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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

Table 1
Behaviours recorded from two wolf packs filmed in Yellowstone National Park in the winter 2008–2009

Type of behaviour	Description
Aggressive behaviours	
Growl	Growl at conspecific with bared teeth; vocalization may be heard
Approach dominant	Move towards another individual, with stiff forelegs and raised tail; piloerection possible
Approach fast	Move quickly towards an individual, by trotting or running; may include jumping on the conspecific or blocking its movement
Chase	Run after a conspecific, with piloerection, ears flattened
Snap	Shut jaws in the air
T-position dominant	Stand as dominant in the T-formation, as the horizontal cross of the T, facing the chest of a conspecific
Push	Push hard against a conspecific with part of body to make him/her move
Ride up	Mount or jump on a conspecific with forelegs, in an aggressive posture (raised tail, may growl, piloerection), without pushing him down
Stand over	Stand over, with piloerection and a stiff tail, a conspecific that is lying down
Nip	Brief inhibited bite, barely touching the conspecific, with insufficient pressure to cause injury
Knockdown	Hit or push down a conspecific
Bite	Bite a conspecific, without inhibition, with enough pressure to cause potential injury
Wrestle	Fight with a conspecific; violent encounter
Affiliative behaviours	
Inspect*	Lick and/or sniff urogenital area of a conspecific
Body contact	Body parts (excluding tails) of two individuals in contact for several seconds
Play	Exaggerated, brief and/or inhibited motor patterns such as jump on, bite, chase, play bow
Lick	Lick part of a conspecific's body, excluding urogenital area
Sniff	Sniff part of a conspecific's body, excluding urogenital area
Greet	Tail wagging, face oriented towards the face of a conspecific, sometimes licking and/or sniffing and/or prolonged nose touch, ears oriented forward
Greeting ceremony	Rally (>4 wolves), howling, greeting, tail wagging
Nose touch	Brief nose touch by one wolf to the face or body of another wolf; no tail wag, ears may be flattened
Submissive behaviours	
Passive submissive	Lay on back or side, present stomach, throat and urogenital area, with tail tucked between legs
Light submissive	Tail tucked between legs, sometimes wagging, with body crouched, ears back; may lick or paw the dominant's muzzle
T-position submissive	Stand as subordinate in the T-formation, as the vertical cross of the T, facing the shoulder of the dominant
Other behaviours	
Immobile	Lay down, sit or stand, look around or sleep
Travel	Walk, trot or run
Howl	Howl (head back, muzzle upward, vocalizing)
Nonsocial behaviours	
Out of sight	Out of sight
Other	Behaviours other than those described above

This ethogram is based on personal observations and on published ethograms of domestic dogs (Cools et al., 2008) and captive wolves (Cordoni & Palagi, 2008).
* Although we considered 'inspect' to be a sexual interaction, not a friendly interaction, we included it in our data set for comparison with previous studies on wolves (Cordoni & Palagi, 2008; Palagi & Cordoni, 2009) and domestic dogs (Cools et al., 2008).

members. To optimize recording of all possible social interactions, two observers guided the cameraman using spotting scopes. We interrupted recordings when individuals went out of sight for more than 1 min, or when wolves were resting.

Video Analyses

Videotapes were loaded on a computer and analysed using the Noldus software, the Observer 5.0. We coded every single agonistic interaction between individuals using the all-occurrences sampling method (Altmann, 1974). We identified individuals based on distinctive external features (presence/absence of a collar, fur colour patterns, age-related characteristics, unique physical characteristics). For each aggressive encounter, we recorded all social behaviours during a postconflict (PC) period of 10 min directly following an aggressive interaction (Palagi & Cordoni, 2009). We focused on the victim, defined as the recipient of the aggression. When the focal individual went out of sight for more than 30 s, the PC period was considered over. For each PC period, we selected a corresponding matched control (MC) period of 10 min to obtain data about baseline behaviour (i.e. without a preceding conflict). An MC period was considered over if the focal individual went out of sight for more than 30 s. We selected the MC periods according to the following criteria: the focal individual was not involved in any conflict during the 10 min preceding the onset of an MC period (de Waal & Yoshihara, 1983); the opponents of the corresponding PC period were within 10 m of each other and thus had the opportunity to interact (Palagi, Antonacci, & Norscia, 2008); inactive (e.g. sleeping, resting) episodes were not used as MC periods. Matched control observations are challenging to acquire in free-ranging populations, and the use of periods immediately preceding a conflict as matched controls may not be representative of baseline conditions (Aureli et al., 2002). To deal with these constraints, each MC period was selected on the first possible day following the corresponding PC period, with a maximum interval of 1 week between PC and MC periods.

For each interaction in PC and MC periods, we identified the initiator and the recipient of the interaction. We recorded all behaviours listed in Table 1, the starting time and the duration of each interaction. Submissive behaviours were not considered as affiliative behaviours.

Statistics

We used SPSS statistical software (version 18.0.0, SPSS, Inc., Chicago, IL, U.S.A.; version 20.0.0, IBM Corp., Armonk, NY, U.S.A.) in data analyses. As the data did not follow a normal distribution, we mostly used nonparametric tests (for one exception see below).

We used a chi-square test to investigate whether there was a difference in the occurrence of affiliative behaviours between PC and MC periods. To avoid pseudoreplication, we used only the first interaction within each pair combination in the analysis.

To discriminate between two consecutive aggressive interactions among the same partners within a given PC period, we

used a bout criterion interval method (Martin & Bateson, 1993). We calculated the minimal period between two distinct conflicts by performing a log survivorship plot. This allowed us to consider an agonistic interaction as renewed aggression when it occurred at least 2 min after the previous agonistic interaction (Palagi & Cordoni, 2009).

If conflict resolution prevails, affiliative interactions should occur earlier in PC periods than in corresponding MC periods. We recorded the latency until the first affiliative behaviour involving the focal individual in both PC and corresponding MC periods. We performed a *t* test that does not assume equal variances between groups. We pooled data from both studied packs and treated each interacting pair as one independent data point. For this analysis, we excluded all cases in which no affiliative behaviour occurred during PC and MC periods.

According to the time-ruled method (Aureli, van Schaik, & van Hooff, 1989), we compared the number of first affiliative contacts occurring each minute in PC and in MC periods. We also grouped the data for each minute in PC and in MC periods.

Conciliatory tendency gives a quantitative indication of the occurrence of reconciliation and is used to compare groups or species (Veenema, Das, & Aureli, 1994). Values close to 50% correspond to a high conciliatory tendency whereas values close to 0% are considered as low (Thierry, 2000). We calculated the corrected conciliatory tendency (CCT) in each wolf pack, including all pairs of opponents. Based on the recorded latency (in min) until the first affiliative interaction between former opponents in each pair of PC and MC periods, we labelled the pair 'attracted' if the first friendly contact occurred earlier or only in the PC period, 'dispersed' if the affiliative contact occurred earlier or only in the MC period, and 'neutral' if the affiliative interaction took place after the same amount of time in both periods or when no such interaction occurred (Veenema et al., 1994). We calculated the CCT as the number of attracted minus dispersed pairs, divided by the total number of pairs.

To assess whether investment in reconciliation is correlated with the intensity of a conflict (estimated as the number of aggressive behaviours displayed in an interaction), we tested whether the total number of aggressive and affiliative behaviours within each PC period were correlated (Spearman rank correlation).

To determine whether a specific affiliative behaviour was preferentially used in reconciliatory interactions, we recorded the occurrence of each type of affiliative behaviour first performed by or towards the focal individual in PC and MC periods. We compared the frequency of these specific behaviours, considering PC periods and MC periods separately.

To investigate the pattern of conflict resolution in the studied packs, we examined which individual (one of the former opponents or a third party) initiated the first affiliative behaviour in PC periods. We analysed interactions between the former opponents separately from interactions involving the victim and a third party. We used chi-square analyses to test the observed values against predicted values of a random distribution (50:50 ratio).

RESULTS

Do Free-ranging Wolves Engage in Postconflict Affiliation?

From a total of 106 h of video recordings (Blacktail Deer Plateau pack: 49 h; Druid Peak pack: 57 h), we collected 68 observation periods (i.e. 34 PC and 34 MC periods; for details see the Appendix).

Considering all conflicts (34 initial, 7 renewed) in PC periods, reconciliation, consolation and solicited consolation occurred following 61.0% ($N = 25$), 4.9% ($N = 2$) and 19.5% ($N = 8$) of the conflicts, respectively. After 14.6% of conflicts ($N = 6$), the victim was not involved in any affiliative interaction. Renewed aggression occurred in 20.5% of PC periods ($N = 7$) but never twice in the same PC period. Redirection of aggression by the victim towards a third party occurred only twice; we did not consider these events as new aggressive encounters.

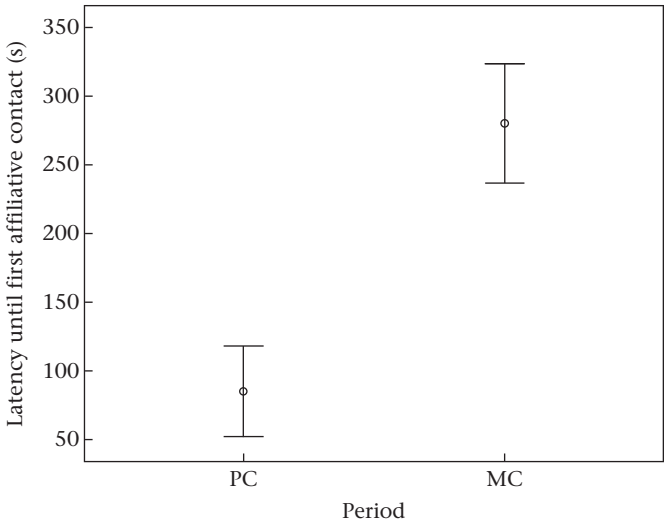

Figure 1. Mean latency ± SE until the first affiliative contact in postconflict (PC) and matched control (MC) periods for both wolf packs.

The first affiliative contact occurred significantly earlier after a conflict (PC) than in the matched control period (MC) (*t* test, not assuming equal variances: $t_{24.9} = -2.5$, $N_{PC} = 30$, $N_{MC} = 24$, $P = 0.02$; Fig. 1).

The number of first affiliative behaviours performed by or towards the focal individual (victim) during the first minute was significantly higher after a conflict (PC) compared to the control situation (MC) (chi-square test: $\chi^2_1 = 6.095$, $N = 42$, $P = 0.014$). After the first minute, there was no significant difference between the two periods (Fig. 2).

Also, the total number of affiliative behaviours performed by or towards the victim was significantly higher in the PC periods than in the corresponding MC periods during each of the first 4 min (minute 1: $\chi^2_1 = 29.032$, $N = 124$, $P < 0.0001$; minute 2: $\chi^2_1 = 12.938$, $N = 65$, $P < 0.0001$; minute 3: $\chi^2_1 = 14.297$, $N = 37$, $P < 0.0001$; minute 4: $\chi^2_1 = 4.167$, $N = 24$, $P = 0.041$). After that, there was no significant difference between the two periods. We calculated a conciliatory tendency of 44.1%.

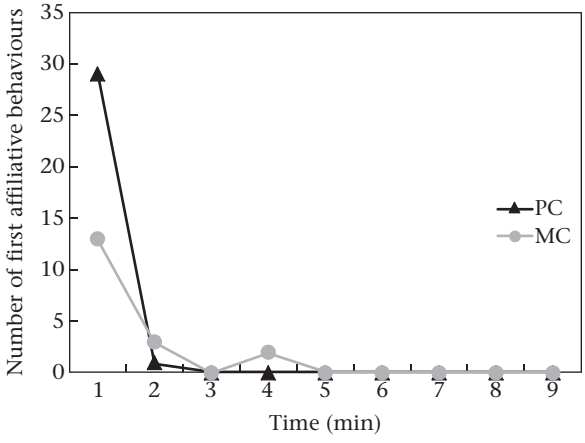

Figure 2. Temporal distribution of the first affiliative contact involving the victim in postconflict (PC) and matched control (MC) periods for both wolf packs.

There was a positive correlation between the number of affiliative and aggressive behaviours displayed during PC periods (Spearman rank correlation: $r_S = 0.379$, $N = 34$, $P = 0.027$).

Which Specific Affiliative Behaviours Are First Displayed After a Conflict?

Overall, there was a significant difference in the occurrence of different types of affiliative behaviours (body contact, greeting, inspecting, licking, nose touch, playing, sniffing) displayed in PC and MC periods ($\chi^2_5 = 27.91$, $N = 46$, $P < 0.001$). In particular, licking ($\chi^2_1 = 9.308$, $N = 13$, $P = 0.002$) and nose touch ($\chi^2_1 = 8.333$, $N = 12$, $P = 0.004$) occurred more often in PC periods, while playing (no statistics, as $N = 4$) and greeting ($\chi^2_1 = 5.333$, $N = 8$, $P = 0.021$) occurred exclusively in MC periods.

Who Initiates Postconflict Affiliation?

Victims were more likely than aggressors to initiate postconflict friendly contact with their former opponent ($\chi^2_1 = 13.542$, $N = 51$, $P < 0.0001$). We found no statistical difference in the propensity of the victim or the third party to initiate postconflict affiliative contact ($\chi^2_1 = 1.978$, $N = 20$, $P = 0.16$; Fig. 3).

Does Postconflict Affiliation Reduce the Likelihood of Renewed Aggression?

When comparing the likelihood of renewed aggressions in PC interactions with friendly postconflict behaviour (no renewed aggression: $N = 24$; renewed aggression: $N = 6$) and without friendly postconflict behaviour (no renewed aggression: $N = 3$; renewed aggression: $N = 1$), we found no significant difference ($\chi^2_1 = 0.05$, $P = 0.81$).

DISCUSSION

We observed reconciliation, consolation and a high conciliatory tendency in free-ranging wolves. Initiation of reconciliation was asymmetric (mostly initiated by subordinates towards dominants), which we suggest can be explained by the higher interest of subordinates to terminate the conflict. Overall, our results are in line with the predictions that postconflict affiliative behaviours are promoted by high, but asymmetric, interdependence among pack members and low within-group conflict but high between-group conflict.

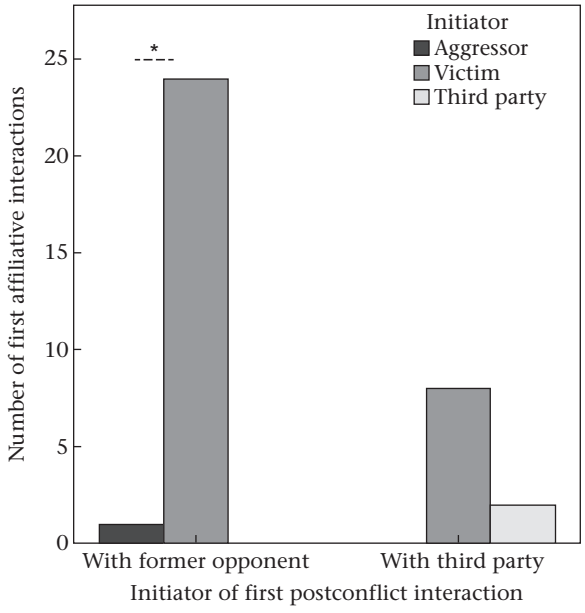

Figure 3. Initiators of the first postconflict (PC) affiliative behaviour in PC periods for both wolf packs. Data are given for interactions between former opponents (aggressor and victim) and between the victim and a third party. *$P < 0.0001$.

Postconflict Affiliation in Wolves

Our results show that postconflict friendly behaviours were mainly initiated by victims (subordinates) and preferentially directed towards the former aggressors (dominants). Hence, subordinates appear to invest in conflict resolution to reduce social tension (de Waal & Yoshihara, 1983) and to prevent further attacks from dominants by signalling that they respect the prevailing dominance relationships. Interdependence (Roberts, 2005), which can also explain asymmetric investments in cooperation (pseudoreciprocity; Connor, 1986), provides an explanation: as subordinates rely on group membership, they invest in their relationship with dominants to benefit from re-established peaceful relationships and to prevent further attacks. In contrast, dominants do not need to invest in their relationships with subordinates because they are not at risk of attack from them.

Former findings in captive wolves (Palagi & Cordoni, 2009) and domestic dogs (Cools et al., 2008) reported consolation (initiated by a third party) and solicited consolation (initiated by the victim). Consolation has been linked to empathy (Romero, Castellanos, & de Waal, 2010), for which there is evidence in dogs (Custance & Mayer, 2012) and which thus seems likely to prevail also in wolves. In our study of free-ranging wolves, solicited consolation occurred frequently while unsolicited consolation was more rare (probably owing to our small sample size). The occurrence of consolation suggests that investments in social peace or in relationships with particular individuals due to interdependence (Roberts, 2005) within a group are potentially relevant in wolves. In addition, solicited consolation appears to result from the direct benefits, such as reduced stress levels, that victims obtain by seeking comfort from third parties (Fraser, Stahl, & Aureli, 2008).

Does Postconflict Affiliation Serve for Conflict Resolution in Wolves?

If postconflict affiliation serves for conflict resolution, renewed aggression between former opponents should be less likely after situations in which postconflict affiliation has occurred compared to situations without postconflict affiliation. Although postconflict affiliation did not reduce the likelihood of renewed aggression in our study (we observed only a few cases of renewed aggression), several lines of evidence suggest that postconflict affiliation in wolves is best explained as conflict resolution.

First, affiliative and aggressive behaviours are typically antagonistic to each other. The finding that friendly behaviours occurred mostly within the first minute after a conflict is typical for conflict resolution and hard to explain alternatively.

Second, as predicted, we found a positive relationship between the level of conflict escalation (i.e. the number of aggressive behaviours) and the number of affiliative behaviours displayed in PC periods. Again, as affiliative behaviours are typically antagonistic to aggressive behaviours, the results suggest that situations with a higher degree of conflict escalation require increased investments in conflict mitigation.

Third, two particular behaviours (licking and nose touch) were the most frequent postconflict friendly behaviours that we observed. Nose touch appears to be specific for conflict resolution in free-ranging wolves. We suggest that individuals use nose touch

as 'excuse' (asking the receiver's forgiveness), which has been suggested to be a prerequisite for reconciliation (Park & Enright, 2000). Specific affiliative behaviours, which seem to have an excuse function, have, for instance, also been described in macaques (Aureli, Veenema, van Eck, & van Hooff, 1993; Thierry, 2000) and cleaner fish (Bshary & Würth, 2001). The use of specific behaviours that are restricted to postconflict situations are characteristic of species with frequent postconflict interactions (Aureli et al., 2002).

Finally, the finding that mostly victims of aggression engaged in friendly behaviours towards the aggressors can most parsimoniously be explained by a conflict resolution function of these behaviours.

Interdependence as an Explanation for Conflict Resolution in Wolves

Friendly postconflict interactions have been found to be particularly likely among mutually valued partners that regularly exchange affiliative behaviours, including pair partners, partners in alliances, or friends (Aureli et al., 2002; de Waal & Aureli, 1997). Such valuable partners should invest in avoiding or mitigating escalated conflicts, which may damage relationships, thereby jeopardizing future benefits of cooperation (Aureli et al., 2002; Kutsukake & Clutton-Brock, 2008). Support for reconciliation among valuable partners comes from primates (Arnold, Fraser, & Aureli, 2010) and birds (Fraser & Bugnyar, 2011).

However, valuable relationships do not explain all observations of conflict resolution as some studies did not find the predicted reconciliation, such as for instance a comparison of human children across cultures (Butovskaya, Verbeek, Ljungberg, & Lunardini, 2000) and investigations on cooperatively breeding callitrichids (Schaffner & Caine, 2000). Asymmetrical investments in conflict resolution by only one partner (as observed in this and other studies: Aureli et al., 1989; Butovskaya et al., 2000; de Waal & Yoshihara, 1983) suggest that the relationship does not necessarily need to be of similar value for both partners. The valuable relationships hypothesis, which has been proposed to explain protection and repair of relationships of mutual value to both partners, is therefore one of several explanations for the occurrence of friendly postconflict behaviour among former opponents (see also Silk, 2000). Here, we suggest that conflict resolution in wolves can be explained by investments of individuals that profit from stable dominance relationships and group membership with no need to invoke particularly valuable relationships.

Cords and Aureli (2000) proposed that three qualities of a relationship might be important to influence conciliatory tendency, that is, the value (what an individual gains from the partner), security (the perceived probability that the relationship will change) and compatibility (the general climate of the relationship resulting, for instance, from the personality of the partners). We suggest that conflict resolution in wolves is partly explained by the security that a dominant gains when a subordinate signals with a friendly behaviour after a conflict that it will respect the existing dominance relationships. This interpretation fits the alternative explanation that friendly postconflict behaviours serve as costly (therefore 'honest') signals that indicate that the conflict is over (Silk, 2000). In wolves, subordinates appear to use costly signals to terminate the conflict and re-establish a peaceful relationship.

Hence, even though particular valuable relationships (which we could not investigate in this study) may also be important to explain reconciliation in wolves, our results suggest that conflict resolution in this species can be explained by interdependence among pack members as a result of the benefits they derive from cooperative hunting, cooperative breeding and cooperation in defence of the territory and related resources (MacNulty et al., 2012; Mech & Boitani, 2003; Packard, 2003). The relevance of interdependence could be tested in future studies. For instance, it has been shown that the benefits of cooperative hunting in wolves increase only up to a certain group size, but then declines thereafter, because some individuals fail to participate in cooperative hunting (free riders), but profit from the effort of others (MacNulty et al., 2012). Therefore, we predict that in larger packs (with lower interdependence among pack members), investments in conflict resolution should be lower compared to that in smaller groups (in which interdependence among group members is higher).

A Comparative Perspective to Conflict Resolution in Wolves

Dominance style has been suggested to be important in explaining the likelihood of reconciliation (de Waal & Luttrell, 1989). High reconciliatory tendencies have been found in species with low levels of conflict, characterized by relaxed and tolerant dominance relationships (Thierry, 2000). Wolves show tolerant dominance relationships and rarely engage in escalated conflicts with pack members (Mech & Boitani, 2003). As predicted, we found a high conciliatory tendency in free-ranging wolves (CCT = 44.1%). Similar high values have been reported in captive wolves (CCT = 53.3%; Cordoni & Palagi, 2008) and in several macaque species showing a relaxed dominance style (CCT > 40%; Thierry, 2000). In contrast, in species with despotic dominance relationships, conciliatory tendencies are much lower (rhesus macaques, *Macaca mulatta*: 9.0%, de Waal & Ren, 1988; chimpanzees, *Pan troglodytes*: 15.5%, Kutsukake & Castles, 2004; brown lemur, *Eulemur fulvus*: 26.6%, Norscia & Palagi, 2011). In species with tolerant dominance relationships, individuals are more likely to initiate a friendly interaction in a situation of conflict as the risk of renewed aggression is low (but see callitrichids, for an exception: Schaffner & Caine, 2000). Accordingly, victims are the main initiator of postconflict affiliative behaviours in species with a high level of tolerance (Aureli et al., 1989), while friendly postconflict interactions are mostly initiated by aggressors in species characterized by despotic dominance relationships (de Waal & Yoshihara, 1983).

Wolf sociality shares many features with human social organization such as cooperative breeding, cooperative hunting and a high level of between-group conflict (Burkart, Hrdy, & van Schaik, 2009; Hawkes, O'Connell, & Jones, 1991; Kramer, 2011). The resulting interdependence has also been proposed to be critical for the evolution of human cooperation (Tomasello, Melis, Tennie, Wyman, & Herrmann, 2012). It would be interesting to investigate conflict management between wolves and humans, which may help to explain why domestic wolves (i.e. dogs) and humans easily communicate with each other, coevolved and still closely coexist within contemporary human societies.

Future studies should attempt to investigate conflict management in various regimes of within-group and between-group conflict (which could be manipulated experimentally) to clarify further the influence of these factors in shaping conflict management across species.

Conclusion

The key question to understand better the evolution of conflict management is: why should individuals invest in mitigating conflicts? We suggest that this question can be better understood by investigating the interplay between ecology and the resulting social system and by a better integration of existing theories of cooperation and conflict management. While valuable relationships seem to be important for the occurrence of reconciliation in many but not all species, our results suggest that more general interdependence among group members may be sufficient, at least partly, to explain

investments in conflict resolution. Investment in social peace as a common good may also be of importance in the occurrence of conflict management strategies in wolves and other species with high interdependence.

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Appendix

Table A1
Data collected from videotapes recorded on two wolf packs in Yellowstone National Park during the winter 2008–2009

Observation	Identity of*			First behaviour displayed in PC	Type of PC-MC pair†
	Focal	Opponent	First partner in MC		
1	F642	ht	None	Moving	D
2	F642	ht	sbl	Body contact	N
3	ht	F693	F693	Nose touch	A
4	mbr	M302	M302	Nose touch	A
5	F642	ht	F693	Nose touch	A
6	bbr	M302	M302	Licking	A
7	bba	hsf	hsf	Body contact	A
8	bbr	M302	M302	Licking	A
9	mbr	M302	M302	Licking	A
10	mbr	M302	M302	Licking	N
11	F642	M302	M302	Nose touch	A
12	mbr	M302	M302	Nose touch	A
13	bbr	M302	M302	Nose touch	A
14	mbr	F693	F693	Sniffing	N
15	F642	M302	F693	Nose touch	N
16	M302	F642	F693	Body contact	A
17	F692	F693	F693	Nose touch	N
18	bbr	M302	M302	Licking	A
19	mbr	M302	M302	Licking	A
20	yearl	F571	F571	Nose touch	A
21	bba	F569	F569	Nose touch	N
22	bbl	M302	bbr	Nose touch	N
23	F693	M302	M302	Licking	N
24	sbl	M302	M302	Licking	N
25	bbr	M302	M302	Licking	A
26	sbl	bbr	F642	Nose touch	A
27	bba	F645	none	Moving	N
28	bbr	M302	none	Other	D
29	bbl	M302	bbr	Body contact	A
30	bba	F569	F569	Licking	D
31	sbl	mbr	none	Moving	N
32	bbr	M302	M302	Licking	A
33	sbl	M302	ND	Licking	N
34	sbl	bbr	mbr	Body contact	N

* ht: half tail; sbl: small blaze; mbr: medium brown; bbr: big brown; bba: bright bar; hsf: high side female; yearl: yearling; bbl: big blaze.
† PC: postconflict; MC: matched control pair for the corrected conciliatory tendency (CCT; Veenema et al., 1994); D: dispersed pair; N: neutral pair; A: attracted pair.