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An ‘unkindness’ of ravens? Measuring prosocial preferences in *Corvus corax*

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In recent years, there has been considerable research effort to determine whether other species exhibit prosocial motivations parallel to those of humans; however, these studies have focused primarily on primates, and with mixed results. We presented captive ravens with a modified prosocial choice task which aimed to address several criticisms of previous methods by including a stringent pretraining regime and a set-up that disentangles motivation to provision a conspecific from motivation to feed next to one. In this task six subjects received no rewards for themselves but could choose to deliver food rewards to either a conspecific or an empty, inaccessible compartment. Subjects did not demonstrate any prosocial tendencies (i.e. they did not preferentially choose to reward a conspecific over the empty compartment), and instead often ceased pulling on test trials when they received nothing for themselves (up to 70% of 80 trials with a partner present, up to 83% of 40 trials in a nonsocial control condition). The relationship between the subject and the partner had no influence on the subject's choices; however, subjects were more likely to pull immediately after performing socio-agonistic displays. Our results contribute to a growing body of evidence that despite their sophisticated social cognitive abilities and range of cooperative behaviours exhibited in the wild, unpaired (or unbonded) ravens do not seem to act to benefit conspecifics in the absence of immediate self-gain.

Humans' extreme prosocial, or ‘other-regarding’, behaviour is unparalleled in nature and is often cited as a defining characteristic of humanity that facilitates human cooperation on a global scale and may have played a key role in the evolution of our complex culture and technology (Fehr & Fischbacher, 2003). Despite its significance, the questions of whether humans alone possess intrinsic prosocial motivations and how our unique levels of prosociality evolved have historically remained unanswered. In recent years, however, these topics have become the centre of much empirical focus and theoretical debate (Burkart, Hrdy, & Van Schaik, 2009; Burkart & van Schaik, 2010; Burkart & van Schaik, 2016; Silk & House, 2011; Thornton & McAuliffe, 2015).

Examples of prosocial behaviour can ostensibly be found throughout the animal kingdom, but the question remains as to whether, on a proximate level, these behaviours are governed by the same underlying psychological mechanisms (i.e. other-regarding concern) as those that prompt many human prosocial behaviours (Jensen, Vaish, & Schmidt, 2014; de Waal & Suchak, 2010). Recent research has aimed at probing the motivational mechanisms underpinning prosociality in other species, yet this has proved difficult to test. For example, a report that rats, *Rattus norvegicus*, behave prosocially towards conspecifics due to an empathetic concern for their welfare (Ben-Ami Bartal, Decety, & Mason, 2011) was later refuted by a lower-level explanation that subjects were motivated by a desire for social contact rather than empathy (Silberberg et al., 2013).

In the last decade, there has been a surge of research aimed at investigating prosociality in nonhuman animals in controlled laboratory settings in order to tease apart these factors. One of the most widely used paradigms for measuring prosocial tendencies in other species is the prosocial choice task (Silk et al., 2005), a provisioning paradigm where subjects may choose between two options, one of which delivers food to both the subject and a nearby conspecific (prosocial choice; often denoted as the 1/1 option with payoffs for the donor and recipient, respectively) and the other which provides food to only the subject (selfish choice; 1/0 option). Reward

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distributions may also be manipulated so that subjects do not receive any rewards for either choice but rather may incur a slight cost for pulling to donate food to a recipient (0/1 option), or must forgo a qualitatively better reward for a less-preferred reward in order to also benefit their partner (HQ-0 versus LQ-HQ; Sterck, Olesen, & Massen, 2015). To further examine the motivations behind prosociality, many researchers have focussed on the interindividual differences in prosocial tendencies based on the relationship between the subject and the partner. In all cases, prosocially motivated subjects are expected to preferentially choose the option that benefits a conspecific at little or no cost to themselves.

Several variations of the prosocial choice task have been used with a range of nonhuman species, with most available data coming from the primate order, and with equivocal results. While some studies have reported other-regarding preferences in several primate species (chimpanzees, *Pan troglodytes*: Horner, Carter, Suchak, & de Waal, 2011; capuchins, *Cebus apella*: Lakshminarayanan & Santos, 2008; Takimoto, Kuroshima, & Fujita, 2010; macaques, *Macaca fascicularis*: Massen, van den Berg, Spruijt, & Sterck, 2010; marmosets, genus *Callithrix*: Burkart, Fehr, Efferson, & van Schaik, 2007; Mustoe, Cavanaugh, Harnisch, Thompson, & French, 2015; tamarins, *Sanguinus oedipus*: Cronin, Schroeder, & Snowdon, 2010; Hauser, Chen, Chen, & Chuang, 2003) other studies with the same species, and in some cases the same individuals, have found contrasting results (chimpanzees: Jensen, Hare, Call, & Tomasello, 2006; Silk et al., 2005; Vonk et al., 2008; Yamamoto & Tanaka, 2010; capuchins: Burkart & Van Schaik, 2012; macaques: Burkart & Van Schaik, 2012; tamarins: Cronin, Schroeder, Rothwell, Silk, & Snowdon, 2009; Stevens, 2010).

These differences have been attributed to various contextual factors and methodological differences between studies including the visibility of food rewards, the relationship between the subject and the recipient and the subjects' understanding of the task (Burkart & Rueth, 2013; Cronin, 2012). For example, when confronted with the same paradigm used with primates, preschool age children fail to show prosociality in a cost-free (1/1) version of the task, but are prosocial in a costly (0/1) version, a finding that has been attributed to the higher attentional demands of the cost-free version rather than a lack of prosociality (Burkart & Rueth, 2013). Prosocial behaviour may additionally be dependent on the ability to appreciate others' goals or needs, and may thus only be expressed in response to signs of need by the recipient (Cronin, 2012; Horner et al., 2011; Schwab, Swoboda, Kotrschal, & Bugnyar, 2012; Vonk et al., 2008). A few studies have examined the effect of the recipient's behaviour on the subject's choices to determine whether direct requests or expression of interest in the reward affect the likelihood of prosocial choices by subjects. Those that have done this have provided mixed results with reports of cottontop tamarins and chimpanzees being less likely to choose the prosocial option on trials where their partner reached out for the reward (Cronin et al., 2009) or produced begging gestures (Horner et al., 2011). In contrast, other studies have reported begging gestures to have no effect on chimpanzee subject choices (Vonk et al., 2008), while general attention-getting behaviours by the partner such as food grunts or hitting the caging had a positive effect on prosocial choices (Horner et al., 2011).

Recently, Tan, Kwetuenda, and Hare (2015) and Marshall-Pescini, Dale, Quervel-Chaumette, and Range (2016) highlighted several methodological limitations with the current paradigms used to test prosocial preferences in nonhuman animals; namely, that very few (Tan et al. calculated 40.9%) include the necessary pretest to ensure that subjects understand the test set-up, and those that do may not be adequately counterbalanced to prevent location biases that may arise from pretraining. Additionally, in studies using a set-up where subjects choose between two horizontally aligned trays, it may be difficult to disentangle motivation to provision a conspecific from motivation to feed next to one (Jensen et al., 2006; Tan et al., 2015). To rule out these confounds in the future the authors suggest a number of methodological changes including a strict self-regard pretest and counterbalancing to avoid location biases (Marshall-Pescini et al., 2016; Tan et al., 2015).

The discrepancies in the current literature highlight the need to explore this topic not only by using consistent methodology between species (e.g. Burkart et al., 2014) that addresses weaknesses in the standard paradigms used, but also by using multiple tasks with the same species (and subjects where possible) before drawing general conclusions on the presence or absence of a particular predisposition (Kim, Martinez, Choe, Lee, & Tomonaga, 2015; Tan et al., 2015). Additionally, research with other species outside the primate order is needed in order to gain a broader understanding of the various factors that may give rise to prosocial behaviour such as breeding system, cognitive ability and social tolerance.

Corvids are frequently cited alongside primates for their complex social cognitive abilities (Emery & Clayton, 2004; Seed, Emery, & Clayton, 2009). Ravens, for example, are able to recognize third-party relationships among both in-group and out-group conspecifics (Massen, Pašukonis, Schmidt, & Bugnyar, 2014) and adjust their pilfering strategies depending on the presence and inferred visual perspectives of others (Bugnyar, 2011). In addition, corvids exhibit a range of cooperative behaviours including food sharing among conspecifics (von Bayern, de Kort, Clayton, & Emery, 2007) as well as the formation of affiliative relationships characterized by agonistic support (Fraser & Bugnyar, 2012) and postconflict consolation and reconciliation (Fraser & Bugnyar, 2010).

Recently, several versions of the prosocial choice task have been used with corvids with results that mirror some chimpanzee studies. Using a set-up similar to that used with chimpanzees (Silk et al., 2005), Di Lascio, Nyffeler, Bshary, and Bugnyar (2013) allowed captive ravens to open one of two boxes, allowing access to food rewards for either themselves and a partner in a neighbouring compartment, or only themselves. The authors found no evidence for prosociality. Importantly, however, subjects continued to choose at random in a post-test condition aimed at exploring whether they understood the consequences of their choices. The negative results of this study may therefore reflect a lack of understanding the apparatus rather than indifference to the partner's payoffs, thus highlighting the importance of conducting knowledge tests prior to testing. Using a slightly modified version of this paradigm, Schwab et al. (2012) found that jackdaws, *Corvus monedula*, preferentially chose the reward option that simultaneously benefited a conspecific, but primarily when the conspecific had already approached that option, a result that the authors attribute to stimulus/local enhancement rather than proactive prosociality. When presented with tokens that could only be exchanged by the partner for a reward, Massen, Lambert, Schiestl, Bugnyar (2015) and Massen, Ritter, Bugnyar (2015) found that subadult ravens generally preferred to cache the tokens rather than transferring them to conspecifics. Finally, in contrast to these negative results, using a group service paradigm (see Burkart et al., 2014), Horn, Scheer, Bugnyar, and Massen (2016) found that azure-winged magpies, *Cyanopica cyana*, do proactively provide food to their group members at very high rates. Nevertheless, overall these previous studies suggest that some species of corvid are not proactively prosocial. There is, however, the possibility that a lack of prosocial performance may alternatively be explained by the peripheral demands of certain prosocial tasks. Convergent evidence from different paradigms is, therefore, needed to resolve tension between naturally occurring cooperative behaviours and inconclusive performance on experimental tasks to date.