

University of Nebraska - Lincoln
DigitalCommons@University of Nebraska - Lincoln

U.S. National Park Service Publications and Papers

National Park Service

2016

Do gray wolves (*Canis lupus*) support pack mates during aggressive inter-pack interactions?

Kira A. Cassidy

Yellowstone Wolf Project, kira_cassidy@nps.gov

Richard T. McIntyre

Yellowstone Wolf Project

Follow this and additional works at: <https://digitalcommons.unl.edu/natlpark>

Cassidy, Kira A. and McIntyre, Richard T., "Do gray wolves (*Canis lupus*) support pack mates during aggressive inter-pack interactions?" (2016). *U.S. National Park Service Publications and Papers*. 146.

<https://digitalcommons.unl.edu/natlpark/146>

This Article is brought to you for free and open access by the National Park Service at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in U.S. National Park Service Publications and Papers by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

Do gray wolves (*Canis lupus*) support pack mates during aggressive inter-pack interactions?

Kira A. Cassidy¹ · Richard T. McIntyre¹

Received: 1 December 2015 / Revised: 3 May 2016 / Accepted: 9 May 2016 / Published online: 19 May 2016
© Springer-Verlag Berlin Heidelberg 2016

Abstract For group-living mammals, social coordination increases success in everything from hunting and foraging (Crofoot and Wrangham in *Mind the Gap*, Springer, Berlin, 2010; Bailey et al. in *Behav Ecol Sociobiol* 67:1–17, 2013) to agonism (Mosser and Packer in *Anim Behav* 78:359–370, 2009; Wilson et al. in *Anim Behav* 83:277–291, 2012; Cassidy et al. in *Behav Ecol* 26:1352–1360, 2015). Cooperation is found in many species and, due to its low costs, likely is a determining factor in the evolution of living in social groups (Smith in *Anim Behav* 92:291–304, 2014). Beyond cooperation, many mammals perform costly behaviors for the benefit of group mates (e.g., parental care, food sharing, grooming). Altruism is considered the most extreme case of cooperation where the altruist increases the fitness of the recipient while decreasing its own fitness (Bell in *Selection: the mechanism of evolution*. Oxford University Press, Oxford 2008). Gray wolf life history requires intra-pack familiarity, communication, and cooperation in order to succeed in hunting (MacNulty et al. in *Behav Ecol* doi:10.1093/beheco/arr159 2011) and protecting group resources (Stahler et al. in *J Anim Ecol* 82: 222–234, 2013; Cassidy et al. in *Behav Ecol* 26:1352–1360, 2015). Here, we report 121 territorial aggressive inter-pack interactions in Yellowstone National Park between 1 April 1995 and 1 April 2011 (>5300 days of observation) and examine each interaction where one wolf interferes when its pack mate is being attacked by a rival group. This behavior was

recorded six times (17.6 % of interactions involving an attack) and often occurred between dyads of closely related individuals. We discuss this behavior as it relates to the evolution of cooperation, sociality, and altruism.

Keywords Altruism · Aggression · Cooperation · *Canis lupus* · Empathy · Fighting · Kin selection · Reciprocal altruism · Support

Introduction

Cooperation is essential for group-living species as group tasks such as hunting, foraging, and protecting young from danger require coordinated effort (Muller and Mitani 2005; Sussman et al. 2005; Nowak 2006; Silk 2007). Coalition or alliance formation has important implications on success in obtaining mates and food, and has been examined during intra-group interactions (Rabb et al. 1967; Watts 1998; Mitani and Watts 2001; Smith et al. 2010). Aggressive interactions also occur between two groups of territorial conspecifics, and these situations often lead to mortality (Heinsohn and Packer 1995, Wilson and Wrangham 2003; Cassidy et al. 2015). Evidence of support for a fellow group member during these encounters is rare (Grinnell et al. 1995).

In *The Descent of Man and Selection in Relation to Sex*, Darwin stated that “animals certainly sympathize with each other’s distress and danger” (1871, p 84), yet in order for altruism to evolve, there must be some benefit to the altruist. Since then researchers have discussed the evolution of altruism with no clear consensus nearly a century and a half later. Many studies have concluded that altruism is not a selfless act and that it ultimately has to benefit the altruist. Inclusive fitness theory through kin selection states

✉ Kira A. Cassidy
kira_cassidy@nps.gov

¹ Yellowstone Wolf Project, Yellowstone Center for Resources, PO Box 168, Yellowstone National Park, WY 82190, USA

that an individual will help others closely related to themselves because it ultimately perpetuates some of the altruist's genes (Hamilton 1964; Maynard Smith 1964; Dugatkin 2007). This is most often cited in species with sterile individuals (Bourke and Franks 1995; Queller and Strassmann 1998) and high levels of cooperative breeding (Reyer 1984; Cockburn 1998).

Reciprocal altruism theory states that an individual should incur the cost of an altruistic act, even if the other individual is not closely related, because in the future the individual might reciprocate (Trivers 1971; Axelrod and Hamilton 1981). Several species' behaviors have been found to fit the reciprocal altruism theory including coalition formation in olive baboons ([*Papio anubis*] Packer 1977) and Przewalski horses ([*Equus ferus przewalskii*] Krueger et al. 2015), cluster roosting position in pallid bats ([*Antrozous pallidus*] Trune and Slobodchikoff 1978), information exchange in spear-nosed bats ([*Phyllostomas hastatus*] McCracken and Bradbury 1981), blood regurgitation in vampire bats ([*Desmodus rotundus*] Wilkinson 1984; Carter and Wilkinson 2015), social grooming in coati ([*Nasua narica*] Russell 1983), and grooming and alliance formation in vervet monkeys ([*Chlorocebus pygerythrus*] Seyfarth and Cheney 1984).

Altruism research is dominated by studies on human subjects (Batson 2011; Rusch 2014; Kurzban et al. 2015), but lately, other group-living species have been studied with regard to altruistic behaviors, such as chimpanzees (Yamamoto et al. 2012; Silk et al. 2013), bonobos ([*Pan paniscus*] Jaeggi et al. 2013; Surbeck and Hohmann 2015), and African elephants ([*Loxodonta africana* and *L. cyclotis*] Jørgensen 2015). Despite investigations into the ultimate benefits of altruistic behavior, a direct mechanism for proximate altruistic behavior was not proposed until de Waal suggested that empathy, an “emotional sensitivity to others,” (de Waal 2008, p 282) may have evolved to direct altruism in ways that satisfy both the kin selection and reciprocal altruism theories. This theory is highly debated in the scientific literature (Hauser 2001; Edgar et al. 2012).

Wolves are social carnivores often living in groups made up of closely related family members (Mech and Boitani 2003). They are highly territorial (Cubaynes et al. 2014) and hunt large prey (Mech, Smith, and MacNulty 2015). Cooperation is necessary during conflicts with conspecific groups (Cassidy et al. 2015) and hunting (MacNulty et al. 2011) and has been proven to be important in other social species (e.g., chimpanzees [*Pan troglodytes*] Boesch 1994; African lions [*Panthera leo*] Heinsohn and Packer 1995; African wild dogs [*Lycaon pictus*] Creel and Creel 1995). Because of their reliance on group activities for success, intra-pack familiarity and communication should be beneficial to many aspects of wolf life history, as has been suggested in primates

(Burkart and van Schaik 2010). Yellowstone National Park (YNP) is an ideal place to examine this behavior because of the high number of individually recognizable, genotyped wolves and wide, open valleys for consistent viewing.

Some behavior classified as possibly altruistic can be difficult to quantify in non-habituated, wild animals (e.g., regurgitation, food sharing, and parental care) when viewing of natural behaviors necessarily takes place at great distance or with a spotting scope. During observations of aggressive inter-pack interactions, we noted which individuals were present and recorded their behavior. We describe aggressive encounters where one wolf is being attacked and its pack mate disrupts the attack. We discuss cooperation and altruism evolutionary theory and possible adaptive advantages of this behavior in a wild, social carnivore.

Study system

We collected all data on the Northern Range (1000 km²) of YNP (8991 km²). The Northern Range is defined by the seasonal movements of the elk (*Cervus elaphus*), and elk are the primary prey (Smith et al. 2004, Metz et al. 2011). Elevations on the NR vary from 1500 to 2400 m, with high elevations characterized by conifer forests and low elevations by open grass meadows and shrub-steppe vegetation (Houston 1982). The area encompasses the territories of between 4 and 8 packs and features a high wolf density fluctuating between 20.1 and 98.5 wolves/1000 km² with an average of 55.8 (Smith et al. 2011). All areas within YNP are protected from consumptive human activities such as development, hunting, and livestock grazing.

Methods

Telemetry collars

As part of its long-term research, the Yellowstone Wolf Project captured 15–30 wolves via aerial darting from a helicopter between December and March each year. Biologists fitted wolves with standard very high frequency radio collars (Telonics, Inc., Mesa, AZ) or Global Positioning System radio collars (Smith and Bangs 2009). The National Park Service approved all capture and handling protocols and confirmed they were in accordance with recommendations from the American Society of Mammalogists (Sikes and Gannon 2011). Radio collars often lasted throughout a wolf's life, but were occasionally replaced if the wolf outlived the battery life of the collar. This resulted in many complete life histories for individual

wolves. Whole blood was collected for genetic analysis and was used to measure relatedness between individuals.

Data collection

Observers recorded wolf behavior during daily tracking of radio-collared individuals. When a signal was detected, we searched for the pack or individual and observed them most often from distances of 0.25 to 6.00 km with 20–60× spotting scopes. During intergroup interactions, we recorded: (1) the individuals present and their age, sex, color, and breeding status, (2) time observation began, (3) time it ended, (4) which group initiated the interaction, (5) the locations of both groups at the beginning and the end of the interaction, (6) the behavior of all individuals in each group related to initiation and participation in the chase, attack, kill, or flight, and (7) the results of the interaction: win or loss. Observations were recorded by voice with digital Dictaphones as the interaction occurred and were later transcribed.

Although non-pack wolves sometimes interacted non-aggressively (usually howling or socializing), we report only aggressive interactions in this study. Aggressive interactions were defined as including a chase at some point during the encounter (even if non-aggressive behavior also occurred during the encounter). A chase occurred if at least one wolf ran toward at least one opposing wolf and that wolf fled. Occasionally wolves or packs ran toward each other and fought before one pack or individual fled. In such cases, a chase was always accompanied by a wolf eventually fleeing. Interactions escalated to an *attack* if at least two opponents made contact (usually biting) and to a *kill* if an individual was attacked and killed or fatally wounded.

We classified aggressive interactions based on both groups' compositions. When two packs of two or more individuals interacted, we considered it a pack–pack (PP) interaction, when a pack interacted with a single, non-pack member, a pack–individual (PI) interaction, and when two single individuals from different packs interacted, an individual–individual (II) interaction. The same classifications and interactions were used in the analysis by Cassidy et al. (2015). Here, we report behavior only for PP interactions so that in each interaction, any wolf has at least one pack mate present and a potential to perform or benefit from interference behavior.

Using presence or absence of a radio collar, body morphology, pelage coloration, and injuries (e.g., permanent limp, tip of tail or ear missing, mange infection patterns) as identifying features, many wolves were individually recognizable after repeated observations. We used year-round observations of urination posture (Peters and Mech 1975) and seasonal observations of breeding

behavior (vonHoldt et al. 2008; Stahler et al. 2013) to determine sex and breeding status of uncollared individuals.

We also gathered demographic information on individuals by recording sex, color, and weight during the capture and radio-collaring process. We used tooth wear to determine age on captured, live individuals and used cementum annuli measurements on dead individuals to determine birth year (Gipson et al. 2000). We considered wolves captured as adults to be known-aged if individually recognized as pups due to some morphological features, such as coloration, sex, and/or injuries.

We determined a wolf was present if it was observed in between the start and end times of the interaction. We then scored individual participation (i.e., participated Yes/No) in each of the major steps of an interaction: chase, attack, kill, and/or flee. We considered a wolf to be more aggressive than another if it participated in a more aggressive level of behavior, defined as follows: kill > attack > chase > present-only > flee. We also recorded individuals that initiated and/or led the major steps of interactions. Based on this, we assigned each wolf an individual aggression score (IAS) from 1 to 10. Some wolves were present during an aggressive interaction yet did not participate in any of the major behaviors.

Each recorded aggressive interaction involving an *attack* was examined for evidence of interference. Confirmed interference behavior required (1) that a wolf was physically attacked and (2) that a pack member of the victim moved to within 30 m of the attack site, while the attack was occurring. This movement had to occur after the attack was in progress, and the individual had to come from a further location. A pack mate <30 m away at the start of an attack that then moved away did not qualify as exhibiting interference behavior. We chose 30 m as a cutoff for the behavior as it is unknown at what distance wolves recognize individuals and assumed that 30 m close proximity is necessary. Also, observations were often made through spotting scopes, and at normal viewing distances (0.25–6.00 km), we could see all wolves within a minimum of 50 m of the focus animals. We chose 30 m to ensure we did not miss recording some interference behavior just out of the scope frame. We referred to the attacked wolf as the recipient and its pack mate as the supporter; both were always in Pack A. We called the attacking pack Pack B.

Results

During >5300 observation days (1 April 1995–31 March 2011), we recorded 121 PP aggressive intergroup interactions. Of these interactions, 34 (28.1 %) escalated to an attack and 11 (9.1 %) resulted in a fatality (Fig. 1). One in

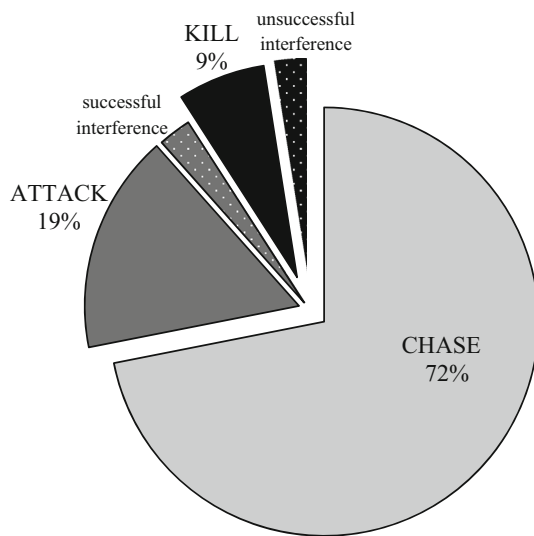


Fig. 1 Escalation level of inter-pack aggressive interactions (i.e., chase, attack, or Kill; $n = 121$), and presence of interference behavior during attacks (interference successful, $n = 3$ of 23 attacks), and Kills (interference unsuccessful, $n = 3$ of 11 kills)

three wolves that was attacked was killed. Six interactions included interference behavior (17.6 % of the attacks), with three recipients successfully escaping the attack. In five of the cases, the supporter was unharmed; once the supporter was bitten on the hind leg but still escaped.

Groups containing the supporter and recipient ranged from 2 to 12 members and averaged 6.2, smaller than the long-term average of 9.9 wolves per NR pack (Smith et al. 2011). There was not a significant difference between group size for interactions without interference (6.3, $n = 28$) and with interference (6.2, $n = 6$, $t\text{-stat} = -0.5$, $p = 0.47$). Of the six dyads of wolves involved, four dyads were closely related, one was a second-order relation, and the last was an unrelated, mated pair with young pups present (Table 1). Four of six supporters were male and ages ranged between 1.5 and 5.6 years old (mean = 3.1, $stdev = 1.4$).

Interaction #1(20 November 2004, 1146 h)

Pack A (11 members of the Slough Creek pack) had an ungulate carcass in thick timber. Pack B (9 members of the Druid Peak pack) traveled into the trees, and all of the wolves came running out. Five members of Pack B attacked a black pup (recipient) from Pack A. An adult male from Pack A (supporter) twice ran within an estimated 10 m of the attack site, and several of the attackers left the black pup to chase the gray adult. At least three Pack B members continued to attack the recipient for 3 min before leaving. Pack A regrouped and chased Pack B out of the area. The recipient got up and traveled into the trees.

Table 1 Details for interactions including possible interference behavior

Interaction #	Date	Pack A	Pack A size	Pack A RPS	Pack B	Pack B size	Supporter	Recipient	Successful interference	Supporter/recipient relatedness
1	11/20/2004	Slough Creek	11	2	Druid Peak	9	Male adult (3.6 years)	Unknown sex pup	No	Parent–offspring
2	6/17/2006	Unknown	4	0	Druid Peak	4	Female adult (2.2 + years)	Male yearling	Yes	Siblings
3	11/8/2007	Silver	6	-10	Druid Peak	16	Male adult (5.6 + years)	Unknown sex pup	Yes	Parent–offspring
4	9/3/2008	Slough Creek	12	1	Druid Peak	11	Female adult (3.4 years)	Female adult	No	Aunt–niece
5	4/14/2009	694F group	2	-3	Cottonwood Creek	5	Male adult (2.0 years)	Female adult and ≥ 2 pups	No	Mated pair and offspring
6	10/28/2009	Druid Peak	2	-1	Hoodoo Creek	3	Male yearling (1.5 years)	Female adult	Yes	Siblings

RPS relative pack size (Pack A size—Pack B size)

After the snow melted in April 2005, we found this wolf dead only 200 m from where it was last seen.

Interaction #2 (17 June 2006, 0716 h)

Pack A (4 members of the Unknown Pack) was bedded as Pack B (4 members of the Druid Peak pack) traveled toward them. When Pack B was within 50 m, Pack A got up and ran away. Pack B caught a black male yearling (recipient) from Pack A and attacked him. An adult female from Pack A (supporter) ran within an estimated 10 m of the attackers, and they chased her for >100 m but then turned around and attacked the recipient again. This repeated 2 more times before Pack B returned to the attack site the third time and could not find the recipient, who had run away. Pack A all went into the trees in slightly different areas and were not observed again. Pack B traveled slowly in the same direction.

Interaction #3 (8 November 2007, 0726 h)

Pack A (6 members of the Silver pack) traveled toward Pack B (16 members of the Druid Peak pack) on a fresh bull elk carcass. Pack B noticed Pack A and chased them. They caught a black pup (recipient) from Pack A and started to attack it. An adult male from Pack A (supporter) ran to within approximately 20 m of the attacking group. The dominant male of Pack B started to chase the supporter, and the rest of Pack B joined him. The recipient got up and ran away. Pack B stopped chasing the supporter and went back to the attack site, but the recipient was running farther away in thick sage. Pack B traveled back toward their elk carcass. Pack A howled and regrouped, and then traveled away from Pack B.

Interaction #4 (3 September 2008, 0738 h)

Pack A (12 members of the Slough Creek pack) were actively hunting a cow elk in the Lamar River as Pack B (11 members of the Druid Peak pack) approached them. Pack B got within 50 m before Pack A realized they were there. Pack B chased and attacked 526F (recipient) as the rest of Pack A scattered. A female from Pack A (supporter) ran to within an estimated 10 m of the attacking group, and the dominant female from Pack B along with at least 5 others chased her. Two wolves continued to attack the recipient until it appeared to be dead. Pack B remained in the area of the dead recipient for 24 min and sniffed around the area Pack A had been bedded. Pack A howled and regrouped about 1 km away, and Pack B chased them several more times. Pack A split up in all different directions, and Pack B moved back to the attack site.

Interaction #5 (14 April 2009, 0717 h)

Pack A (2 adults from 694F group plus at least 2 four-day-old pups) were near their den as Pack B (5 members of Cottonwood Creek pack) traveled toward them. The female from Pack A went into the den where she had at least 2 pups (we refer to the female and the pups as the recipients, in this case) as the male (supporter) ran away. All five Pack B members chased the supporter four times, but each time turned back toward the den and the recipient. The longest chase was estimated at 300 m and the shortest at 20 m. Before the last two chases, the supporter approached Pack B to within approximately 30 m, while they were within 10 m of the recipient in the den. Pack B then ignored the supporter and attacked the recipients in the den. They killed the adult female and at least two of Pack A's pups. The supporter ran away then bedded approximately 1 km away as Pack B remained in the area for 5 h then travelled away. At 1500 h, 694F's radio signal is still in active mode, but by 0705 h the next morning, it is in mortality. Upon examining the area 2 weeks later, we found the recipient dead in the den with many bite wounds on her head, neck, stomach, and groin. There was also blood on the rock walls inside of the den. The den was under several large boulders wedged together and had two openings. This likely made it impossible to defend from multiple attackers, unlike a typical tunnel underground with one entrance. This encounter is also described by Smith et al. (2015) as it relates to inter-pack den attacks resulting in infanticide.

Interaction #6 (28 October 2009, 0804 h)

Pack A (2 members of the Druid Peak pack) and Pack B (3 members of the Hoodoo Creek pack) ran toward each other. At the last second, Pack A split and Pack B caught the adult female (recipient) of Pack A. All three wolves from Pack B attacked the recipient. The yearling male (supporter) ran in and attacked one of Pack B. All three members of Pack B started to chase the supporter, but went back to the recipient and attacked her again. The supporter ran in again and attacked one of Pack B. Pack B chased the supporter (biting him on the hind leg), and the recipient crossed the Lamar River and ran away. The recipient ran away and also crossed the river in a different spot. Pack B stopped chasing.

Discussion

Aggressive interactions between wolf packs can be chaotic. This confusion can make detailed data collection difficult, so we include only the most easily observed data (i.e., a wolf actively being attacked) as many wolves are

concentrated in one place and the attacks lasted more than a few seconds, sometimes several minutes. In all six cases, we report here the supporter approached the attackers and the recipient. Although the approach by the supporter functioned to distract the attackers, it is feasible that the supporter approached for several reasons; therefore, we cannot make assumptions concerning the supporter's intent. The supporter may have approached out of curiosity, or even to determine whether pack mates were attacking a rival, instead of the other way around. Perhaps a benign approach coincidentally worked to distract the attackers, and interference was never the purpose. Several interactions involved multiple interference behaviors by the supporter, and we report on all recorded instances of this behavior.

Kin selection was originally proposed as the most likely explanation for cooperative breeding and altruistic behaviors (Hamilton 1964), yet has been criticized as some studies found no correlation between helping behavior and relatedness (Dunn, Cockburn and Mulder 1995; Magrath and Whittingham 1997). This cooperative gene theory—where the supporter benefits in that the recipient passes on their shared genes—is likely appropriate for many species as they often live in family-structured groups with high levels of intra-group relatedness. Wolf packs usually consist of an unrelated pair and their offspring from multiple years (vonHoldt et al. 2008), and five of the six interference events reported here involved closely related dyads of wolves (and once a wolf and his mate with their litter of offspring), who are highly familiar with each other having lived in the same pack their whole lives.

It is unknown by what mechanism and to what extent wolves measure and understand their relatedness to others. Glandular secretions and excrement likely contain information related to individual identity (Bronson 1968, Mech and Boitani 2003) and may be used to gauge genetic similarities or differences as has been found in beavers ([*Castor canadensis*] Sun and Müller-Schwarze 1998), European storm petrels ([*Hydrobates pelagicus*] Bonadonna and Sanz-Aguilar 2012), and meerkats ([*Suricata suricatta*] Leclaire et al. 2013).

If kin discrimination influenced wolf behavior, we may assume that wolves would treat their close kin favorably even if they were in a different pack—which often happens when new packs form in territories adjacent to the natal pack. It is unknown if wolves tolerate or avoid aggression with packs containing close kin, or if relatedness has any bearing on behavior at all. African lion territorial behavior was unaffected by relatedness ([*Panthera leo*] Spong and Creel 2004), and it may be that wolf packs are aggressive toward all neighbors, regardless of relatedness.

Reciprocal altruism is most often studied within a group and focuses on behaviors where the opportunity to

reciprocate in the form of grooming (Kaburu and Newton-Fisher 2015), support during aggression (Fraser and Bugnyar 2012, Krueger et al. 2015), or food sharing (Carter and Wilkinson 2015) is very likely to present itself in the future. Some reciprocation even happens immediately as when female chimpanzees exchange food for sex (Boesch 1994; Gomes and Boesch 2009). Does gray wolf interference behavior fit with the reciprocal altruism theory, especially if the opportunity to reciprocate is rare? Presumably inter-pack aggressive interactions are somewhat infrequent as only 121 were recorded in 16 years of data collection. However, comparing observed mortalities of collared wolves ($n = 3$) to all recorded mortalities of collared wolves ($n = 35$) suggests the interactions observed only represent about 10 % of the interactions that occurred. These interactions are likely not distributed equally among packs as there is some suggestion that the smallest packs avoid aggressive interactions and most encounters occur between packs of similar size (Cassidy et al. 2015). While the chances the recipient will have opportunity to reciprocate during an inter-pack aggressive encounter in the future are not guaranteed, the recipient may provide other benefits to the supporter in the future.

Group size is an important factor in many facets of wolf life history. Territorial interactions between neighbors are often won by the larger pack, with the effect of just one additional wolf increasing a pack's odds of winning by 140 % (Cassidy et al. 2015). With such a dramatic difference adding just one wolf makes, supporting a pack mate makes evolutionary sense in order to maintain competitiveness, especially for small packs where each individual increases the likelihood, the pack is larger than their neighbors. Winning these encounters is important to adult survival (Cubaynes et al. 2014) and pack longevity, creating a positive feedback loop for the most successful packs.

Supporting a pack mate in order to maintain a larger pack size may be particularly important for small packs in relation to elk hunting, where ideal pack size is 4 (MacNulty et al. 2011) and reproduction, where ideal pack size is 8 (Stahler et al. 2013) and may be less important for packs larger than those thresholds. This is one possible reason pack size for groups in which interference was recorded (6.2) was smaller than the long-term average group size (9.9).

In addition to their own pack size and pack size relative to their opponent, the group size of the attacking pack may be important to the decision by the supporter to even attempt to interfere. A potential supporter may be more likely to act the fewer the number of attacking wolves are present as the danger to itself is decreased. We found no significant difference in the average attacking pack size when interference did or did not occur, but sample size was extremely small.

Although wolves are highly social mammals, most wolves disperse from their natal pack between 1 and 2 years old (Gese and Mech 1991), and most of them leave alone (Mech and Boitani 2003). Perhaps because of the high density of wolves in the NR, there are many cases of wolves dispersing in groups, usually with same-sex siblings (Yellowstone Wolf Project unpublished data). This may be an adaptive strategy to maneuvering through a wolf-dense system, and selectively benefit any wolf having a pack mate present during aggressive interactions. If group dispersal can be classified as a type of coalition formation, similar to bottle-nosed dolphins (*Tursiops aduncus*] Möller et al. 2001), chimpanzees (Watts 1998), and African lions (Packer et al. 1991), it likely helps new packs become established in a hypercompetitive environment.

While kin selection and reciprocal altruism are feasible evolutionary explanations for the ultimate benefits of altruistic behavior, this does not explain the proximate decision-making process resulting in an altruistic act. Empathy has been proposed as the reason why an individual would choose to perform a behavior that is costly in the short-term (Batson 1991). de Waal describes empathy as the ability to “relate to the emotional states of others, which is essential for the regulation of social interactions, coordinated activity, and cooperation toward shared goals,” (2008, p 282) all important factors in the life of a social carnivore (Bailey et al. 2013). The capacity for animals to experience empathy continues to be debated (Hauser 2001). Even if one animal could relate to another in distress, an attempt to alleviate the distress may still be selfish and not related to any emotional connection to the distressed (Edgar et al. 2012). In all of the attacks we report, the supporter and the recipient were both in stressful, and potentially deadly, situations. The possibility that the supporter approached the attack to alleviate its own distress, and not necessarily the recipient’s, cannot be discounted. Given this, the best strategy for the supporter would have been to flee the area and perhaps fittingly, in 83 % of the attacks recorded, potential supporters did just that.

Although interference behavior was recorded only rarely, we believe there is likely some evolutionary mechanism behind the behavior that relates closely to successful group-living and perpetuation of shared genes. Wolves perform many group-level activities where group size and coordination are essential for success. Cooperating in these shared goals results in direct and indirect benefits to the individuals (Axelrod and Hamilton 1981). Nowak (2006) stated that evolution forms new organizational levels from multicellular organisms to social insects to human societies because of cooperation among increasingly complex organisms and the evolution of cooperation requires one or more mechanisms in order to become an

evolutionary stable strategy. Wild gray wolf packs are on that spectrum of complex organizational societies. Although we cannot know exactly the motivations behind some of their behaviors, we examine behavioral patterns and attempt to determine how those behaviors have shaped gray wolf ecology and life history.

Summary

Evidence for and against altruism will continue to be a much debated topic among ethologists. Although altruism often has ultimate benefits to the actor, there is presumably some proximal explanation for the occurrence of a costly behavior. The evolution of empathy, especially in social species, may fit this requirement as individuals relate to the emotional state of another and can choose to act in a potentially costly way to alleviate their own and the other individual’s distress. In gray wolves, the behavior observed during inter-pack fights where one wolf interferes as its pack mate is being attacked by several opponents potentially fits this pattern as the supporter could easily escape yet puts itself in danger, often successfully allowing the recipient to escape. Cooperation is essential to successfully hunt large prey, to raise pups, and to defend territory for gray wolf packs. The long-term benefits of cooperative supporting behavior, kin selection and reciprocal altruism, would ultimately favor supporters over non-supporters.

Acknowledgments We would like to thank Douglas Smith, Daniel Stahler, Erin Stahler, Matt Metz, Emily Almberg, Nathan Varley, Laurie Lyman, and numerous technicians for their assistance in field data collection and recording of details in the events described here. We also thank donors to the Yellowstone Wolf Project: Valerie Gates, Annie and Bob Graham, and Frank and Kay Yeager, as well as the U. S. National Park Service, and National Science Foundation (DEB-0,613,730 and DEB-1245373). Any use of trade, firm, or product names does not imply endorsement by the U.S. government.

Compliance with ethical standards

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the American Society of Mammalogists at Yellowstone National Park, WY (IUCUC Protocol Approval Number: IMR_YELL_Smith_Wolf_2012; National Park Service Scientific Research and Collecting Permit Number: YELL-2014-SCI-1818).

Conflict of interest The authors declare they have no conflict of interest.

References

- Axelrod R, Hamilton WD (1981) The evolution of cooperation. *Science* 211:1390–1396

- Bailey I, Myatt JP, Wilson AM (2013) Group hunting within the Carnivora: physiological, cognitive and environmental influences on strategy and cooperation. *Behav Ecol Sociobiol* 67:1–17
- Batson CD (1991) The altruism question: toward a social-psychological answer. Psychology Press, New York
- Batson CD (2011) Altruism in humans. Oxford University Press, United Kingdom
- Bell G (2008) Selection: the mechanism of evolution. Oxford University Press, United Kingdom
- Boesch C (1994) Cooperative hunting in wild chimpanzees. *Anim Behav* 48:653–667
- Bonadonna F, Sanz-Aguilar A (2012) Kin recognition and inbreeding avoidance in wild birds: the first evidence for individual kin-related odour recognition. *Anim Behav* 84:509–513
- Bourke AFG, Franks NR (1995) Social Evolution in Ants. Princeton Univ Press, NJ
- Bronson FH (1968) Pheromonal influences on mammalian reproduction. In: Diamond M (ed) Perspectives in reproduction and sexual behavior. Indiana University Press, Bloomington, pp 341–361
- Burkart JM, van Schaik CP (2010) Cognitive consequences of cooperative breeding in primates? *Anim Cogn* 13:1–19
- Carter G, Wilkinson G (2015) Social benefits of non-kin food sharing by female vampire bats. *P Roy Soc B-Biol Sci*. doi:10.1098/rspb.2015.2524
- Cassidy KA, MacNulty DR, Stahler DR, Smith DW, Mech LD (2015) Group composition effects on aggressive interpack interactions of gray wolves in Yellowstone National Park. *Behav Ecol* 26:1352–1360
- Cockburn A (1998) Evolution of helping behavior in cooperatively breeding birds. *Annu Rev Ecol Syst* 29:141–177
- Creel S, Creel NM (1995) Communal hunting and pack size in African wild dogs, *Lycan pictus*. *Anim Behav* 50:1325–1339
- Crofoot MC, Wrangham RW (2010) Intergroup aggression in primates and humans: the case for a unified theory. In: Kappeler PM, Silk J (eds) Mind the Gap. Springer, Berlin, pp 171–195
- Cubaynes S, MacNulty DR, Stahler DR, Quimby KA, Smith DW, Coulson T (2014) Density-dependent intraspecific aggression regulates survival in northern Yellowstone wolves (*Canis lupus*). *J Anim Ecol* 83:1344–1356
- Darwin C (1871) The descent of man and selection in relation to sex. John Murray, London
- de Waal FBM (2008) Putting the altruism back into altruism: the evolution of empathy. *Annu Rev Psychol* 59:279–300
- Dugatkin LA (2007) Inclusive fitness theory from Darwin to Hamilton. *Genetics* 176:1375–1380
- Dunn PO, Cockburn A, Mulder RA (1995) Fairy-wren helpers often care for young to which they are unrelated. *P Roy Soc Lond B Bio* 259:339–343
- Edgar JL, Paul ES, Harris L, Pentum S, Nicol CJ (2012) No evidence for emotional empathy in chickens observing familiar adult conspecifics. *PLoS One* 7:e31542
- Fraser ON, Bugnyar T (2012) Reciprocity of agonistic support in ravens. *Anim Behav* 83:171–177
- Gese EM, Mech LD (1991) Dispersal of wolves (*Canis lupus*) in northeastern Minnesota, 1969–1989. *Can J Zool* 69:2946–2955
- Gipson PS, Ballard WB, Nowak RM, Mech LD (2000) Accuracy and precision of estimating age of gray wolves by tooth wear. *J Wildlife Manage* 64:752–758
- Gomes CM, Boesch C (2009) Wild chimpanzees exchange meat for sex on a long-term basis. *PLoS One* 4:e5116
- Grinnell J, Packer C, Pusey AE (1995) Cooperation in male lions: kinship, reciprocity or mutualism? *Anim Behav* 49:95–105
- Hamilton WD (1964) The genetical evolution of social behavior. *J Theor Biol* 7:17–52
- Hauser MD (2001) Wild minds: what animals really think. Macmillan, London
- Heinsohn R, Packer C (1995) Complex cooperative strategies in group-territorial African lions. *Science* 269:1260–1262
- Houston D (1982) The northern Yellowstone elk: ecology and management. Macmillian Publishing Company, New York
- Jaeggi AV, De Groot E, Stevens JMG, Van Schaik CP (2013) Mechanisms of reciprocity in primates: testing for short-term contingency of grooming and food sharing in bonobos and chimpanzees. *Evol Hum Behav* 34:69–77
- Jørgensen S (2015) Empathy, altruism and the African elephant. Dissertation, Swedish University of Agricultural Sciences
- Kaburu SK, Newton-Fisher NE (2015) Egalitarian despots: hierarchy steepness, reciprocity and the grooming-trade model in wild chimpanzees, *Pan troglodytes*. *Anim Behav* 99:61–71
- Krueger K, Schneider G, Flauger B, Heinze J (2015) Context-dependent third-party intervention in agonistic encounters of male Przewalski horses. *Behav Process*. doi:10.1016/j.beproc.2015.10.009
- Kurzban R, Burton-Chellew MN, West SA (2015) The evolution of altruism in humans. *Annu Rev Psychol* 66:575–599
- Leclaire S, Nielsen JF, Thavarajah NK, Manser M, Clutton-Brock TH (2013) Odour-based kin discrimination in the cooperatively breeding meerkat. *Biol Lett* 9:20121054
- MacNulty DR, Smith DW, Mech LD, Vucetich JA, Packer C (2011) Nonlinear effects of group size on the success of wolves hunting elk. *Behav Ecol*. doi:10.1093/beheco/arr159
- Magrath RD, Whittingham LA (1997) Subordinate males are more likely to help if unrelated to the breeding female in cooperatively breeding white-browed scrubwrens. *Behav Ecol Sociobiol* 41:185–192
- Maynard Smith J (1964) Kin selection and group selection. *Nature* 201:1145–1147
- McCracken GF, Bradbury JW (1981) Social organization and kinship in the polygynous bat *Phyllostomus hastatus*. *Behav Ecol Sociobiol* 8:11–34
- Mech LD, Boitani L (2003) Wolves: behavior, ecology, and conservation. University of Chicago Press, Illinois
- Mech LD, Smith DW, MacNulty DR (2015) Wolves on the Hunt. University of Chicago Press, Illinois
- Metz MC, Smith DW, Vucetich JA, Stahler DR, Peterson RO (2011) Seasonal patterns of predation for gray wolves in the multi-prey system of Yellowstone National Park. *J Anim Ecol* 81:553–563
- Mitani JC, Watts DP (2001) Why do chimpanzees hunt and share meat? *Anim Behav* 61:915–924
- Möller LM, Beheregaray LB, Harcourt RG, Krützen M (2001) Alliance membership and kinship in wild male bottlenose dolphins (*Tursiops aduncus*) of southeastern Australia. *P Roy Soc Lond B Bio* 268:1941–1947
- Mosser A, Packer C (2009) Group territoriality and the benefits of sociality in the African lion, *Panthera leo*. *Anim Behav* 78:359–370
- Muller M, Mitani JC (2005) Conflict and cooperation in wild chimpanzees. *Adv Stud Behav* 35:275–331
- Nowak MA (2006) Five rules for the evolution of cooperation. *Science* 314:1560–1563
- Packer C (1977) Reciprocal altruism in *Papio anubis*. *Nature* 264:441–443
- Packer C, Gilbert DA, Pusey AE, O'Brien SJ (1991) A molecular genetic analysis of kinship and cooperation in African lions. *Nature* 351:562–565
- Peters RP, Mech LD (1975) Scent-marking in wolves. *Am Sci* 63:628–637

- Queller DC, Strassmann JE (1998) Kin selection and social insects. *Bioscience* 48:165–175
- Rabb GB, Woolpy JH, Ginsburg BE (1967) Social relationships in a group of captive wolves. *Am Zool* 7:305–311
- Reyer HU (1984) Investment and relatedness: a cost/benefit analysis of breeding and helping in the pied kingfisher (*Ceryle rudis*). *Anim Behav* 32:1163–1178
- Rusch H (2014) The evolutionary interplay of intergroup conflict and altruism in humans: a review of parochial altruism theory and prospects for its extension. *P Roy Soc Lond B Bio* 281:20141539. doi:10.1098/rspb.2014.1539
- Russell JK (1983) Altruism in coati bands: nepotism or reciprocity. In: Wasser S (ed) *Social Behavior of Female Vertebrates*. Academic Press, United Kingdom, pp 263–290
- Seyfarth RM, Cheney DL (1984) Grooming, alliances and reciprocal altruism in vervet monkeys. *Nature* 308:541–543
- Sikes RS, Gannon WL (2011) Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *J Mammal* 92:235–253
- Silk JB (2007) The adaptive value of sociality in mammalian groups. *Philos Trans R Soc Lond B Biol Sci* 362:539–559
- Silk JB, Brosnan SF, Henrich J, Lambeth SP, Shapiro S (2013) Chimpanzees share food for many reasons: the role of kinship, reciprocity, social bonds and harassment on food transfers. *Anim Behav* 85:941–947
- Smith JE (2014) Hamilton's legacy: kinship, cooperation and social tolerance in mammalian groups. *Anim Behav* 92:291–304
- Smith DW, Bangs EE (2009) Reintroduction of wolves to Yellowstone National Park: History, values, and ecosystem restoration. In: Hayward MW, Somers M (eds) *Reintroduction of top-order predators*. Wiley-Blackwell, United Kingdom, pp 92–125
- Smith DW, Drummer TD, Murphy KM, Guernsey DS, Evans SB (2004) Winter prey selection and estimation of wolf kill rates in Yellowstone National Park, 1995–2000. *J Wildlife Manage* 68:153–166
- Smith JE, Van Horn RC, Powning KS, Cole AR, Graham KE, Memenis SK, Holekamp KE (2010) Evolutionary forces favoring intragroup coalitions among spotted hyenas and other animals. *Behav Ecol Arp* 181:284–303
- Smith DW, Stahler DR, Albers E, McIntyre R, Metz M, Irving J, Raymond R, Anton C, Cassidy-Quimby K, Bowersock N (2011) *Yellowstone Wolf Project, Annual Report, 2010*. Yellowstone Center for Resources, Yellowstone National Park
- Smith DW, Metz M, Cassidy KA, Stahler EE, McIntyre RT, Alberg ES, Stahler DR (2015) Infanticide in wolves: seasonality of mortalities and attacks at dens support evolution of territoriality. *J Mammal* 96:1174–1183
- Spong G, Creel S (2004) Effects of kinship on territorial conflicts among groups of lions, *Panthera leo*. *Behav Ecol Sociobiol* 55:325–331
- Stahler DR, MacNulty DR, Wayne RK, vonHoldt B, Smith DW (2013) The adaptive value of morphological, behavioral, and life history traits in reproductive female wolves. *J Anim Ecol* 82:222–234
- Sun L, Müller-Schwarze D (1998) Anal gland secretion codes for relatedness in the beaver, *Castor canadensis*. *Ethology* 104:917–927
- Surbeck M, Hohmann G (2015) Social preferences influence the short-term exchange of social grooming among male bonobos. *Anim Cogn* 18:573–579
- Sussman RW, Garber PA, Cheverud JM (2005) Importance of cooperation and affiliation in the evolution of primate sociality. *Am J Phys Anthropol* 128:84–97
- Trivers RL (1971) The evolution of reciprocal altruism. *Q Rev Biol* 46:35–57
- Trune DR, Slobodchikoff CN (1978) Position of immatures in pallid bat clusters: a case of reciprocal altruism? *J Mammal* 59:193–195
- vonHoldt BM, Stahler DR, Smith DW, Earl DA, Pollinger JP, Wayne RK (2008) The genealogy and genetic viability of reintroduced Yellowstone grey wolves. *Mol Ecol* 17:252–274
- Watts DP (1998) Coalitionary mate guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Behav Ecol Sociobiol* 44:43–55
- Wilkinson GS (1984) Reciprocal food sharing in the vampire bat. *Nature* 308:181–184
- Wilson M, Wrangham R (2003) Intergroup relations in chimpanzees. *Annu Rev Anthropol* 32:363–392
- Wilson ML, Kahlenberg SM, Wells M, Wrangham RW (2012) Ecological and social factors affect the occurrence and outcomes of intergroup encounters in chimpanzees. *Anim Behav* 83:277–291
- Yamamoto S, Humle T, Tanaka M (2012) Chimpanzees' flexible targeted helping based on an understanding of conspecifics' goals. *P Natl Acad Sci USA* 109:3588–3592