

MINI-SERIES

The psychology of cooperation in animals: an ecological approach

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Introduction

Cooperative behavior, where one individual acts in a manner that provides a benefit to another, has been a central puzzle in evolutionary biology since the time of Darwin (1859). Cooperation presents an apparent paradox because situations in which individuals' efforts to assist others appear to be at odds with the genes'-eye view of natural selection (Dawkins, 1976). This paradox has largely been resolved through extensive theoretical and empirical research pointing to three main explanations for the evolution of cooperation. Perhaps the most prominent class of explanation stems from Hamilton's (1964) insight that cooperation is often favored by kinship structures, in which individuals reap indirect benefits from assisting those with whom they share genes. A second class of explanation relies on contingency: individuals may be expected to assist those who have assisted them (direct reciprocity: Trivers, 1971) or other group members (indirect reciprocity: Nowak, 2006) in the past to trade goods and services with others (biological market theory; Noë & Hammerstein, 1994) or to punish uncooperative individuals (Clutton-Brock & Parker, 1995). Although such contingent explanations have garnered a great deal of theoretical support (Trivers, 1971; Axelrod & Hamilton, 1981; Nowak & Sigmund, 1992, 1998; Noë & Hammerstein, 1994), empirical evidence remains scarce (Clutton-Brock, 2009; Hauser, McAuliffe & Blake, 2009; Cheney, 2011). A third class of explanation removes the apparent paradox by emphasizing that cooperation can evolve

Abstract

There has been a recent push to study the psychological processes supporting cooperation in nonhuman animals. However, progress has been limited thus far due to differences in approaches between psychologists and behavioral ecologists. Although the former tend to use controlled experiments to pinpoint precise cognitive mechanisms, these experiments often lack ecological validity. In contrast, behavioral ecologists seek to understand the adaptive function of cooperative behavior of animals in the wild but typically neglect the underlying psychological mechanisms. Here we appraise and integrate evidence from these two approaches to understand the potential cognitive solutions to four fundamental challenges that animals face during cooperative interactions under natural conditions: (1) when to cooperate; (2) with whom to cooperate; (3) what to do in cooperative interactions; (4) how much to contribute to cooperation. We argue that an ecologically motivated approach is critical to understanding the psychological mechanisms of cooperation and how these mechanisms evolve.

in cases where individuals gain direct benefits from their actions (Clutton-Brock, 2002). Classic examples of this occur not only in inter-species mutualisms where both parties benefit (e.g. algae and coral; Hopley, 2011) but also within species when self-serving actions produce a benefit to others as a by-product (by-product mutualism; Clutton-Brock, 2002). Although the evolutionary function of cooperation is now fairly well understood, relatively little is known about the psychological mechanisms that underpin cooperative behavior in animals.

Part of the reason these mechanisms remain poorly understood is due to a tension between two contrasting approaches within animal behavior. Behavioral ecologists seek to understand the adaptive value of behavior by examining its fitness consequences, often through studies of animals in their natural environments. However, the cognitive mechanisms that underpin these behaviors are largely neglected. Moreover, when cognition is addressed in behavioral ecology, there is often a tendency to assume that cognitive mechanisms can be inferred from behavioral observations alone (Byrne & Bates, 2011). In contrast, psychologists highlight the fact that mechanisms, unlike behavior, are unobservable: a given behavior could be underpinned by a variety of different underlying mechanisms (see Tomasello & Call, 2007 response to Boesch, 2007). Consequently, they use controlled experiments, often under laboratory conditions, to pinpoint the role of specific cognitive mechanisms. Although rigorous experimental methods provide valuable insight into the range of possible

mechanisms that animals may use to solve cooperative problems, tests often lack ecological validity and may not reflect the mechanisms that animals use to solve problems in the wild. Here we argue that an approach that integrates these two perspectives is necessary to understand both the mechanisms supporting cooperation in animals and how these mechanisms evolved.

Within psychology there are strong debates as to the extent to which animals employ computationally complex, human-like mechanisms. Many psychologists' interest in animal cognition lies in understanding the evolutionary origins of human cognition (e.g. de Waal, 1999). Consequently, they test animals to determine whether they show evidence for high-level cognitive processes known to be involved in human cognition. By contrast, others emphasize the use of relatively simple heuristics or rules of thumb and conserved general mechanisms like associative learning (Gigerenzer, Todd & Group, 1999; Heyes, 2012). An ecological approach can be instrumental in establishing which mechanisms are likely to be important in allowing animals to solve the problems they face in natural environments (McAuliffe & Thornton, 2012). For example, studies of food-caching birds have brought together evidence from ecological field studies, neuroanatomy and experimental psychology to show that these birds' ability to retrieve hundreds or sometimes thousands of stored food items relies on an enlarged hippocampus supporting long-term memory retention (e.g. Biegler *et al.*, 2001). A similar ecologically motivated approach is likely to be invaluable in furthering our understanding of the psychological and evolutionary basis of animal cooperation.

In this paper we aim to unite perspectives from behavioral ecology and comparative cognition to generate an ecologically grounded framework for understanding the challenges that animals face during cooperative interactions and how evolution has shaped the cognitive solutions to these challenges. This is very much a two-way street: rigorous psychological experiments are critical to uncover mechanisms underlying behavior, but they must be informed by a thorough understanding of the problems that animals face in their natural environments. We focus on four main classes of cooperative problem that animals face in their natural environment. Although these categories are not mutually exclusive, we hope they provide a new framework for examining the decisions that animals face during the course of cooperative interactions. The classes of cooperative problem that we focus on are (1) when to cooperate; (2) with whom to cooperate; (3) what to do in cooperative interactions; (4) how much to contribute to cooperation.

Four cooperative problems and potential cognitive solutions

When to cooperate?

In cooperative societies, individuals must decide when to engage in cooperation. For instance, helpers in cooperative breeding societies must decide when to eat a procured food item or give it away to dependent young. Similarly, in species

that exhibit group territory defense or hunting, individuals must decide when to participate. Different disciplines approach this question in contrasting ways. Behavioral ecologists typically focus on *extrinsic* factors imposed by others that compel individuals to cooperate (reviewed in Clutton-Brock, 1998). In contrast, psychologists tend to emphasize *intrinsic* motivations, termed prosocial motivations or other regarding preferences (Burkart, Hrdy & van Schaik, 2009), which lead individuals to help whenever possible. Here we consider each of these perspectives in turn by examining the possible mechanistic underpinnings of two extrinsic factors, solicitation and aggression, and by appraising the ecological validity of evidence for intrinsic prosocial motivations.

Signals of solicitation may provide a clear and honest indicator of when help is needed. Evolution is likely to favor signals that tap into preexisting psychological biases in the receiver, making the signal easy to detect, discriminate, learn and remember (Guilford & Dawkins, 1991). One extreme example is seen in chicks of the brood parasitic Horsfield's hawk-cuckoo *Cuculus fugax*, which have brightly colored gape-like marking under their wings. These markings, along with the chick's own open gape, mimic the appearance of three begging chicks, deceiving host parents into feeding the tricky intruder at very high rates (Tanaka & Ueda, 2005). Signals comprised of multiple components (i.e. multicomponent signals) are thought to be particularly effective, especially when they tap into multiple sensory modalities (Rowe, 1999). Most begging chicks, for instance, employ both acoustic and visual signals to solicit feeding from adults (Kilner, 2002).

In addition to solicitation, individuals can elicit help from others through other extrinsic cues, such as aggressive behavior. Theoretical models of cooperation often assume that individuals will defect whenever possible (Houston & Davies, 1985; Clutton-Brock, 1998). If this is the case, then cooperation may only be stabilized by punishment, where one individual harms a cheat, causing them to cooperate in future, or by coercion, where one individual is forced to cooperate even though it is in their interest to defect (Raihani, Thornton & Bshary, 2012). From a psychological point of view, aggression could play an important role in enforcing cooperation if aggressors must identify and react to actions and/or victims must learn to desist from cheating in future interactions. For instance, attacks by male cleaner fish (*Labroides dimidiatus*) can cause their female partners to desist from biting clients and only eat ectoparasites rather than client mucous (their preferred food) in the future (Raihani, Grutter & Bshary, 2010). In this example, the male need only monitor and recognize a single outcome (the sudden departure of the client) that is particularly salient because it results in the immediate removal of a food source. From the perspective of the cheater, future cooperation is enforced by operant conditioning, whereby the female learns to associate her deviant behavior with a negative outcome. In addition to punishment, individuals may also be forced into cooperation through harassment. Harassment differs from punishment in that it benefits both the harasser and the defector simultaneously and immediately (Stevens, 2004), whereas the benefits of punishment are delayed. The harasser benefits through forcing cooperation

(e.g. forcing the defector to donate food) and the defector benefits through avoiding costly conflict. Harassment may be quite common in food sharing in primates, particularly under conditions where the costs of food defense outweigh costs of sharing food (Stevens, 2004). For example, a detailed study of food sharing in Gombe chimpanzees *Pan troglodytes* demonstrated that harassment by others largely explains incidents of sharing (Gilby, 2006).

Some authors have argued that aggressive behaviors such as punishment may induce desired behavior as well as inhibiting unwanted actions. For instance, according to the pay-to-stay hypothesis, helpers in cooperatively breeding societies are allowed to stay on their home territory if they contribute to cooperative activities. Such contributions are enforced by attacks by dominant individuals on helpers that do not pull their weight (Gaston, 1978). Empirical evidence for cooperation enforced by this type of punishment under natural conditions is scarce (but see Balshine-Earn *et al.*, 1998) and equivocal (see Raihani *et al.*, 2012). The apparent rarity of punishment-mediated cooperation in nature may be explained in part by psychological constraints. From the point of view of the aggressor, it would be necessary to monitor, encode and remember the relative contributions of all helpers and to recognize when a helper has failed to help (Raihani *et al.*, 2012). All of these tasks are likely to be cognitively demanding, and recognizing a failure to help may be especially challenging given that omissions are unobservable and have no causal consequences (Baron & Ritov, 2004). From the point of view of victims, learning as a result of aggression to do something that they had previously failed to do may be extremely difficult. Such learning is only likely to be effective if the range of possible responses to aggression is tightly constrained. In a Skinner box containing no features other than walls and a lever, a rat that is subjected to shocks may exhibit a range of escape behaviors and, in so doing, may learn through negative reinforcement that pressing the lever causes the shocks to cease (Sidman, 1953). In contrast to such artificially restricted conditions, an individual in the wild may be performing a range of behaviors at any given time. It would thus be difficult for an animal to learn an association between the absence of a behavior and a negative reinforcer like punishment. Instead, the animal is likely to respond to aggression by avoiding the punisher rather than learning to perform the targeted cooperative behavior. Humans may get around this using language to explain which omitted behavior was punished (Raihani *et al.*, 2012).

Thus far we have considered situations in which individuals are compelled to help either by solicitation or by aggression. Some authors have argued that humans and certain other species are intrinsically motivated to help (Burkart & van Schaik, 2010). Such motivations could, in theory, eliminate the temptation to defect, negating the need for external motivators. For example, Burkart *et al.* (2010, 2014) have argued that food donation in some cooperative breeders is not the result of coercion or solicitation but is rather the product of an intrinsic desire to assist others. Because psychological motivations are unobservable and thus hard to study in the field, researchers have used carefully controlled laboratory experiments to

explore whether animals may have intrinsic preferences for assisting others. The paradigm that has been used most frequently to study this is based on food sharing behavior and gives individuals an opportunity to choose between actions that deliver varying food rewards to themselves and a social partner. For instance, Silk *et al.* (2005) showed that chimpanzees were equally likely to choose between a 'selfish' action that would deliver food only to themselves and a 'prosocial' action that delivered food both to themselves and to another individual, indicating that chimpanzees are indifferent to each other's welfare (see also similar results in Jensen *et al.*, 2006). In contrast, Burkart *et al.* (2007) found that common marmosets *Callithrix jacchus* preferred to deliver a 'prosocial' option (0 for actor, 1 for recipient) over a no-food option (0 for actor, 0 for recipient), whereas they did not show this preference in the absence of a partner. Burkart *et al.* interpreted this as evidence that these cooperatively breeding primates are motivated to help one another (but see Thornton & McAuliffe, 2015 for a detailed discussion of these results). Evidence from these tasks is ambiguous, with different studies producing different results (Silk & House, 2011) and results are often hard to interpret. At first glance, negative results may be relatively straightforward: if an individual fails to deliver a reward to a partner even in situations when doing so entails no cost (Silk *et al.*, 2005; Jensen *et al.*, 2006), this would seem to provide compelling evidence for the absence of prosocial motivations. However, negative results could also indicate that the animal has not understood the structure of the task. Positive results on these tasks may be even more difficult to interpret: because donations entail no cost, it is not clear how such motivations could relate to cooperative behavior shown in the wild where cooperation often involves donating previously acquired resources (Thornton & McAuliffe, 2015). One possible explanation for why marmosets prefer the 'prosocial' option in the Burkart *et al.* (2007) task is that the presence of a partner increases the salience of the single food item, making individuals more likely to select that option. Similarly, Heyes (2012) and Chang, Winecoff & Platt (2011) have argued that apparently prosocial choices in chimpanzees and macaques *Macaca mulatta* may be explained by associative learning of reward contingencies during the course of experiments. For example, Heyes (2012) argues that chimpanzees tested in a token-based prosocial study by Horner *et al.* (2011) may have made apparently prosocial choices because they learned an association between the food and the sound of food being unwrapped (conditioned reinforcer). The 'prosocial' choice resulted in two pieces of food being unwrapped and thus delivered two hits of the conditioned reinforcer whereas the selfish choice resulted in only one reinforcer. Under this view, therefore, apparent prosociality is a mere artifact of the experimental setup. We argue that any attempt to evaluate the merits of competing mechanistic explanations or the plausibility of claims for prosociality or other high-order psychological interpretations must take into account the challenges animals face in their natural environments.

Laboratory findings often seem at odds with behavior exhibited under natural conditions. For example, in contrast with claims of prosociality in experiments on chimpanzees and

callitrichids (Burkart *et al.*, 2007; Horner *et al.*, 2011), active food sharing in the wild is very rare in the former and largely restricted to offspring provisioning in the latter (Gilby, 2006; Rapaport & Ruiz-Miranda, 2006). This tension reflects a common tendency to conflate explanations based on proximate mechanisms and adaptive functions. In other words, observing that an animal chooses a prosocial option under laboratory conditions cannot be interpreted as evidence that prosocial motivations have been shaped by selection as a means of promoting cooperation (see Scott-Phillips, Dickins & West, 2011 for a discussion of the ultimate–proximate distinction in behavioral research). Conversely, there is no reason to assume that behaviors that are functionally prosocial are supported by prosocial mechanisms. For example, two recent papers reported rescue behavior in which individuals helped to release a trapped conspecific, in ants *Cataglyphis cursor* (Nowbahari *et al.*, 2009) and rats *Rattus norvegicus* (Bartal, Decety & Mason, 2011). Whereas the former made no mention of underlying mechanisms, the latter claimed that rats' rescue behavior was motivated by empathy, a prosocial motivation whereby individuals share emotions with others. Vasconcelos *et al.* (2012) argued powerfully that such an explanation is unwarranted because apparently helpful behaviors need not be underpinned by helpful motivations. As they explain, evidence for empathy hinges on the demonstration that individuals represent others' emotional states and intentionally attempt to improve others' welfare. Despite claims of evidence for components of empathy in chickens *Gallus gallus domesticus*, rodents, dogs *Canis familiaris* and primates (Anderson, Myowa-Yamakoshi & Matsuzawa, 2004; Joly-Mascheroni, Senju & Shepherd, 2008; Palagi *et al.*, 2009; Bartal *et al.*, 2011; Edgar *et al.*, 2011), no study has yet met these requirements. Moreover, the theoretical plausibility of empathy as an evolved mechanism (as opposed to an artifact of testing conditions) is difficult to assess as laboratory studies rarely consider if and how empathetic concern would be favored by selection in the natural environment. Rather than focusing on anthropocentric mechanisms, future studies investigating how animals decide when to cooperate could benefit from considering ecological and psychological explanations in concert. Such an approach could help behavioral ecologists by pointing to mechanisms that enable and constrain decisions as to when to cooperate, and assist psychologists in designing experiments that reflect the cooperative problems that animals face in the wild.

With whom to cooperate?

In addition to deciding when to cooperate, animals must also make decisions about with whom to cooperate. Given the costs of cooperation, individuals should not help indiscriminately. There are two main classes of explanation for such discriminate helping. First, individuals may preferentially help those that meet particular criteria, such as age, sex, rank or relatedness. For instance, male baboons *Papio cynocephalus* preferentially come to the assistance of their offspring during conflicts (Buchan *et al.*, 2003) and spotted hyenas preferentially support high-ranking individuals in agonistic interac-

tions (Engh *et al.*, 2005). Alternatively, the propensity to help other individuals may be contingent on their past behavior. For example, wild chimpanzees appear to reciprocate grooming over the long term (Gomes, Mundry & Boesch, 2009). Similarly, there is evidence that in long-tailed macaques *Macaca fascicularis*, individuals are more likely to groom those who have provided grooming in the recent past (Hemelrijk, 1994).

Among cases where help is based on particular criteria, the best-studied examples are those where help is directed towards kin. Across taxa from amoebae to primates, individuals preferentially assist group members that are most closely related to themselves (Clutton-Brock, 2002; Mehdiabadi *et al.*, 2006; Silk, 2009). A range of mechanisms have been proposed to explain how individuals discriminate between relatives and non-relatives (Hepper, 2005). In cases where kin are consistently found in a predictable location, such as nesting birds, a simple rule, such as 'feed any chick in my nest', may suffice (Komdeur & Hatchwell, 1999). In other cases, where kin are not distributed predictably in space, kin recognition may rely on the assessment of other cues and individuals may need to learn to recognize these cues (Komdeur & Hatchwell, 1999). For instance, cooperatively breeding long-tailed tits *Aegithalos caudatus* show kin-biased care, discriminating between kin and non-kin using vocal cues learned from adults during the nesting period (Sharp *et al.*, 2005).

In cases where individuals regularly cooperate with non-kin, help may be contingent on previous interactions. Mechanistically, one of the simplest form of contingent helping is generalized reciprocity, whereby individuals who receive help in the past have an increased propensity to help any individual in the group (Pfeiffer *et al.*, 2005). Here it is sufficient for individuals to base their decisions on the outcome of their last interaction with no requirement for recognizing and remembering who helped. Despite the simplicity of this mechanism, evidence for generalized reciprocity is currently restricted to two laboratory studies. Most recently, a study of capuchin monkeys *Cebus apella* demonstrated that individuals who had received food subsequently gave food of equivalent value to the next individual with whom they interacted (Leimgruber *et al.*, 2014). Rutte & Taborsky (2007) found a similar result between unfamiliar and unrelated partners in a study of Norway rats (*R. norvegicus*). However, the ecological validity of this finding is questionable given that rats typically attack and often kill strangers (Ewer, 1971; Blanchard & Blanchard, 1977). Thus, rather than reflecting an evolved mechanism for cooperation among strangers, we suspect this result may be an artifact of experimental reinforcement regimes.

Other forms of reciprocity may require mechanisms for recognizing individual conspecifics and remembering their past behavior. The need for recognition and memory is likely to depend on the extent to which cooperative interactions are spatially and temporally restricted (see Table 1). In experiments inspired by natural cleaner fish–client relations, for example, Bshary & Grutter (2006) showed that clients select cleaners on the basis of observations of their past cleaning interactions, a phenomenon known as image scoring (Wedekind & Milinski, 2000; Bshary & Grutter, 2006; Russell

Table 1 Basic cognitive prerequisites for contingent cooperation

	Spatially predictable	Spatially unpredictable
Short term	No memory No individual recognition (e.g. image scoring in cleaner fish–client interactions)	
Long term	Memory No individual recognition (e.g. mobbing in pied flycatchers)	Memory Individual recognition (e.g. grooming in chimpanzees)

The top right box is empty because in short-term, one-shot interactions the location of a partner is predictable.

et al., 2008). Here, the interaction is both spatially predictable and short term: cleaners occupy spatially discrete ‘cleaning stations’ and clients approach cleaners immediately following a bout of observation (Bshary, 2001). Consequently, clients may be able to make decisions that are contingent on past cleaner behavior without needing to recognize cleaners as individuals or remember their behavior over the long term. In other cases, individuals may need to remember who has helped over longer time frames. If individuals’ locations are spatially predictable, however, this may be achieved through remembering where the last helping event took place rather than by individual recognition *per se* (see Proops, McComb & Reby, 2009; Wiley, 2013 for discussion of the cognitive demands of true individual recognition). For example, a recent study suggested that pied flycatchers (*Ficedula hypoleuca*) show direct reciprocity whereby breeding pairs join in mobbing predators at the nests of pairs who have helped them drive away predators in the past (Krams *et al.*, 2008; for a review of this study and other examples of reciprocity see Raihani & Bshary, 2011). However, as Russell & Wright (2009) point out, this seemingly contingent behavior may not require individual recognition or score keeping. Russell and Wright did not specify the cognitive mechanisms that may be involved, but one possibility is that flycatchers employ a rather simple rule of thumb: remember where pairs that helped you came from and preferentially join in mobs at those locations in the future. Indeed, this type of location-based contingent behavior may be relatively common. For instance, a recent study of symbiotic interactions between plants and mycorrhizal fungi showed that plants reward good fungal partners with increased donations of carbohydrates and those fungal partners reciprocally reward plants with increased nutrient transfer (Kiers *et al.*, 2011).

Where the location of partners varies unpredictably over space and time, individual recognition is likely to be a fundamental requirement of contingent cooperation (Table 1). For instance, a study of chimpanzees showed that individuals may use image scoring, a form of partner choice linked to indirect reciprocity, to preferentially recruit collaborators who have helped others in the past (Melis, Hare & Tomasello, 2006; see Vail, Manica & Bshary, 2014 for a similar result in trout-moray eel mutualisms). Unlike image scoring in cleaner–client interactions, individuals must remember interactions they

observed the previous day and, critically, the identity of potential partners cannot be predicted by their previous location. Direct reciprocity, whereby individuals selectively help those who have helped them in the past (Trivers, 1971), may require additional mechanisms beyond individual recognition and memory. These cognitive requirements have been discussed at length elsewhere (Stevens & Hauser, 2004) but, at a minimum, are additionally likely to involve learning, the ability to discriminate between quantities and temporal discounting. These cognitive prerequisites may help to explain why evidence for reciprocal altruism (*sensu* Trivers, 1971) in nature is scarce (Clutton-Brock, 2009; Hauser *et al.*, 2009; Cheney, 2011). Psychological investigations of direct reciprocity thus provide a clear example of how consideration of cognitive requirements can inform our understandings of constraints on the evolution of particular types of cooperation. Operating on the principle of parsimony, behavioral ecologists generally are reluctant to ascribe complex cognitive mechanisms to their study animals, but they seldom specify concrete alternative mechanistic explanations (for a discussion of parsimony see Heyes, 2012). An ecologically motivated approach to the psychology of cooperation, testing the cognitive mechanisms that support animal behavior observed in the wild, can shed important light on animals’ decisions as to with whom to cooperate.

What to do in cooperative interactions?

Once an animal has decided to cooperate and whom to assist, it may additionally face a choice between different forms of cooperation or need to select a strategy to achieve a particular outcome. For example, cooperatively breeding meerkats *Suricata suricatta* engage in a variety of cooperative activities so helpers must choose between investment in sentinel behavior, burrow maintenance, pup feeding and babysitting (Clutton-Brock, Russell & Sharpe, 2003).

The distribution of work by helpers across different categories of cooperation is largely determined by individual characteristics. The most striking examples of this are caste systems in eusocial insects, in which individuals are morphologically and physiologically specialized for particular activities (Wilson, 1971). Among vertebrates, division of labor is not strictly caste based, but rather varies by age, sex and size (such behavioral differences between categories of individuals are known as ‘polyethisms’; e.g. naked mole rats *Heterocephalus glaber*; Lacey & Sherman, 1991, 1997; meerkats; Clutton-Brock *et al.*, 2003; white-winged choughs *Corcorax melanorhamphos*; Heinsohn & Cockburn, 1994; and cichlids *Neolamprologus pulcher*; Brintjes & Taborsky, 2008). In cases where work is divided strictly by caste or other polyethisms, individuals may not need to actively decide what to do. However, there are many instances in which individuals are faced with a choice and their decisions can be roughly categorized into two explanatory classes: simple heuristics and more complicated cognitive assessment of different options.

Simple heuristics may often be sufficient to generate seemingly complex decision rules, attuned to the specific requirements of the situation. For example, when a meerkat helper finds a prey item, it must first decide whether to eat the item or

provision it to a pup. These decisions are based largely on characteristics of the prey: helpers are most likely to feed large and rare prey items to pups (Thornton, 2008). Helpers must also decide what state to provision the item in as part of a continuous process where they teach young pups to handle prey. This decision is based on a simple rule: provision dead prey in response to the begging calls of young pups and live prey in response to the calls of old pups (Thornton & McAuliffe, 2006).

In highly dynamic contexts in which individuals' access to information is unpredictable or unreliable, simple rules of thumb may not suffice and more complex cognitive appraisals may be needed to guide their decisions about what to do in cooperative interactions. Some authors have argued that in certain populations of collaboratively hunting species, individuals assume specific roles and coordinate their hunting behavior with hunting partners (lions *Panthera leo*; Stander, 1992; dolphins *Tursiops truncatus*; Gazda *et al.*, 2005; and chimpanzees Boesch, 2002). Boesch (2005) has suggested that coordinated hunting among Tai chimpanzees may involve complex cognitive mechanisms such as perspective taking, and the sharing of goals and intentions (see Gilby & Connor, 2010; Vail *et al.*, 2014 for discussion of simpler alternatives). However, no study has specifically tested the psychological mechanisms underlying collaborative hunting. The development of high-resolution animal tracking technologies such as accelerometers and global positioning systems (e.g. Wilson *et al.*, 2013) may provide researchers with an opportunity to track, for the first time, the precise movements of individuals and their responses to one another during coordinated hunts. A clear picture of these roles could then inform the design of controlled experiments testing possible cognitive mechanisms.

Given the difficulties of investigating cognitive mechanisms in the wild, to date more progress has been made in understanding how animals decide what to do in cooperative interactions in controlled laboratory tests. For instance, Warneken & Tomasello (2006) demonstrated in a series of experiments, which did not involve food rewards, that chimpanzees recognize when help is needed and spontaneously assist both human and conspecific partners. Additionally, many researchers have used variants of the classic Crawford (1937) task, wherein two individuals must pull a rope together in order to access food rewards. To solve this task, individuals may need to (1) recognize that a collaborator is necessary to complete the goal; (2) attend to and coordinate their behavior with that of their partner. Hirata & Fuwa (2007) importantly extended the paradigm with a design that required complete synchronization between the two partners. In this task, if one individual fails to pull the rope this means that neither individual can access the food. A number of species, including some birds (Seed, Clayton & Emery, 2008), mammalian carnivores (Drea & Carter, 2009; Ostojić & Clayton, 2013), elephants (Plotnik *et al.*, 2011) and primates (Crawford, 1937; Cronin, Kurian & Snowdon, 2005; Hattori, Kuroshima & Fujita, 2005; Melis *et al.*, 2006; Hirata & Fuwa, 2007) have been found to succeed in these tasks. However, the extent to which they use complex mechanisms is ambiguous. For instance, Seed & Jensen (2011) argue that a simple learnt rule whereby individuals pull the

rope only when a collaborator is present may often be sufficient to explain successes on this task. Arguably a stronger test for the role of complex cognitive processes in collaborative interactions comes from a recent study by Yamamoto, Humle & Tanaka (2012). Here, captive chimpanzees were paired with a partner who needed a tool to access a reward. The partners did not have access to tools but could solicit help from a collaborator in an adjacent cage who had access to a tray of potential tools. In order to help effectively, the collaborator needed to select an appropriate tool and deliver it to the partner. When collaborators could see the task facing their partner, they selected and donated an appropriate tool at higher rates than when they could not see their partner's task. This finding was interpreted as evidence that collaborators decided what to do on the basis of an understanding of the partner's goal. Although these results are thought provoking, this paper illustrates the difficulty of generating clear evidence for mental state attribution because the same results could be achieved if collaborators acted on their own perceptual access to and prior experiment with the task. Moreover, given that chimpanzees do not routinely share tools in the wild, it is unclear how this task maps onto collaborative or cooperative challenges that chimpanzees face in nature.

To fully understand how animals decide what to do in cooperative interactions, experimental tasks should be designed with the species' ecology in mind. Two recent ecologically motivated studies have examined the possible roles of desire and knowledge state attribution in animal cooperation. One captive study exploited the courtship feeding behavior of male Eurasian jays *Garrulus glandarius*, where males provision their mate with food items. When females have eaten a large amount of one type of food, they subsequently show a preference for different food types, a phenomenon known as food-specific satiety. If a male has not seen what his mate has been eating, he feeds her according to his own preferences. On the other hand, if he has seen what she has been eating, he preferentially gives her a different food type, raising the possibility that males act on the basis of an understanding of females' desires (Ostojić *et al.*, 2013). In a second experiment, Crockford *et al.* (2012) used presentations of model snakes to examine whether chimpanzees selectively inform ignorant conspecifics about the presence of danger. Here, when focal chimpanzees came across a model snake they were most likely to alarm call if in the presence of individuals who they had not seen encountering the snake. This finding suggests that decisions about whether to inform conspecifics about potential danger may, in some cases, rely on reasoning about what others know. Although there is some debate about the interpretation of these results (Seyfarth & Cheney, 2012), this study provides a strong illustration of a highly ecologically valid test of the psychology of cooperation.

How much to contribute to cooperation?

One problem individuals face is how much to contribute to cooperative interactions. For example, cooperatively breeding cotton-top tamarin *Saguinus oedipus* helpers must decide when to transfer the young that they are carrying to another

individual (Sanchez *et al.*, 1999). Similarly, individuals across many species of primates must decide when to terminate a grooming bout. One striking feature of cooperative animal societies is that there is typically extensive variation in how much different individuals contribute to helping (Bergmüller, Schurch & Hamilton, 2010; English, Nakagawa & Clutton-Brock, 2010). Much of this inter-individual variation can be explained by age, sex and other polyethisms (Komdeur, 2006; Bergmüller *et al.*, 2010). For instance, female meerkats contribute more to pup feeding than do males, presumably because as the philopatric sex they derive greater benefits from pup survival (Brotherton *et al.*, 2001). From a proximate point of view this can be explained, in part, by sex differences in adult meerkats' responsiveness to pup begging calls (English *et al.*, 2008), although the psychological underpinnings of this difference in responsiveness are unknown.

Individual variation in contributions to cooperative care is also strongly determined by body condition. In cases where cooperation results from by-product mutualism or pseudo-reciprocity, individuals derive direct benefits from their actions and thus it may be in their interest to invest when they can afford to do so. A classic example of this is seen in meerkat sentinel behavior. Here, individuals climb onto high vegetation to spot predators and use alarm calls to alert group members of impending danger. Sentinels are thought to benefit from being on guard because they are the first to spot predators and can thus make a speedy escape. Supplemental feeding experiments show that satiated helpers are most likely to go on guard, indicating that the decision to go on guard is at least partly driven by current energetic state (Clutton-Brock, 1999); although note helpers are also more likely to guard in the presence of pups (Santema & Clutton-Brock, 2013). Condition may additionally play an important role in explaining variation in investment in cooperation when benefits of helping are delayed. Indeed, across cooperative societies, investment in cooperative activities such as offspring care and territory defense, is typically condition dependent (Heinsohn & Legge, 1999). Even after accounting for polyethisms between categories of helpers and the influence of individual condition, there is still substantial unexplained variation in how much individuals contribute to cooperative behaviors (Bergmüller *et al.*, 2010; English *et al.*, 2010; Carter & English, 2014). For instance, in some eusocial insect species certain individuals, known as elite workers, show unusually high levels of cooperation that cannot be explained by known physiological or morphological characteristics of workers (Hölldobler & Wilson, 1990; Robson & Traniello, 1999).

From a psychological perspective, one important factor influencing individuals' decisions about how much to help is the availability of information about how much help is required. In many cases, this information may be provided by the potential recipients of help (e.g. chicks begging). In other cases individuals may attend to and process information about the extent to which their social partners are helping, and use this information to guide their own contributions. This information can either be generated inadvertently or actively by social partners. For instance, in great tits *Parus major* that

show biparental care, the rate at which one parent provisions the chicks provides the other parent with a cue as to how much feeding is necessary (Hinde, 2005). In this case, information transfer is a by-product of parental feeding rates. In certain other cases, helpers may actively provide information to others. In many cooperative species sentinels produce a distinctive call, known as the watchman's song, which signals that they are on guard. This may play a role in informing foraging group members of current risk (Bell *et al.*, 2009; Ridley, Raihani & Bell, 2010; Kern & Radford, 2013) and perhaps in coordinating guard duty (Manser, 1999; Bell *et al.*, 2010).

Although body condition and the availability of information are likely to play a major role in influencing how much individuals contribute to cooperation, some authors have argued that animals may be driven by psychological processes akin to the human sense of fairness (Brosnan, 2006, 2011). Specifically, animals may show an aversion to situations in which their returns from cooperation are low relative to those of others. Such disadvantageous inequity aversion could, in theory, play a role in regulating individuals' investments in cooperative activities. For instance, young children will protest volubly when rewarded less than a peer for having done the same amount of work tidying a room (LoBue *et al.*, 2010), indicating sensitivity to the relationship between relative investment in and rewards from working together.

Given the theorized importance of fairness norms in stabilizing human cooperation (Fehr & Schmidt, 1999; Fehr & Fischbacher, 2004), some psychologists have sought to examine the evolutionary roots of fairness preferences in other animals by studying whether they show an aversion to disadvantageous inequity. Evidence for such an aversion is controversial, with different studies generating contradictory results (e.g. pro: Brosnan & de Waal, 2003; Brosnan, Schiff & de Waal, 2005; con: Henrich, 2004; Wynne, 2004; Bräuer, Call & Tomasello, 2006; Bräuer, Call & Tomasello, 2009). In these experiments, pairs of individuals are differentially rewarded for performing the same action, for example, handing a token to an experimenter. Results of some of these studies have shown that the individual that has received the relatively poor reward may reject the reward and becomes less likely to continue performing the action (Brosnan & de Waal, 2003; Brosnan *et al.*, 2005; Range *et al.*, 2009). However, a number of other studies using similar protocols have failed to find these effects (Bräuer *et al.*, 2009; Silberberg *et al.*, 2009; Horowitz, 2012), and there is strong debate whether reward rejections are due to inequity aversion (Brosnan, 2006, 2011). An alternative explanation is that reward rejections are due to frustration: individuals reject food rewards both in the presence and absence of partners, if a better reward is within view (Wynne, 2004; Roma *et al.*, 2006; Silberberg *et al.*, 2009). Other tests of inequity aversion in humans have used methods based on the ultimatum game (Güth, Schmittberger & Schwarze, 1982), widely used to test inequity aversion in humans. These studies, like those discussed above, have produced mixed results (pro: Proctor *et al.*, 2013; con: Jensen *et al.*, 2007). Minimally, results from inequity aversion experiments suggest that, in some contexts, animals attend and react

to relative pay-off distributions. Such attention may have little to do with cooperation and instead result from non-cooperative foraging strategies (Chen & Santos, 2006). For instance, individuals may base their foraging decisions both on personally acquired information about prey distributions and public information generated by foraging partners. Thus, rejections in the absence of a social partner can be explained by perceptions of better rewards elsewhere; the presence of a partner eating a better reward provides additional public information about resource distributions in the environment. Minimally, results from inequity aversion experiment suggest that, in some contexts, animals attend and react to relative pay-off distributions. Such attention may have little to do with cooperation and instead result from non-cooperative foraging strategies (Chen & Santos, 2006). For instance, individuals may base their foraging decisions both on personally acquired information about prey distributions and public information generated by foraging partners. Thus, rejections in the absence of a social partner can be explained by perceptions of better rewards elsewhere; the presence of a partner eating a better reward provides additional public information about resource distributions in the environment. Future work could test this idea on species where inequity aversion has been claimed by combining observations in the wild (e.g. do animals tend to abandon relatively poor resources if nearby conspecifics are feeding on better food?) with field or laboratory experiments to explore the how foraging decisions are influenced by the presence and returns of others (e.g. how much better must the partner's food be to motivate resource 'rejection?').

Studies of apparent inequity aversion in animals provide a strong illustration of how the interpretation of results from cognitive experiments can be informed by insights from ecological theories. Here, the extensive body of work on optimal foraging in behavioral ecology can allow us to make sense of apparently puzzling results. Moreover, when one considers animal behavior in the wild, it is difficult to imagine scenarios under which rejecting rewards would be beneficial. Additionally, the design of these experiments bears little resemblance to the cooperative activities documented among animals in their natural environments (Wilson, 1971; Stacey & Koenig, 1990; Dugatkin, 1997; Solomon & French, 2007).

Conclusion

Animals face a variety of problems in their cooperative interactions but the psychological mechanisms supporting their solutions to these problems remain poorly understood. An integrative approach, uniting insights and methods from behavioral ecology and psychology, offers the promise of allowing us to understand both *how* and *why* animals cooperate.

In recent years such an approach to the study of animal cooperation has begun to bear fruit. For instance, studies of cleaner fish–client mutualisms have started to shed light on the decisions involved in clients' choices of cleaners, cleaners' strategies to maximize their rewards from clients and interactions within female–male pairs of cleaners (Bshary, Gingsins & Vail, 2014). This work has shown, among other things, that

clients are able to select cooperative cleaners and influence their future cooperative behavior (Bshary & Grutter, 2006; Pinto *et al.*, 2011), cleaners can learn to select an option that provides delayed rewards (Salwiczek *et al.*, 2012) and females learn to cooperate in response to male punishment (Raihani *et al.*, 2010). Further psychological work can help pinpoint the precise cognitive mechanisms enabling these decisions. Moreover, because these fish have relatively small brains such work is fundamental in helping us understand the minimal cognitive requirements for apparently complex cooperative interactions (see Chittka & Skorupski, 2011 for a similar argument about insects).

Studies of cleaner–client mutualisms stand out from most other studies of cooperative cognition because they are explicitly designed to test hypotheses rooted in an understanding of the cooperative challenges that these species face in the wild. Similar ecologically motivated approaches are likely to prove invaluable in furthering our understanding not only of mutualistic interactions but also in arguably more puzzling forms of cooperation wherein individuals incur costs to confer benefits to others. Greater efforts to combine field ecologists' deep understanding of natural animal behavior with psychologists' knack for rigorous experimental design will pave the way for research programs that are both ecologically valid and psychologically informed. This can allow us to make strides in understanding the psychological mechanisms of cooperation and how these mechanisms evolve.

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