



Pattern of individual participation and cheating in conflicts between groups of free-ranging dogs

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Cooperative intergroup aggression provides an example of a costly cooperative behaviour whose benefits spill over to noncooperative animals as well. Consequently, investigating factors that promote individual participation in intergroup contests should prove useful for understanding how cooperation may persist in animal societies despite cheating. Here, we examined variables affecting individual participation in naturally occurring conflicts between groups of free-ranging dogs, *Canis lupus familiaris*. The overall proportion of cooperating group members decreased significantly with an increasing number of group members present. In one pack, the individual probability of active participation decreased significantly when this pack had a numerical advantage over opponents. Dogs belonging to the smallest pack tended to be more cooperative than those belonging to larger groups. Social prestige (measured as the number of submissions received during greeting) did not appear to be a consequence of cooperative behaviour. Individual participation increased with an increasing number of affiliative partners. Young and high-ranking dogs tended to cooperate more when their group was outnumbered by opponents but did not stay at the front of the pack during conflicts. These results emphasize the greater opportunity for cheating in larger groups and the complexity of dogs' behaviour. Cooperation appears to be conditional on both the 'adversity of the environment' (as measured by relative group size) and the identity/behaviour of companions.

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In animal social groups, cooperation has been broadly defined as a joint action by two or more individuals that is carried out to achieve a common goal (reviewed in Boesch & Boesch 1989). Since cooperative behaviour is usually costly to group members that actively participate in the collective action and the resulting benefits may often spill over to group members that have not participated, from an evolutionary perspective cooperation may be destabilized by the threat of 'cheating' (or 'free riding' or 'defecting'; Dugatkin 1997; Nunn 2000; Nunn & Lewis 2001). Thus, one of the central questions in behavioural biology remains how cooperation in animals could evolve and remain stable despite some individuals benefiting more by exploiting other individuals' cooperative actions and avoiding paying any costs than they would by cooperating. Several evolutionary mechanisms have been hypothesized: in kin selection, cooperation is stable if the recipients of the

benefits of the cooperative actions are close relatives of the cooperating individuals, even if such recipients do not incur the costs of these actions (Hamilton 1964; Lehmann & Keller 2006); in mutualism, cooperation pays more than defection in terms of fitness and thus individuals cooperate to gain immediate individual benefits that outweigh the costs paid (Mesterton-Gibbons & Dugatkin 1992; Clements & Stephens 1995; Lehmann & Keller 2006); in reciprocal altruism, or reciprocity, cooperation may be stable in repeated interactions between the same individuals if they play a strategy such as 'Tit for Tat' (always cooperate during the first interaction and then retaliate against cheating by withholding further cooperation; Trivers 1971; Axelrod & Hamilton 1981; Olendorf et al. 2004); finally, in the handicap principle individuals are thought to gain social prestige, and thus to increase their direct fitness, by cooperating (Zahavi & Zahavi 1997; Roberts 1998; Lotem et al. 2003).

Free riding is expected to undermine cooperation, especially in sizeable groups where reciprocity is less likely to evolve (Boyd & Richerson 1988, 1992) and relatedness between group members is usually lower (Frank 1995). Moreover, Nunn (2000) and Nunn & Lewis (2001) pointed out that even mutualistic benefits may be

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limited as groups become larger, given that a smaller proportion of group members would be required to provide efficiently a collective good, thus leading to some level of free riding.

Cooperation during intergroup conflicts in social species provides an example of a cooperative behaviour that is costly to participants, because it involves considerable expenditure of energy and risk of injury, and that often results in benefits to both cooperating and noncooperating group members in terms of increased access to contested resources (Nunn & Deane 2004). These are exactly the conditions under which cheating is expected to destabilize cooperation and, consequently, it is important to understand which factors may explain individual variation in cooperation and cheating in intergroup conflicts. Studies investigating individual participation and cheating in cooperative intergroup aggression have been carried out using playbacks of recorded intruders' vocalizations to simulate territorial intrusions (e.g. lions, *Panthera leo*: Grinnell et al. 1995; Heinsohn & Packer 1995; Heinsohn et al. 1996; chimpanzees, *Pan troglodytes*: Wilson et al. 2001; black howler monkeys, *Alouatta pigra*: Kitchen 2004), or have studied animals living in semifree-ranging conditions (e.g. ringtailed lemurs, *Lemur catta*: Nunn & Deane 2004), owing to the rarity of natural intrusions. All of these studies have documented consistent individual differences in the extent of active participation in intergroup conflicts. For instance, in an influential study, Heinsohn & Packer (1995) concluded that female lions could be classified according to four different cooperative strategies: 'unconditional cooperators' which always lead the group response to the simulated territorial intrusion (stay at the front of the group thus bearing the costs of fighting); 'unconditional laggards' which always stay at the rear of the group, thus avoiding the risks of fighting; 'conditional cooperators' which lead only when the group is outnumbered by the simulated opponents, that is, when their cooperation is most needed; and 'conditional laggards' which lag even farthest when their group is outnumbered. Heinsohn & Packer (1995) suggested that 'leaders' and 'laggards' (or 'cooperators' and 'free riders') may coexist in a mixed evolutionarily stable strategy. Such individual variation was not explained by variables such as body size (a measure of fighting ability), age or kinship but it could have been related to differences in temperament with 'bold' animals at the front of the group and 'shy' individuals at the rear.

However, in other species individual variation in the level of cooperation may be explained by asymmetries in the benefits accrued from an intergroup conflict and in the costs incurred (Nunn 2000; Nunn & Lewis 2001; Nunn & Deane 2004). For instance, in species with dominance hierarchies high-ranking individuals often enjoy priority of access to resources (food and mates), and thus may be more motivated than subordinates to defend such resources against opposing groups or, alternatively, may simply experience fewer costs of fighting strangers because of their better fighting ability (Nunn 2000; Nunn & Lewis 2001; Nunn & Deane 2004).

In this study, we investigated the mechanisms underlying cooperation and the pattern of individual participation and defection during conflicts between groups of free-ranging dogs, *Canis lupus familiaris*. Unlike most previous studies on cooperative intergroup aggression (see above) we did not use playback experiments to simulate intrusions but, instead, exploited the abundance and accessibility of dogs to record naturally occurring conflicts.

Free-ranging dogs live in packs consisting of multiple breeding males and females which are cooperative in conflicts against strangers (Font 1987; Daniels & Bekoff 1989; Macdonald & Carr 1995; Boitani et al. 1995; Pal et al. 1998, 1999; Cafazzo 2007). Although their morphology, physiology and behaviour have been partially modified during domestication (Clutton-Brock 1995; Coppinger & Schneider 1995), they still have a complex social organization (Cafazzo 2007; Pal 2008; Cools et al. 2008) in which

the dominance hierarchy predicts intrapack access to resources (Cafazzo 2007; Cafazzo et al., in press). Also, they seem to be able to assess relative group size in intergroup conflicts and to adjust their intergroup agonistic behaviour according to the odds of winning; that is, they are more likely to attack opposing groups the lower the ratio of the number of opponents to that of companions, and more likely to retreat the higher this ratio (R. Bonanni, E. Natoli, S. Cafazzo & P. Valsecchi, unpublished data).

Here, we assumed that adaptive behaviour observed in dogs would have evolved in wolves, *Canis lupus*, which are the dogs' wild ancestors (Vià et al. 1997), before domestication. We expected that if cooperation during intergroup conflicts in dogs is based on mutualism, then individuals should be more likely to participate in conflicts when the individual benefits of cooperating are higher, that is, when the participation of an additional animal is likely to increase substantially the probability of winning. Consequently, we predicted that: individuals should be more likely to cooperate when attacking an opposing pack that outnumbers their own pack than when attacking an opposing pack that is smaller than their own pack; the proportion of cooperating animals should increase when the aggressive behaviour is directed towards larger packs (or should decrease when the aggressive behaviour is directed to smaller packs); on average, individuals belonging to smaller packs should be more cooperative than those belonging to larger packs.

Unlike mutualism, in both reciprocity and kin selection cooperation is conditional on the behaviour and identity of the recipients of the benefits of cooperation (see above). Specifically, if cooperation is based on these mechanisms, then one could expect that the individual level of cooperation will increase with an increasing number of group companions that are either kin or that are likely to reciprocate the support provided. A rigorous test for reciprocity should demonstrate experimentally that the support given is contingent upon that received previously, and also control for the effects of kinship (see for example Hauser et al. 2003; Rutte & Taborsky 2008). However, in the absence of this information, a tentative prediction for reciprocity would be that individual cooperation in dogs should increase with an increasing number of socially bonded group companions. This is because animals seem to behave altruistically preferentially towards their affiliative partners (Scheid et al. 2008; de Waal et al. 2008; Schino & Aureli 2009), and thus these should be more likely to reciprocate favours.

As regards the handicap principle, we predicted that if cooperation in dogs is based on this mechanism, then the amount of social prestige obtained by each individual (defined as the degree to which dominance rank is recognized by companions, Zahavi & Zahavi 1997) should be positively correlated with the amount of costly cooperative behaviour performed, that is, cooperation during conflicts against larger packs and frequency of staying at the front of the pack during conflicts. In other words, the display of costly cooperative behaviour should replace aggression as a means of achieving high social status and, consequently, subordinates should recognize high-ranking individuals as valuable social partners (Zahavi & Zahavi 1997).

METHODS

Study Area

The research was carried out in a suburban area in the south-western outskirts of Rome, Italy, traditionally called 'Muratella'. It covered a total surface area of about 300 ha and was delimited to the north, west and south by roads with heavy traffic and to the east by cultivated areas. The area was split by another road into two sectors, one in the southwest and another in the northeast. The southwest sector was urbanized, although not densely populated,

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