With a little help from my (*Psittacidae*) friends

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Summary

Understanding the distribution of and mechanisms underlying prosocial behavior in other species has been hampered by methodological differences among studies, questions about animals' interpretations of the designs, and low phylogenetic diversity. Brucks and von Bayern's recent report that African gray parrots are proactively prosocial reiterates the importance of social tolerance and suggests a role for perspective taking, but additional work using identical procedures across taxa is needed to verify the cognitive mechanisms underpinning prosocial behavior.

Understanding the degree to which animal species make active choices to benefit conspecifics is key for both hypotheses about the evolution of social behavior (i.e., the cooperative breeding hypothesis) and questions of human distinctive traits. Despite a growing body of research, answers remain elusive, in part due to methodological differences among studies that make comparisons difficult. Test paradigms generally fall into one of two categories, the “prosocial choice tasks” (PCTs), in which the target individual chooses one of two distributions of food that reward the subject and/or the partner, and the “helping tasks” (HTs), in which the target individual has the option to help a partner, such as retrieving an object or opening a door. Despite both exploring whether subjects take others' needs into account, results suggest that the animals see these tasks very differently; chimpanzees more often show prosocial behavior in HTs than PCTs, whereas capuchin monkeys show the opposite pattern. Intuitively, they appear to tap into different phenomena, and/or require different cognitive skills. PCTs are hypothesized to require less perspective taking because it is assumed that the subjects understand that the partner wants food. Nonetheless, these tasks still require the subject to understand that they will not get all of the food and to inhibit their prepotent responses in the presence of food. HTs require that the subject understands the partner's needs, suggesting more advanced perspective taking, but avoid visible food. This may be more ecologically valid, especially for species for which food sharing is rarely observed.

Even within this split, there is substantial variation. PCT choices can be made by choosing between two tokens, two icons on a computer screen, or two trays containing food rewards. Despite the conceptual similarity, dogs' responses differ depending on whether the task is a token, a computer, or a bar-pull design (Dale et al., 2019). Reward distributions also differ across tasks; actors in PCTs receive the same outcome no matter what their choice in order to remove any self-oriented motivations, but that can be the same reward for either choice or nothing at all. In the case of the former, it has been argued that the presence of a reward for the actor overwhelms any ability to focus on the recipient's outcomes, but the absence of any reward makes this an altruism task, and could potentially trigger inequity aversion in some species. In addition, animals may be poor at inhibiting the prepotent response in the presence of food, but the use of tokens or icons representing food rewards adds a level of abstraction, which may also be challenging. Finally, recent work suggests that the primates may not always understand these paradigms as a chance to benefit their partners. Simple tweaks that give the actor experience as the recipient or make the recipient an active participant, rather than passive recipient, change decisions in chimpanzees.

In another variant, subjects have access to tokens that they can pass to their partner, who can then exchange them to an experimenter for food rewards. Aspects of the design are simple – for instance, the subject has to choose whether or not to engage, rather than choosing between two options. On the other hand, the task requires subjects to recognize that tokens that are useless to them may be useful to another, and the controls require a subtle understanding on the part of the subjects. As with PCTs, there is always a partner-absent control, but in this case, to verify that subjects recognize that the tokens are only useful to the partner when they can exchange

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them to the experimenter, there is a control in which the exchange port is blocked. To pass, subjects have to recognize that even though the experimenter and partner are present, there is no need to pass tokens. Thus, both recognizing that the partner needs the tokens in the first place, and then recognizing when they cannot use them, require a fairly high degree of both nuance and perspective taking.

Indeed, so far, neither capuchins, who do pass PCTs, nor ravens, who do not, have passed the required controls (Massen et al., 2015; Skerry et al., 2011). In Brucks and von Bayern's study, however, African gray parrots (AGPs) actively passed tokens to their partners and passed all controls, suggesting a fairly high level of understanding and/or motivation, while blue-headed macaws (BHMs), another *Psittacidae*, did not (Brucks & von Bayern, 2020). They ruled out several alternative explanations. The AGPs' choices could not be explained entirely by reciprocity; although subjects had the opportunity to reciprocate, and did so, seven of eight parrots showed prosocial behavior on the very first trial, suggesting it is not the only motivation. In addition, while recipients' attention getting behaviors were positively correlated with overall token transfers, the recipients' frequency of these behaviors did not differ among the experimental conditions, suggesting either that begging played no role in subjects' choices, or that we need to be looking at more subtle cues.

AGPs' prosocial behavior was also influenced by their long-term social relationships. AGPs were more prosocial with individuals with whom they had a more affiliative relationship. Wolves, dogs, and several species of primate also show increased prosocial behavior towards familiar or ingroup individuals compared to strangers or outgroup members, a consistency that suggests that this is an important factor in shaping and/or selecting for prosocial behavior. AGPs did not, however, show any changes in affiliation patterns subsequent to prosocial behavior, suggesting that the effect is based on the long-term relationship rather than on immediately preceding actions.

The AGPs' performance was impressive; they are proactively prosocial, and do so in the absence of either reciprocity or the tweaks that have been needed to generate prosocial behavior in chimpanzees. Their results also suggest the importance of perspective taking in prosocial behavior. They not only had to recognize their partner's need of a token that was useless to them, but recognize when the partner couldn't use the token because the exchange port was blocked. However, this paradigm is not directly comparable to the PCT or traditional HT. This makes it difficult to know if perspective taking is needed for proactively prosocial behavior, which suggests fairly sharp limits on which species will show it, or if it was needed for this particular task, but that in general prosocial behavior can be achieved without perspective

taking. Given the variability in subjects' responses across different paradigms, answering this will require testing a broad range of species on a variety of tasks that differ in the degree to which perspective taking is required and, for those species that have yet to show evidence of prosocial behavior, seeing how they behave with the variations that helped the chimpanzees succeed.

Ultimately, we want to answer the million dollar questions – what do subjects understand about their choices, what are the underlying mechanisms (cognitive and other) that support these choices, and what were the social and ecological factors that selected for them? As this study shows, we learn a lot by studying these paradigms across multiple species. Future work needs to continue this trend, ideally using identical procedures to test multiple paradigms in the same study, both within taxon and across taxa (i.e., Amici et al., 2014). But in doing so, we need to take care to ensure that our test subjects get a fair chance to succeed. As evidenced by this and previous research, this means paying attention to subjects' relationships, ensuring that subjects receive adequate experience with the task to understand both their and their partner's roles, and designing tasks that the subjects interpret in the way that we intended. Indeed, if, as these results suggest, prosocial behavior does rely on some degree of perspective taking, then the aforementioned cautions are particularly relevant; if subjects do not understand what their partner needs, they will not recognize their opportunity to help even if they are motivated to do so.

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