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Conflict management in free-ranging wolves, *Canis lupus*

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Individuals should invest in conflict management when the costs of conflicts outweigh their benefits. We investigated whether free-ranging wolves engage in conflict resolution. We predicted that reconciliation and consolation should occur because pack members are highly interdependent upon each other owing to the benefits that group members derive from cooperative breeding, cooperative hunting and cooperation in between-group conflicts. As within-group conflict in wolves is low, in accordance with tolerant dominance relationships among pack members, we also predicted a high conciliatory tendency. We collected behavioural data from two packs in Yellowstone National Park (U.S.A.). We report reconciliation, mainly initiated by victims and directed towards aggressors, and solicited and unsolicited consolation. As predicted, the conciliatory tendency was high and comparable to the values reported in primate species with a tolerant dominance style. We suggest that conflict management is favoured in wolves, and more generally in species with a sufficiently high degree of interdependence among group members, as interdependence can explain investment in conflict mitigation without the need to invoke particular relationships of mutual value.

The benefits of sociality almost invariably come along with costs of conflicts arising from competition over resources. Costs of conflicts involve the risk of injuries, increased stress levels or degradation of social relationships, which can lead to exclusion from a group or death (Aureli, Cords, & van Schaik, 2002; Aureli & de Waal, 2000). To alleviate the negative consequences of prolonged or escalated conflicts, conflict management strategies prevail across many taxa (Aureli et al., 2002; Aureli & de Waal, 2000; Shino, 2000).

Conflict management involves behavioural strategies that prevent escalated conflicts before they occur, mitigate them while they occur, or help to avoid potential negative consequences after they occur (Cords & Killen, 1998). Measures that individuals take to reduce the likelihood that a conflict will occur or escalate include avoiding each other (Kutsukake & Clutton-Brock, 2008), maintaining stable dominance relationships (Preuschoft & van Schaik, 2000), investing in social relationships through social grooming and greeting behaviours (Colmenares, Hofer, & East, 2000), displaying submissive behaviours (Bergmüller & Taborsky, 2005) or pre-emptive helping (Bergmüller & Taborsky, 2005). Finally, post-conflict affiliative interactions have been proposed to serve for restoring peaceful interactions by means of conflict resolution (Aureli et al., 2002; Aureli & de Waal, 2000). Different types of conflict resolution have been distinguished, including 'reconciliation' (a friendly contact between former opponents shortly after a conflict: de Waal & Van Roosmalen, 1979), 'consolation' (an affiliative interaction initiated by a third party towards the victim of a conflict: de Waal & Van Roosmalen, 1979) or 'solicited consolation' (an affiliative contact initiated by the victim towards a third-party: Watts, Colmenares, & Arnold, 2000). We use 'friendly' and 'affiliative' as synonyms to refer to nonagonistic and nonsexual social interactions between pack members.

The Evolution of Conflict Resolution

Engaging in a friendly interaction with another individual during or shortly after a conflict involves costs and therefore constitutes an investment. An investment in conflict resolution is seemingly 'altruistic' as it involves an immediate cost to the actor (engaging in friendly behaviour in a situation of conflict) and a benefit to the receiver, which needs to be compensated for by a direct or indirect benefit to the actor; otherwise this behaviour would involve net fitness costs and should be removed by selection (West, Griffin, & Gardner, 2007). Thus, from an evolutionary perspective the key question that needs to be addressed is: why

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should an individual invest in conflict resolution? Investments in conflict resolution have been proposed (1) to restore relationships that are particularly important to individuals such as coalitions, alliances, partnerships or friendships (the 'valuable relationship hypothesis': de Waal & Aureli, 1997), (2) as 'honest' signals to social partners indicating that a conflict is over (Silk, 2000), or (3) to support the wellbeing of a valuable social partner such as kin, or other individuals with strong mutual attachments such as friends (consolation: Watts et al., 2000).

Here we propose that cooperation theory integrates these potential explanations. According to the concept of interdependence (Roberts, 2005) one individual should promote or invest in another, when the fitness of the donor depends on the fitness of the receiver. Valuable relationships can be considered as a special case of interdependence in which both partners profit from the valuable relationship. As the concept of interdependence is a more general explanation for cooperative investments, it can also explain asymmetrical investments in conflict resolution. While selection should favour reconciliation when the investment is of self-serving interest to the donor (e.g. to protect a relationship that is valuable to the donor), selection should favour consolation when the donor has an interest in the fitness of the receiver. Interdependence can also explain investments in common goods such as social peace within a group (Roberts, 2005).

Ecological Factors Favouring Conflict Resolution

In primates, species with tolerant dominance relationships show a high conciliatory tendency while species with more despotic dominance relationships tend to engage more rarely in reconciliation (Thierry, 2000). The socioecological model of Sterck, Watts, and van Schaik (1997) predicts despotic dominance relationships in primates when within-group competition is high and when between-group competition is low. In contrast, tolerant dominance relationships prevail under the opposite conditions: when within-group competition is low and between-group conflict is high (Sterck et al., 1997). This leads to the prediction that low levels of within-group conflict and associated tolerant dominance relationships should favour investments in conflict resolution. Under these conditions, individuals can engage in friendly behaviour in a situation of conflict with low risk of incurring renewed aggression. In line with several studies suggesting that between-group conflict can foster within-group cooperation (Radford, 2011; Sterck et al., 1997; West et al., 2006), high levels of between-group conflict have been proposed to foster within-group investments in conflict resolution (Shino, 2000).

Should Conflict Resolution Be Predicted in Wolves?

Members of a wolf pack are interdependent as individuals rely on the benefits they derive from cooperative hunting, cooperative breeding (also referred to as 'alloparental care'; Packard, 2003) and cooperation in between-group contests (MacNulty, Smith, Mech, Vucetich, & Packer, 2012; Mech & Boitani, 2003; Packard, 2003).

In free-ranging wolves, agonistic interactions between pack members rarely escalate (Mech & Boitani, 2003). In contrast, the territoriality of the species leads to elevated between-group conflict with potentially highly injurious encounters (Mech & Boitani, 2003; Packard, 2003). In accordance with the predictions of the primate socioecological model (Sterck et al., 1997), wolf sociality is characterized by relaxed dominance relationships. Pack members use elaborate displays that prevent conflict escalation and physical harm in agonistic interactions. Subordinates also spontaneously use submissive displays towards dominants, thereby acknowledging dominance relationships. While postconflict affiliative interactions have recently been reported in captive wolves (Cordoni & Palagi, 2008; Palagi & Cordoni, 2009) and domestic dogs (Cools, Van Hout, & Nelissen, 2008), they have not yet been investigated in free-ranging wolves (Packard, 2012).

Predictions

We predicted investments in conflict resolution, including reconciliation and consolation, in wolves because of the interdependence among pack members and because levels of conflict within groups are low but those between groups are high. Given the tolerant dominance style in wolves, we predicted a high conciliatory tendency. As subordinates should be more interested in terminating conflict, and as the risk of renewed aggression is low, we expected victims of aggression to be more likely to invest in reconciliation than aggressors. As elevated levels of conflict should require higher investments in conflict mitigation, we predicted a positive relationship between the number of aggressive behaviours and the number of postconflict friendly behaviours among former opponents. As is typical in species showing frequent postconflict interactions (Aureli et al., 2002), we also expected specific friendly behaviours in postconflict situations.

METHODS

Study Site and Individuals

The fieldwork took place in Yellowstone National Park, U.S.A. (44°60′N; 110°55′W) from 1 November 2008 to 31 March 2009, in agreement with the national park policy (permits YELL-2008-SCI 5716 and YELL-2009-SCI 5716). We studied two free-ranging packs of grey wolves, the Druid Peak pack and the Blacktail Deer Plateau pack, whose home ranges were located on the northern range of the park (Smith et al., 2008, 2009). The Druid Peak pack was established in 1996 (Smith & Ferguson, 2005) and consisted of 16 wolves (12 females, four males). It was structured as a nuclear family (Packard, 2003) with all members born into the pack except for the breeding male. By the end of 2008, the pack consisted of six pups, two yearlings and eight adults. The Blacktail Deer Plateau pack was founded in November 2008 and consisted of dispersing males from the Druid Peak pack and dispersing females from the Agate Creek pack. In November 2008, the pack consisted of 10 individuals (7 yearlings (5 males) and 3 adults (1 male)). One of these individuals (a yearling female) probably died, and two others (yearling males) dispersed during the winter (Smith et al., 2008, 2009; C. Baan & B. Molnar, personal observation).

Fieldwork

Animals are captured and radiocollared every year for the purpose of local research, under the approval and authority of the Institutional Animal Care and Use Committee of the United States National Park Services. Our study was not involved in these processes and we did not use any advice allowing location of animals. To locate the packs, we collaborated with the local crew, who used telemetry, and also relied on tracks, howls and bird activity around carcasses. The studied individuals were accustomed to the daily presence of distant observers and our filming did not appear to affect their behaviour.

We filmed the studied packs daily, from dawn to dusk, given suitable weather conditions and sufficiently short distances to the animals, which ranged from approximately 100 to 1500 m. We used an adapted camcorder (Canon XL-H1 camcorder, Canon EF adapter XL, Canon EF 100–400 mm f/4.5–5.6L IS USM photo lens, Canon extender EF 2× II) to record social interactions among group