Proximate mechanisms underlying cooperation in carnivores

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Abstract While the evolution of cooperative behaviors has generated an intense debate among evolutionists and animal behaviorists, the proximate mechanisms underlying cooperative relationships have received much less attention. In recent years, it has become clear that an understanding of proximate causation of cooperation is needed in order to obtain a more balanced and complete picture of the phenomenon. The proximate cause of cooperation refers to the immediate situation that triggers behavior, and the role of learning, memory, physiology, and neural processes. Since from an evolutionary point of view cooperative relationships are maintained because of the subsequent benefits they bring, there has been the tendency to erroneously assume that they are also motivated by their future benefits. This assumption would imply that animals engage in social interactions in order to gain future benefits, or that they are able to remember the services given by another individual in order to offer a service in return at a later date. While this "rational" calculation offers a possible explanation, it is currently unclear whether or not some animal species have these cognitive capacities. Here I will argue that, while complex cognitive mechanisms may be present in some species, less-cognitively demanding mechanisms, based on emotions, could be at the basis of the flexibility needed to form complex, enduring cooperative relationships in both human and non-human animals.

Key words : cooperation, proximate mechanisms, carnivores, emotions, oxytocin

The problem of cooperation: A few concepts

A cooperative behavior is a behavior that provides a benefit to another individual (recipient) and that it has evolved — at least partially — because of its benefit for the recipient (for reviews see Lehmann & Keller, 2006; Sachs, Mueller, Wilcox, & Bull, 2004; West, Griffin, & Gardner, 2007). The evolution of such behaviors poses a fundamental problem for evolutionary biologist because one has to reconcile its existence with a theory of evolution which rests on the assumption that individuals compete to survive and breed (Darwin, 1859/1958). In other words, natural selection favors selfish individuals who do not cooperate. Despite this contradiction, there is evidence of cooperation throughout all organisms, from microbes to vertebrates at scales that range from intra-genomic to inter-specific, suggesting that there must be a solution to the problem. Current theoretical explanations for the evolution of cooperation are rooted in Hamilton's concept of inclusive fitness (kin selection, Grafen, 2006; Hamilton, 1964), and it is now widely accepted that selection operating through benefits gain from aiding related individuals is commonly involved in maintaining cooperative behaviors (Clutton-Brock, 2009; West, El Mouden, & Gardner, 2011). In spite of these successful explanations, there are still many unresolved problems and empirical evidence for many proposed solutions is quite sparse (e.g.

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Brosnan & Bshary, 2010; Clutton-Brock, 2009; Lehmann & Rousset, 2010).

Mixing proximate and ultimate explanations

When studying cooperation, or any other behavior, it is important to distinguish between proximate and ultimate explanations (Mayr, 1961; Tinbergen, 1963). Ultimate explanations of a behavior are concerned with its fitness consequences, while proximate causations are concerned with the causal mechanisms underlying the behavior. These different methodologies, although complementary to each other, ask different questions and therefore, provide different answers. For cooperation, the ultimate question is why is cooperation maintained? The possible answer is because it provides either direct and/or indirect fitness benefits to the actor. The proximate question is how is cooperation maintained? The answer to this is a predisposition to cooperate, which refers to the immediate situation that triggers cooperation, and the role of learning, memory, ontogeny, physiology, and neural processes. Most research about cooperative behaviors has focused on the conditions under which cooperation may promote individual's fitness (i.e. ultimate explanations), and as a consequence its proximate causation has been until recently largely neglected. A detailed understanding of the proximate mechanisms of cooperation is important in order to obtain a more balanced and complete picture of the phenomenon. It will also help to elucidate possible constrains on the evolution of cooperation and define realistic assumptions in theoretical models. For instance, many models assume that individuals have a perfect memory, that each individual is able to perform all different behavioral options, or that gaining information is free; which are unlikely to be realistic for any empirical example (Brosnan, Salwiczek, & Bshary, 2010).

Although proximate and ultimate causes are clearly different (i.e. individual motivation to perform a behavior vs. possible reasons for the evolution of the behavior), it is not uncommon to find hypotheses that fail to distinguish between both approaches. A key point here is that to explain the evolution of cooperation evolutionary biologists consider the average consequences of a behavior and not the consequences of every single instance. That is, evolutionary explanations state that cooperative relationships are maintained because of the *subsequent* benefits they bring to the actor's inclusive fitness over its lifespan. Maybe because of this emphasis on overall consequences, there has been the tendency to erroneously assume that cooperative relationships are also motivated by their future benefits (e.g. Stevens & Hauser, 2004). This assumption would imply that animals are aware of the long-term outcome of their actions and that they engage in social interactions in order to gain them. However, evidence for such awareness or cognitive ability to remember the outcome of social exchanges over time is currently unclear (Cheney, 2011; Melis & Semmann, 2010; Schino & Aureli, 2009). Thus, the fitness-enhancing properties of cooperative behaviors should not be taken as an explanation of what motivates individuals to interact in a cooperative way (Schino & Aureli, 2009).

Here, I will present some examples of less-cognitively demanding mechanisms that could be at the basis of the flexibility needed to form complex, enduring cooperative relationships in animals. In this respect, mammalian carnivores represent an excellent model. Many species of carnivores live in large, permanent social groups that contain both male and females from several overlapping generations. Social carnivores are known to stablish enduring cooperative relationships with group mates that often last many years (e.g. Watts & Holekamp, 2007). Help from group members is often required while hunting large preys, or while defending their kills or territories (Macdonald, 1983). Sentinel behavior, in which individuals scan for predators and alert other group members of danger, is also found in some social carnivores (e.g. Clutton-Brock et al., 1999; Kern & Radford, 2013). In addition, allies are critical during within-group

disputes (e.g. Fentress, Ryon, McLeod, & Havkin, 1986; Gompper, 1997), which can be extremely intense in some species (e.g. Smith et al., 2010). Furthermore, some carnivores are cooperative breeders, with most or all group members contributing to guarding and feeding the young (e.g. Clutton-Brock et al., 1998). Thus, the study of the enduring cooperative relationships found among long-living carnivores can help to uncover whether proximate mechanisms not necessarily reliant on cognitive processes are sufficient to explain complex cooperative patterns. The present work is not meant to be a review of the current knowledge of proximate mechanisms of cooperation in vertebrates in general, and carnivores in particular. Major reviews and theoretical debates are well covered elsewhere (Brosnan et al., 2010; de Waal, 2008; Schino & Aureli, 2009; West et al., 2011). By providing examples of possible mechanisms underlying cooperation in carnivores, the present work aims to emphasize the importance of studying such mechanisms in a wide range of taxa in order to gain a more complete understanding of cooperation in both human and non-human animals.

Partner choice in agonistic support

Probably one of the clearest examples of confounding ultimate and proximate explanations can be found in the debate about the mechanisms underlying reciprocal altruism (Trivers, 1971). Evolutionary biologists classify social behaviors as *selfishness*, *spite*, *altruism*, and *mutually beneficial* depending on the lifetime benefits and costs for the actor and the recipient (Hamilton, 1964; West et al., 2007). According to this classification, behaviors that involve lifetime mutual benefits, such as group hunting, cooperative breeding, or coalitionary agonistic support, are easily explained by individual selection. That is, they are favored because the reproductive success of the individual who performs the cooperative behavior is increased. It should be note that behaviors classically termed as "reciprocal altruism" (see below) would be included under this heading. While the

theory on the evolution of cooperation provides a unified explanation for all of these examples of mutual benefits, the proximate mechanisms involved on each of them are likely to be disparate. The reason is the heterogeneity in the timing of the benefits and costs for each of the individuals involved. For instance, wolves (*Canis lupus lupus*) hunting together a large prey will obtain immediate benefits from the cooperative hunt, and the proximate mechanisms involved do not need to be particularly complex. Although cognition may help make coordination more efficient (Bailey, Myatt, & Wilson, 2013), a recent study suggest that coordinated hunting in wolves could arise as each wolf follows simple rules such as getting the closest safe distance to the prey and getting the best view of the prey (Muro, Escobedo, Spector, & Coppinger, 2011).

A complication arises when there is a time lag between costs and benefits. That is, the actor incurs immediate costs and receives delayed benefits that depend on the future behavior of the recipient. This is what has been classically termed reciprocal altruism, although it is now usually referred to as "direct" or "cost-counting" reciprocity (Clutton-Brock, 2009). Examples of carnivore behaviors that benefit other individuals at (little) cost for the actors are agonistic support, tolerance, and food sharing (e.g. Fentress et al., 1986; Romero & Aureli, 2008; Stander, 1992). Since the evolutionary stability of reciprocity depends on individuals' strategies — and counter-strategies — aimed at maximizing benefits and minimizing costs (i.e. detecting and avoiding individuals that fail to provide benefits later), many authors have assumed that animals are (proximately) motivated to engage in social interactions in order to gain future benefits. The limited understanding that animals have of future events (Roberts, 2002), their tendency to devalue future rewards (Stevens, Cushman, & Hauser, 2005), and their limited ability to wait for a desired reward (e.g. Dufour, Pele, Sterck, & Thierry, 2007), inevitably led to the conclusion that due to cognitive limitations reciprocal altru-

ism, when it occurs, must be immediately reciprocated (e.g. Dufour et al., 2007; Ramseyer, Pele, Dufour, Chauvin, & Thierry, 2007).

In contrast with this view, other researchers argue that hypotheses about proximate mechanisms should not be modeled on ultimate functions and that reciprocal altruism is not motivated by future benefits, but by previous benefits animals received (Barrett, Henzi, & Rendall, 2007; de Waal, 2008; Schino & Aureli, 2009). Furthermore, the view that reciprocal altruism must be immediately reciprocated contrasts with examples of direct reciprocity in animals that occurs over longer time frames. For instance, agonistic support in within-group disputes are central features in various carnivore species from spotted hyenas (*Crocuta crocuta*: Smith et al., 2010; Zabel, Glickman, Frank, Woodmansee, & Keppel, 1992), to African wild dogs (*Lycaon pictus*: de Villiers, Richardson, & van Jaarsveld, 2003), and from wolves (Fentress et al., 1986) to coatis (*Nasua spp.*: Gompper, 1997; Romero & Aureli, 2008). Support in aggressive conflicts can be viewed as a service that can be exchanged for a similar act or another service or commodity, such as food, tolerance, grooming or mating (de Waal, 1997; Noë & Hammerstein, 1995). Indeed, ring-tailed coati females (*Nasua nasua*) give agonistic support preferentially to those individuals that support them most, and support less frequently those individuals that intervene against them during agonistic disputes (Figure 1; Romero & Aureli, 2008). Given the relative rarity of agonistic support (hourly rate<0.01, Romero & Aureli, unpublished data), immediate reciprocation is inherently unlikely. Furthermore, the observed patterns of reciprocity cannot be explained as a by-product of the time coatis spend in proximity, nor as an interchange with other positive social behaviors — such as grooming. Thus, it is likely that some form of scorekeeping may be involved in reciprocity of agonistic support. This however does not necessarily imply that coatis employ complex cognitive processes in their reciprocity of support. For example, partner choice in

Figure 1. Support in aggressive conflicts is a common feature in coatis (*Nasua sp.*). This behavior is reciprocally exchanged for itself or another service — such as grooming — in a manner seemingly as complex as in primates. Group grooming session in ring-tailed coatis (photo by Filippo Aureli).

agonistic support may depend on animals having a positive emotional attitude toward a partner as a consequence of previous friendly interactions (Romero & Aureli, 2007, 2008; see Schino, di Sorrentino, & Tiddi, 2007 for a similar argument applied to primates). This is what Brosnan and de Waal (2002) called *attitudinal reciprocity* in which the need to keep track of multiple interactions with multiple partners over time can easily be avoided by a proximate mechanism based on emotional mediation rather than cognition (Aureli & Schaffner, 2002; Brosnan & de Waal, 2002; de Waal, 2000). In this view, the exchange of services (i.e. reciprocity) triggers partner-specific emotional variations that in turn affect animals' decisions over subsequent interactions (Schino et al., 2007). As such, emotions may constitute a relatively simple mechanism that may well act in long time frames and explain how animals negotiate the uncertainty and time lag between cost and benefits (Schino & Aureli, 2009).

Physiological underpins of cooperative bonds

While much discussion about proximate mechanisms of cooperation focuses on cognitive aspects, relatively less research has been done with respect to the physiological

mechanisms that underlie individual tendencies to help others. Of the major hormone families acting on social behavior in vertebrates, i.e. sex steroids, stress steroids, and neuro-hormones (Adkins-Regan, 2005; Soares et al., 2010), the latter has recently attracted the attention regarding the neurochemical basis of prosocial and cooperative behaviors (there are several comprehensive reviews, e.g. Bartz, Zaki, Bolger, & Ochsner, 2010; Heinrichs, von Dawans, & Domes, 2009; Insel, 2010; Olff et al., 2013; Ross & Young, 2009 for the interested reader). Extensive animal research has shown that the hypothalamic neuropeptide oxytocin plays a central role in various reproductive effects in mammals, such as parturition and lactation, and that it is involved in pair-bonding, parental care, sexual behavior and social memory (for reviews see above). In human and non-human primates, oxytocin also regulates many complex forms of social behavior and cognition, such as trusting behavior, generosity, or social perception (for reviews see above). Although these findings show that oxytocin modulates social behavior in a range of species, the evidence of oxytocin involvement in mediating enduring, cooperative bonds remains scant, especially outside reproductive contexts.

In carnivores, there is some evidence that variation in oxytocin levels affects alloparental care (Madden & Clutton-Brock, 2010). After peripheral administration of oxytocin (i.e. intramuscular injection), free-living meerkats (*Suricata suricatta*) increase their contribution to communal, cooperative activities such as digging, guarding or pup-feeding, and decrease initiation of aggressive interactions (Madden & Clutton-Brock, 2010). In addition, a recent study provides behavioral evidence that oxytocin modulates social bonding in domestic dogs (Romero, Nagasawa, Mogi, Hasegawa, & Kikusui, 2014). Specifically, the intranasal administration of oxytocin caused dogs to engage in higher levels of affiliation, social orientation, and social approach with their owners and dog partners, which constitutes the basis for the formation of any

stable social bond. That exogenous oxytocin promotes a suite of behaviors directly related with social bonding in dogs supports the idea that the same hormonal and neuroendocrine factors that promote parental behavior and pair bonding in mammals (i.e., the oxytocinergic system) also contribute to the formation of other types of cooperative relationships (Insel, 2010; Ross & Young, 2009). Furthermore, in dogs, as well as in primates (e.g. Feldman, Gordon, Schneiderman, Weisman, & Zagoory-Sharon, 2010; Nagasawa, Kikusui, Onaka, & Ohta, 2009), the exchange of socio positive behaviors associated with bond maintenance triggers the release of endogenous oxytocin (Odendaal & Meintjes, 2003; Romero et al., 2014). As it has been suggested before, the proximate motivation to develop a cooperative relationship is most likely not modeled on the subsequent benefits (i.e. ultimate functions), but on previous rewards individuals received (de Waal, 2008; Schino & Aureli, 2009). Because oxytocin enhances reward via dopamine-dependent mesolimbic reward pathways (Donaldson & Young, 2008), it is likely that positive emotional feedback, through behaviorally induced oxytocin secretion, facilitates repeated interactions with individuals with whom positive interactions have already occurred. While the specific mechanisms through which behaviors could modulate the release of central oxytocin are not well understood, and there is an ongoing debate about whether oxytocin affects social behavior by reducing social anxiety, altering the perceptual salience of social cues, or by increasing motivation to affiliate (Bartz et al., 2010), the current evidence suggests that oxytocin might be an important mechanism that allowed the evolution of enduring cooperative bonds between related and unrelated individuals without requiring any cognitive understanding or estimate of the probability of future benefits (Romero et al., 2014).

Conclusions
Although the study of cooperation has

traditionally focused on the evolutionary aspects of the behavior, in recent years there has been a growing interest in its proximate causation. This switch of attention from ultimate to proximate mechanisms is leading to a more complete view of the phenomenon of cooperation in both human and non-human animals. For instance, while emotions have been included as a significant aspect of human cooperation, it has not been until recently that this less-cognitively demanding mechanism has been considered for non-human animals. In this new picture, however, non-primate species are conspicuously absent since most research has been done in primates. It is hoped that the examples of research on carnivores presented here may help to stimulate new research in a wide range of species.

Acknowledgements

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