild observations do not show evidence of theory of mind; even the great apes species show only limited abilities to take the perspective of others, and predicting conspecifics' future actions is complicated no matter what level of social cognition a species possesses.

Another hypothesized mechanism is empathy, the phenomenon in which one individual's emotional or mental state is affected by the emotional state of another (de Waal 2009). While this can be quite complex, it can also be as simple as mirroring of another's emotional state, which may be sufficient to induce pro-social behavior in many species. This would allow pro-social behavior without complex social cognition; if another's distress or desire causes discomfort to an actor, that actor is likely to act in a way that alleviates that discomfort. For instance, when rats act altruistically to help a conspecific, it may be that the recipient's distress causes cognitive

discomfort in the actor, who then acts to alleviate that discomfort (Bartal et al. 2014). Therefore, pro-social behavior does not seem to require such complex social cognition, but instead may use a much simpler mechanism to achieve the same end of group cohesion.

## Future Directions

Pro-social behavior is hypothesized to be important in animal social groups, but more work is needed to determine the degree to which it is seen across species and contexts, as well as the underlying mechanisms. For instance, one prominent hypothesis for the evolution of pro-social behavior is the cooperative breeding hypothesis, but to date it is based on evidence from only primates and corvids. Future work should expand to other cooperatively breeding species. In addition, an area that needs more exploration is how pro-social behavior differs toward individuals who are new immigrants to the group, or strangers versus a long-term groupmates. This is likely to vary depending on whether the new individual is seen as a threat or a potential mate and will presumably also differ depending on the residents' status in the group. In particular, it would be interesting to see how pro-social behavior changes in pair bonded species across the course of their relationship, from pair bond formation through reproduction.

Finally, more work is needed to clarify underlying mechanisms of pro-social behavior. It is not clear in which contexts perspective taking is useful, nor do we know much about the underlying hormonal correlates. It would also be useful to determine how pro-social behavior changes depending on whether the context is to provide help, to provide a good (i.e., food), or to help an individual avoid or escape a negative reinforcer. As the current literature consists of a mix of methods, it can be challenging to compare results from different species or contexts to one another. Understanding this complexity and the subtleties of context will be critical in further exploring pro-social behavior.

## Cross-References

▶ Cooperation
▶ Cooperative Breeding
▶ Cooperative Hunting
▶ Empathy
▶ Helping Behavior
▶ Reciprocity
▶ Social Behavior
▶ Social Grooming

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