

Studying the evolution of cooperation and prosociality in birds

Cooperation and prosociality are hallmarks of human behavior, and it is generally believed that our extra-ordinary levels of cooperation have contributed to the success of our species (Vygotskian intelligence hypothesis: Moll & Tomasello, 2007). Prosocial tendencies, that is an attitude to provide benefits to others, in turn may serve as a motivational drive to facilitate that cooperation (Silk, 2007). The evolution of our cooperative nature, however, has been a hotly debated topic for decades. Many theoretical advances have been made, and different evolutionary pathways have been modeled. Whereas these models inform us about possible, evolutionary stable pathways, they do not necessarily reflect the actual evolutionary history of cooperation and prosociality as traits, or human cooperation more generally. However, comparisons with other species may elucidate the evolutionary history and selection pressures promoting cooperation.

Taking a phylogenetic approach, many ethologists and/or comparative psychologists have reverted to comparisons of human cooperative behavior with that of other animals. Cooperation is ubiquitous in the animal kingdom (Clutton-Brock, 2009; Dugatkin, 1997). By studying its degree and complexity in different species, either observationally or experimentally, phylogenetic pathways can be traced. Traditionally, most of the comparative work has been conducted on non-human primates in general, and great apes in particular. Unfortunately, up to very recently, the belief remained that studies on, for example, chimpanzee cooperation are still the most relevant or “sophisticated” (Schmelz & Call, 2016). Whereas I do not want to disregard the importance and ground-breaking nature of the studies on cooperation in our closest living relatives, found similarities between non-human great apes and humans inform us about homologies only. With our common ancestor as only reference point, the testing of evolutionary pressures is logically not possible (Fitch, Huber, & Bugnyar, 2010).

In contrast, studying cooperation and prosociality in more distantly related species can provide us with information about phylogenetic lineages where a specific trait may have evolved convergently. Comparisons of the socio-ecology of this increased sample of different species/lineages may subsequently help us to pinpoint specific selection pressures that may have facilitated the evolution of cooperation (Massen, Behrens, Martin, Stocker, & Brosnan, 2019). Since we share a common ancestor with birds that lived ~310–330 million years ago, similarities in cooperation and prosociality and their underlying socio-cognitive traits have most probably evolved convergently. Moreover, birds do show much cooperation in the wild, such as cooperative parental care (Remeš, Freckleton, Tökölyi, Liker, & Székely, 2015), cooperative

breeding with aid of (un)related helpers (Riehl, 2013), or mobbing of neighboring groups (Radford & Fawcett, 2014). Consequently, birds are an excellent group to study the evolution of cooperation, and relatedly, prosociality.

Over the past decades studies on social cognition in birds have steadily accumulated (for a review see Bugnyar & Massen, 2017). Several seminal papers have also experimentally studied cooperative, reciprocal interactions in different bird species and whether these birds do, or do not, follow tit-for-tat decision rules (e.g., Reboreda & Kacelnik, 1993; Stephens, McLinn, & Stevens, 2002). Since then the study of cooperation in birds has taken flight. To date, several other studies on reciprocal altruism in birds have seen the light (e.g., Krams, Krama, Igaune, & Mänd, 2008; St-Pierre, Larose, & Dubois, 2009), as well as a number of studies on birds simultaneously co-operating an apparatus to receive a reward that they could not have gained on their own (Massen, Ritter, & Bugnyar, 2015; Schwing, Jocteur, Wein, Noë, & Massen, 2016; Seed, Clayton, & Emery, 2008). Similarly, prosociality, defined here as helping another individual at low or no cost, has recently gained increasing attention of ornithologists. And whereas initial studies reported negative findings (e.g., Lambert, Massen, Seed, Bugnyar, & Slocombe, 2017; Massen, Lambert, Schiestl, & Bugnyar, 2015), others have now reported positive findings regarding prosociality in birds (Brucks, & von Bayern, in press; Duque, Lechner, Ahmann, & Stevens, 2018; Horn, Scheer, Bugnyar, & Massen, 2016).

The time thus seems ripe to review the state of the art with regard to studies on cooperation and prosociality in birds, not just to see what species can do what, and what that might tell us about the potential phylogenetic pathways of a given trait, but also to investigate the proximate mechanisms that underlie such convergently evolved traits.

The current special issue thus elaborates on recent findings of cooperation and prosociality in birds. For example, Tassin de Montaigu and colleagues show that blue-throated macaws can cooperate in an experimental task; that is the loose-string paradigm. However, when there was no partner present the birds also pulled the rope suggesting that they do not fully understand the contingencies of the task (Tassin de Montaigu, Durdevic, Brucks, Krashennikova, & Bayern, 2020). Schwing and colleagues, however, show that kea significantly improve their performance in the same task over time, suggesting that the contingencies of the task may be learned when given enough experience (Schwing, Reuillon, Conrad, Noë, & Huber, 2020). The pay-off structure of effort and reward of cooperation seems also important for birds, as Laumer and colleagues show that Goffin's cockatoos have a tendency to refuse to work when their

partners are receiving the same reward, yet do not have to work for it (Laumer et al., 2020).

Heaney and colleagues find in an experiment where kea could choose between a selfish token that delivered a reward to the subject only, and a prosocial token that also delivered food to its partner, some tentative evidence that kea may also be prosocial (Heaney, Bastos, Gray, & Taylor, 2020). This in contrast to the findings of Wascher and colleagues in a slightly different paradigm testing crows and ravens, which showed that these corvids were not willing to provide their conspecifics with tokens that had no value to themselves, yet had value to those partners (Wascher, Feider, Bugnyar, & Dufour, 2020). Both studies, moreover, find no evidence for reciprocal exchange in the kea, and crows and ravens, respectively (Heaney et al., 2020; Wascher et al., 2020), which may be suggestive of the cognitive limits of these species, be it for interactions within these specific paradigms or for (calculated) reciprocity in general. Similarly, Dufour and colleagues show in a risky exchange task where the birds have to choose between a medium quality reward or a lottery of one out of six rewards that can either be of lower or higher quality that carrion crows, hooded crows, common ravens and rooks do not base their decisions on the odds of success, which were shown to them prior to the choice; that is how many lower and higher quality rewards there are in this lottery, but rather use simple heuristics (Dufour, Broihane, & Wascher, 2020). This further suggests cognitive constraints of at least these birds with regard to cooperative decision-making. These results corroborate recent theoretical advances that suggest that cooperative decision rules, in non-human animals and humans alike, may not always rely on cognition but rather have a more affective character (Brosnan & de Waal, 2002; Massen et al., 2019; Schino & Aureli, 2009). Nevertheless, other-regard would require some sort of self-regard, which is what Clary and colleagues investigated in California scrub jays. And although they do not find positive evidence of mirror-self-recognition in the classic mirror-mark test, they do show that these jays do not increase their cache protection strategies when in front of a mirror, in contrast to when a conspecific is observing, suggesting that they at least not treat their own mirror image as a conspecific (Clary, Stow, Vernouillet, & Kelly, 2020). Thus, the birds tested show some evidence of cooperation and prosociality, yet the cognitive underpinnings of this behavior seem relatively constraint.

The emotional underpinnings of cooperation predict a strong effect of social bonds on cooperation and prosociality. To show that birds, like primates initiate and maintain specific social bonds, outside the pair-bonds, Morales-Picard and many colleagues set up a large collaborative effort of observational data on 6 corvid species and 9 parrot species. They show that allopreening, like allogrooming in great apes, is predictive of such social bonds, especially when considering preening of more vulnerable body parts like the head (Morales-Picard et al., 2020). Studying these allopreening patterns in more detail in juvenile large-billed crows, Miyazawa and colleagues show that the function of allopreening is dependent on the sex combination of giver and receiver, with between sex allopreening potentially functioning to develop and/or maintain social bonds, while

within sex allopreening seems to function as a status or dominance signal (Miyazawa, Seguchi, Takahashi, Motai, & Izawa, 2020). Sierro and colleagues show that ravens actively seek support from socially bonded individuals at difficult feeding opportunities (e.g., through contest competition) using food-calls. Whereas these food-calls advertise broadly, the ravens tend to stop calling as soon as their affiliation partners had arrived (Sierro, Loretto, Szpl, Massen, & Bugnyar, 2020). Duque and colleagues investigated the proximate mechanisms of social bonding, focusing specifically on the effect of the neuropeptide hormone mesotocin in pinyon jays. However, in contrast to recent findings on oxytocin, the mammalian homologue of mesotocin, the administration of mesotocin did not seem to have a detectable effect on the formation and maintenance of bonds in these jays (Duque, Rasmussen, Rodriguez, & Stevens, 2020). Consequently, these studies show that social bonds are as important for birds as they are for primates, that birds actively seek support from said friends, yet that we need additional studies to investigate the proximate mechanism of social bonding in birds.

Finally, cooperation not only takes the form of mutual collaboration or the sharing of resources, but also of sharing of information; that is birds may learn from each other socially. Pendergraft and colleagues examine such social learning regarding problem-solving in American crows using the classic string-pulling paradigm; that is a piece of reward is attached to a string that hangs from a branch, and the question is how to get to the reward. They find that although their crows do not master the task faster when a model is available, they do tend to converge towards the solution of their model neighbors (Pendergraft, Lehnert, & Marzluff, 2020). Bobrowicz and Osvath subsequently investigate how such a social context influences short-term memory in cache recovery task and find that whereas humans had a lower performance when they also had to keep track of a partner's actions that got access to the caches before them in comparison with an individual task, ravens did not show such a decline in performance when the task became social rather than individual (Bobrowicz and Osvath (2020). Hence, birds are not only able to learn from each other, they also seem able to memorize what others have done.

The results presented in this special issue reflect the state-of-the-art with regard to the investigation of social cognition in birds. As such they provide further evidence of cooperation and prosociality in birds, while simultaneously unraveling some of the underlying mechanisms. Consequently, the results suggest convergent evolution of cooperative and prosocial traits in birds with primate cooperation and prosociality. It should, however, be noted that all studies in this special issue were conducted on either corvid or parrot species, and thus there is a large sampling bias that restricts the generalizability of these results across all birds. This sampling bias stems from the fact that most research on social cognition in birds is being done on corvids and parrots, as these groups have traditionally been considered "intelligent," and this intelligence is often referred to as paralleling that of apes (Emory, 2004; Lambert, Jacobs, Osvath, & Bayern, 2019). Recent comparisons of brain tissue also highlight similarities in extra-ordinary high neuron numbers of primates, corvids and parrots, and clearly set the corvids and parrots apart from other birds (Olkowicz et al., 2016).

Nevertheless, I would like to encourage studies on cooperation and prosociality in non-corvid/parrot bird species. Such studies may reveal unexpected capacities in less brainy birds or, when these other bird species lack the capacity for cooperation and prosociality, they will function as an outgroup for phylogenetically controlled studies. Such studies will also reveal whether these skills have evolved as a result of a homology or analogously in parrots and corvids. But also, and maybe even more importantly, studies on less brainy birds might find similar results, because the cognitive requirements for specific cooperative decision rules are often also not met by the corvids, parrots, or primates, as evidenced by some studies in this special issue. And in fact, the cognitive requirements for cooperation and/or prosociality need not be high, and alternative mechanisms, like for example emotions (Massen et al., 2019) may be at play.

In sum, this special issue provides further evidence for convergent evolution of cooperation and prosociality in primates, corvids and parrots. Moreover, it highlights (the lack of) specific cognitive proximate mechanisms to explain said cooperative behavior. I hope as such it will inspire future studies into the cooperative and prosocial behavior of birds, since only understanding (the lack of) cooperation and prosociality in a broad array of bird species will elucidate the selection pressures that lead to cooperation and prosociality.

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