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Studying the Evolution of Cooperation and Prosociality in Birds

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The Evolution of Cooperation

The social brain hypothesis (Humphrey, 1976) poses that the intricacies of social life may have been a significant selection pressure for the evolution of mind. This evolution may act on competition between group members and strategies to outcompete others (Machiavellian intelligence hypothesis: Byrne & Whiten, 1988), or on cooperative tendencies between group-members that provide benefits that cannot be reached by a single individual (Vygotskian intelligence hypothesis: Moll & Tomasello, 2007). The latter hypothesis, however, creates an evolutionary conundrum, as cooperation is prone to free-riders, and with defection being an evolutionary stable system, the occurrence and complexity of cooperation in humans and other animals remains a puzzle. Several theoretical advances have been made to explain the evolution of cooperation nonetheless, with kin-selection (Hamilton, 1964) and reciprocal altruism (Trivers, 1971) being the most prominent ones. However, the proximate mechanisms that foster the strategies proposed in the Vygotskian intelligence hypothesis and the required cognition in nonhuman animals, remain a hotly debated topic (see Massen et al., 2019).

Birds

Most studies on cooperation in non-human animals have focused on primates. Such studies are helpful in unraveling the evolutionary history of a cooperation within the primate lineage. However, to study potential selection pressures that may have shaped the evolution of a certain behaviour, comparative studies within a certain taxon are restricted, since the common ancestor becomes the only reference point if a certain trait is found among the members of that taxon. As the behaviour and socio-ecology of that common ancestor remains largely obscured because it left no fossils, inferences about potential selection pressures are impossible (Massen, 2020). In contrast, comparing a trait like cooperation in more distantly related species (e.g. birds) may allow ruling out common ancestry when that trait is not present in the majority of all living descendants, and subsequently generates data from a lineage where this trait has evolved convergently. Subsequent comparisons of the socio-ecologies of the species from the different lineages in which this trait is then found may help us pin-point specific selection pressures that may have generated the evolution of this trait (Massen, 2020). Such studies have now revealed striking similarities between primates and birds like corvids and parrots that emphasize the role of social tolerance (Massen, Ritter & Bugnyar, 2015; Schwing et al., 2016) and partner choice (Asakawa-Haas et al. 2016) when cooperating, while also pin-pointing some more elaborate cognitive skills that may be involved in animal cooperation, like understanding the need for a partner (Massen, Schaake & Bugnyar, 2020), long-term memory for direct reciprocity (Müller et al. 2017) and inequity aversion (Laumer et al., 2020).

Prosociality

In human literature it has been suggested that a prosocial attitude may enhance cooperation, and this connection has recently been shown in non-human animals too (Martin et al., 2021). As such, prosociality may contribute to the spread of cooperators in a population and thus to the evolution of cooperation. However, the problem of free-riders remains, and it is thus of significant interest to investigate the socio-ecological selection pressures that may have mitigated this problem. Interestingly, prosocial tendencies have been difficult to find among primates, even when considering our closets living relatives (e.g., Silk et al., 2005). Similarly, clear prosocial tendencies seem absent in another highly social and intelligent animal, the common raven (Massen et al. 2015; Lambert et al. 2017). In contrast, prosociality was found in the cooperatively breeding common marmoset, and it is this cooperative breeding lifestyle, which these New World primates share with humans, that has led to the formulation of the cooperative breeding hypothesis (Burkart, Hrdy & van Schaik, 2009). This hypothesis states that the requirements of this lifestyle have facilitated the evolution of prosociality. So far, however, proof for this hypothesis only came from primate studies, and with only two families showing such cooperative breeding among the primates, i.e., Homo sapiens and the callitrichidea, interpretations remained inconclusive.

To study the generalizability of the cooperative breeding hypothesis, my lab has started investigating prosociality among birds, which as a class show a much higher prevalence of cooperative breeding and thus provide the possibility for more elaborate comparisons. So far, in line with the cooperative breeding hypothesis, we have shown high levels of prosociality in a cooperative breeding corvid, i.e. the azure-winged magpie (Horn et al. 2016; Massen, Haley & Bugnyar, 2020). Moreover, a comparison of prosocial tendencies across 8 different corvid species, indeed showed that a cooperative breeding lifestyle predicts proactive prosociality (Horn et al. 2020). Currently, we are extending our test-sample to parrots (Laumer et al., *in review*; Dam & Massen, *in prep*), as well as investigating the required cognition and ecological relevance of the tests used to establish evidence for prosociality (Horn et al., *in review*).

In sum, studies investigating the evolution of cooperation and prosociality have long suffered a too narrow focus on primates, and a broader scope of comparisons across different animals with different socio-ecological backgrounds was needed. Consequently, recent advances in the study of social cognition of birds have not only informed us about the remarkable cooperative and prosocial skills of these birds, but it has also been proven paramount in identifying the selection pressures that have shaped the evolution of cooperation and prosociality.

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