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Douglas Smith

Yellowstone National Park, doug_smith@nps.gov

Matthew C. Metz

Yellowstone National Park

Kira A. Cassidy

Yellowstone National Park

Erin E. Stahler

Yellowstone National Park

Richard T. McIntyre

Yellowstone National Park

See next page for additional authors

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Authors

Douglas Smith, Matthew C. Metz, Kira A. Cassidy, Erin E. Stahler, Richard T. McIntyre, Emily S. Almberg, and Daniel R. Stahler



Infanticide in wolves: seasonality of mortalities and attacks at dens support evolution of territoriality

DOUGLAS W. SMITH,* MATTHEW C. METZ, KIRA A. CASSIDY, ERIN E. STAHLER, RICHARD T. MCINTYRE, EMILY S. ALMBERG, AND DANIEL R. STAHLER

Yellowstone Center for Resources, Wolf Project, P.O. Box 168, Yellowstone National Park, WY 82190, USA (DWS, MCM, KAC, EES, RTM, ESA, DRS)

* Correspondent: doug_smith@nps.gov

Evidence for territoriality is usually correlative or post hoc as we observe the results of past selection that are challenging to detect. Wolves (*Canis lupus*) are considered territorial because of competition for food (resource defense), yet they exhibit classic intrinsic behaviors of social regulation (protection against infanticide). This emphasis on prey and infrequent opportunity to observe wild wolf behavior has led to little investigation into the causes of or competitive underpinnings in the evolution of wolf territoriality. We report 6 cases of territorial wolf packs attacking neighboring packs at or near their den; 2 attacks were observed in detail. In all cases, except perhaps one, the attacking pack killed adult wolves either at the den or near it; in 4 cases, pups were probably lost. Loss of pups led to future loss of territory and in one case pack cessation. Intraspecific killing (measured in collared adults only) peaked in April, the month when pups were born and helpless in dens, even though aggressive interactions were at their seasonal low. Twelve of 13 (92%) of the wolves killed during the denning season (March, April, May) were reproductive (males and females), and 8 of 12 were dominant individuals (highest ranking wolf for that sex in the pack). Wolf–wolf killings were also high in October and December, the beginning and middle of the nomadic season, respectively. Aggressive interactions were more frequent during the nomadic season when wolves were roaming their territory as a group compared to the denning season when wolf activity was centered on the den and pack members less cohesive. We conclude that attacks on dens are a more effective form of interpack competition than interference during the breeding season, the current best-supported hypothesis, and that protected pup-rearing space is the primary cause of wolf territoriality.

Key words: *Canis lupus*, denning, infanticide, pups, reproduction, territoriality, trespass, wolves, Yellowstone National Park

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Intrinsically regulated animals (i.e., territorial), as opposed to extrinsically regulated (nonterritorial, food regulated—Wolff 1997), control territory size and positioning to maximize acquisition of food and create social space for offspring protection and rearing (Pimlott 1967; Macdonald 1983; Rich et al. 2012). Territoriality in wolves (*Canis lupus*) is well studied and serves to space packs to avoid excessive amounts of conflict and mortality (Mech 1973; Packard and Mech 1980; Mech and Harper 2002). Among wolf packs, territories are maintained both through nonaggressive (e.g., howling and scent marking) and aggressive behavior. Aggressive interactions may sometimes lead to the death of individual wolves and these mortalities have been used as a measure of intraspecific strife within wolf populations (Mech and Boitani 2003). Peaks in wolf–wolf killing during the breeding season (mid-winter), presumed to disrupt breeding, have been interpreted as a form of interference competition (Mech and Boitani 2003). But estrus in wolves

averaged 9 days in 1 study (Seal et al. 1979) and 15 in another (Zimen 1976), and Kreeger (2003:194) described estrus duration variable and potentially lasting up to a month. Therefore, it would potentially be difficult for another pack (a competitor) to interfere with breeding because estrus may be long providing many opportunities to breed. Further, we found wolf–wolf killings peaked during the denning season (March, April [highest], and May), yet this is the season packs were least likely to encounter each other. Together these findings suggest that attacks during the breeding season (February) are not purposeful attempts to disrupt breeding, rather consequences of wolves circulating their territory and encountering each other, or opportunistic attacks on a competitor. On the other hand, attacks on dens usually lead to mortality of pups or adults, a more evolutionarily effective behavior to interfere with breeding.

Mech and Boitani's (2003) finding that mortalities peak during mid-winter (“...in the few months before and after the

breeding season...”—Mech and Boitani 2003:28) may be a result of intensive winter monitoring and high pack cohesion making discovery of a mortality more likely. In summer, mortalities are more likely to be missed due to typically less intense monitoring (most wolf studies focus on winter field seasons—Mech 1974) and individuals are more difficult to locate and hence missed. Packs are less cohesive in the pup-rearing season (Peterson et al. 1984; Metz et al. 2011) and circulate an often larger territory (e.g., Demma and Mech 2009) making encounters with neighbors less likely and probably less aggressive (fewer wolves/encounter and lower chance of encountering high ranking wolves). In short, territory defense declines in favor of more efficient acquisition of prey and pup care (Metz et al. 2011; Cassidy 2013). The den becomes the activity center where wolves locate one another and exchange information (i.e., location of kills—Demma and Mech 2009). This has the side-effect of disengaging packs from each other and should lead to less conflict, and this is consistent with the Mech and Boitani (2003) explanation, yet despite this, we found it does not. With more data, we found conflict is more often fatal during denning (which takes place more than a “few months” after the breeding season (Mech and Boitani 2003—see above) and attempts to interfere with breeding in winter are probably ineffectual due to pack mobility and the potential of multiple breeders (Smith 2005; Smith and Bangs 2009). Winter is also the time of year when wolves defend territories more vigorously (Fig. 1), unlike summer, which could make a den vulnerable (Peters and Mech 1975; Zimen 1976; Harrington and Mech 1979; Cassidy 2013).

Therefore, we hypothesize that attacks on denning wolves that are currently considered rare (Mech 1994; Latham and Boutin 2011) may have been overlooked as a cause of wolf territoriality (protection of rearing space—Wolff 1997). Further, when considering Wolff’s (1997) definition of intrinsic versus extrinsically regulated species, wolves are currently considered

extrinsically regulated (resource defense—Packard and Mech 1980; Kruuk and Macdonald 1985; Fuller et al. 2003) despite exhibiting every characteristic of an *intrinsically* (social or protected rearing space) regulated species. Because denning wild wolves are rarely observed in detail, our objective was to test the prediction of offspring rearing space and infanticide as being critical to wolf territoriality as proposed by Wolff (1997). We also wanted to test the prediction that patterns of intraspecific strife among wolf packs differed seasonally, or the intensity of territory defense varies throughout the year. We tested this because there are substantial differences in foraging (Peterson et al. 1984; Metz et al. 2011) and territorial behavior (Jedrzejewski et al. 2001, 2007) between denning (i.e., when wolves typically utilize a “homesite”: April–September on the northern ungulate wintering range [NR—Houston 1982] of Yellowstone National Park (YNP)) and nomadic seasons (October–March). If territorial behavior varies, as the above citations suggest, a more appropriate test may be to examine timing of aggression and mortality (and they should be correlated) to more fully explain wolf territoriality.

MATERIALS AND METHODS

Background.—Examination of these ideas was possible because of high wolf density (21–98 wolves/1,000 km²; 3–7 packs) combined with observability of wolves in the northern reaches (NR; also called the northern ungulate wintering range—Houston 1982) of YNP. Competition between packs on the NR of YNP was intense (Smith 2005; Smith and Bangs 2009). Annual territories were small (96–448 km²) and overlap was great (10–60%) with little interstitial space (Smith 2005; Smith and Bangs 2009). This high density and overlap led to high rates of intraspecific killing and was the leading cause of wolf death in YNP (Smith 2005; Smith et al. 2009).

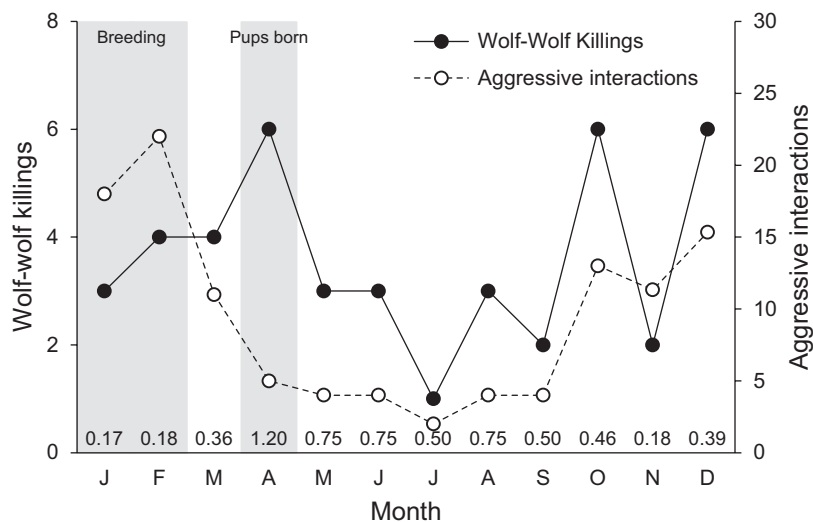


Fig. 1.—Number of wolf–wolf (*Canis lupus*) killings of radiocollared Northern Range wolves and observed interpack aggressive interactions by month, April 1995–March 2013. Interpack aggressive interactions were scaled to reflect changes in observation effort. Numbers displayed above the x-axis represent the interaction effectiveness index value (wolf–wolf killings divided by interpack aggressive interactions) for each month of the year.

Study area.—YNP was mountainous and temperate creating extreme variation in climate and weather patterns. Elevations ranged from approximately 1,500–3,800 m. Vegetation varied from grassland (Idaho fescue [*Festuca idahoensis*] and blue-bunch wheatgrass [*Pseudoroegneria spicata*]) to alpine with high mountain meadows and treeless plateaus but forests of Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), and spruce (*Picea engelmannii*)-fir (*Abies lasiocarpa*) are common (Despain 1990). Sagebrush (*Artemisia tridentata*) is abundant in nonforested areas to about 2,500 m.

Average mean monthly temperatures ranged from 12°C to –13°C and annual precipitation ranged from 25 to 180 cm, depending on elevation (Despain 1990). Winter length can vary significantly with snow cover beginning as early as October and lasting at higher elevations into July, but mean duration of snow cover was 213 days at 2,200 m (Despain 1990). Lower elevations were typically snow free by late April. During our study, most winters were mild, except the winters of 1996–1997 and 2010–2011, which were considered severe and the winters of 2005–2006 and 2007–2008, which were of average severity (based on snow water equivalents [SWE; a measure of snowfall]).

Wolf data.—Approximately 35–40% of NR wolves have been outfitted with very high frequency (Telonics Inc., Mesa, Arizona) or GPS (Televilt, Lindesberg, Sweden; Lotek, Newmarket, Ontario, Canada) radiocollars during each year between 1995 and 2013 (see Smith and Bangs 2009). The handling of all wolves was carried out in strict accordance with approved veterinarian and National Park Service protocols; handling of all wolves conformed to guidelines of the American Society of Mammalogists (Sikes et al. 2011).

Population and behavioral data were gathered on NR wolves through routine radiotracking from both the air and ground throughout the year from April 1995 to March 2013 (see Smith and Bangs 2009). We determined the population of NR wolves via annual early winter counts and used this to calculate population density. As weather permitted, wolves were monitored daily from both the air and ground for two 30-day periods of the year (March and mid-November to mid-December—Smith et al. 2004). For the remainder of the year, wolves were monitored approximately once per week from the air but were typically still monitored daily from the ground, although the number of ground-based observer groups was less (see below). We discovered mortalities from a switch in the radiocollar activated when the collar was motionless for 5 h, which doubled the pulse rate and triggered an investigation from us into cause of death. When we discovered a radiocollared wolf mortality, we investigated the carcass to determine cause of death.

Interpack encounters were recorded throughout the year and were classified as nonaggressive (no chasing; usually howling only) or aggressive (included a chase or physical attack of at least 1 individual). Encounters were also categorized as either pack–pack (at least 2 wolves present from each pack), pack–individual (at least 2 wolves interacting with a single wolf from another pack), or individual–individual (single wolves from different packs). Herein, we present data on aggressive interactions observed via ground-based observations on the NR. We

used only aggressive, pack–pack encounters because interactions involving individuals (pack–individual and individual–individual) were highly likely to occur during the breeding season and include nonaggressive behavior (i.e., breeding and socializing between non-pack members). Further, aggressive, pack–pack encounters were more likely to cause mortalities (14 of 15 observed mortalities) than any encounters involving individuals and better reflect pack–pack competition.

Due to the aforementioned intensive monitoring periods during March and November–December, observation effort from the ground varied throughout the year. An average of 4 observer groups per day were present during March, 3 during November (2 from 1–14 November, 4 from 15–30 November), 3 during December (4 from 1–14 December, 2 from 15–31 December), and 2 per day during the rest of the year. To account for this variation, we adjusted the number of observed aggressive interactions for each month to reflect the number expected to be observed by 2 observer groups. To do this, we divided the number of aggressive interactions by 2 in March and by 1.5 in November and December. The remaining months were not adjusted. Because wolf–wolf killings and aggressive interactions are relatively infrequent, we then pooled each of these metrics of intraspecific strife across years for each month.

Seasonality of intraspecific strife.—To evaluate this prediction, we conducted *t*-tests to evaluate whether wolf–wolf killings and/or observed aggressive interactions differed between seasons. We used regression analysis to assess the prediction that wolf–wolf killings are correlated with aggressive interactions. In addition, for each month of the year, we also calculated an interaction effectiveness index (IEI):

$$\text{IEI} = k / a$$

where *k* is the number of wolf–wolf killings of radiocollared wolves and *a* is the number of observed aggressive interactions (adjusted for observer effort as described above). An IEI of 0 occurs when no mortalities are recorded no matter the number of observed aggressive interactions and an IEI of 1 occurs when the number of mortalities equals the number of observed aggressive interactions. Of note, IEI is an index and not a proportion because only observed aggressive interactions were included.

Attacks on dens.—We describe the details and consequences of 6 interpack interactions at or near dens that we discovered through our routine monitoring (Table 1). Four of the interactions were only partially observed or results of the interaction were inferred from radiotracking, and inspection of the site, and necropsy of individual wolves. Two interactions were observed in their entirety and detailed data were obtained. The interaction between the Slough Creek and Unknown packs in April 2006 was the most detailed, took place over 2 weeks, and was observed from the park road through spotting scopes using multiple observers (Supporting Information S1). The other completely observed interaction was observed in the same manner (Table 1; den attack #5), but unlike the Slough Creek/Unknown observations transpired over several hours, not days. For all interactions, observation through a spotting scope was combined with use of a dictaphone and notes that were later transcribed and analyzed.

Table 1.—Details of interpack attacks on wolf dens in Yellowstone National Park April 1995–March 2013.

Den attack #	Date(s) of attack	Attacking pack	Attacking pack whelp date(s)	Denning pack	Denning pack whelp date	Adult(s) killed	Pups lost	Territory changes for denning pack
1	16 May 1996	Druid Peak	Did not den	Crystal Creek	17 Apr. 1996	4M	Yes, entire litter of unknown size	Lost entire territory, moved to new territory 30 km away
2	22 Apr. 1997	Druid Peak	19 Apr. 1997 and 28 Apr. 1997	Rose Creek	12 Apr. 1997	19F	Yes, entire litter of 4	No loss of territory
3	5 May 2002	Geode Creek	15 Apr. 2002	Leopold	8 Apr. 2002	7F	No, pack mates raised pups	No loss of territory
4	4–28 Apr. 2006	Unknown	27 Apr. 2006	Slough Creek	13 Apr. 2006	489M, 377M	Yes, both packs lost entire litters	Lost significant part of territory, 72% decline in territory size
5	14 Apr. 2009	Cottonwood Creek	15 Apr. 2009	694F Group	9 Apr. 2009	694F	Yes, entire litter of unknown size	Lost entire territory because pack ceased to exist
6	25 Apr. 2012	Mollie's	28 Apr. 2012	Lamar Canyon	21 Apr. 2012	None confirmed, possibly uncollared male yearling	No	No loss of territory

RESULTS

Wolf population

Post-reintroduction, the NR wolf population grew rapidly. December wolf densities were modest from 1995 to 1999 (19–42 wolves/1,000 km²), but increased to high density 2000 through 2008 (54–98 wolves/1,000 km²) before dropping back to moderate levels from 2009 to 2013 (34–40 wolves/1,000 km²). Territorial clashes increased as density increased. From April 1995 to March 2012, we documented 66 natural deaths of collared NR wolves. Among these, 65% (43 of 66) were due to wolf–wolf killing (2.4 ± 0.5 radiocollared NR wolves killed/biological year [$\bar{X} \pm SE$]; range = 0–7). Prime-aged adults (2.0–5.9 years old) made up the largest percentage of wolves killed by other wolves (53%), with 30% being old adults (> 6.0 years), and 16% being yearlings. No pups (< 1 year of age) were recorded killed by other wolves; however, these data include collared wolves only and because we captured wolves during winter, radiocollared pups were usually collared for less than 3 months before becoming yearlings. The dominant breeders made up the highest percentage of wolves killed by other wolves (53%), followed by subordinates (30%), unknown social class (9%), and dominant nonbreeders (7%). Based on collared wolves, these mortalities were proportional to availability (Kolmogorov–Smirnov D_n at $P = 0.05$ is 0.14 with the highest $D = -0.077$).

Seasonality of intraspecific

Wolf–wolf killings peaked during the denning season (March, April, and May; final stages of pregnancy and pups born in dens), October (beginning of nomadic phase), and December (Fig. 1; Table 1). Of the wolves killed during denning, 12 of 13 (92%) were reproductively active (Table 2). Aggressive interactions between packs peaked in February (peak of breeding season) and were also high October–January (Fig. 1). Our evaluation of seasonal differences in intraspecific strife indicated that aggressive interactions were greater during the months of the nomadic season ($t_{5,5} = 6.28$, $P = 0.001$), but wolf–wolf killings were not ($t_{10} = 1.24$, $P = 0.25$).

Monthly wolf–wolf killings were not correlated with the number of observed aggressive interactions for that month ($R^2 = 0.15$, $P = 0.21$; Fig. 1). April was one of the months with the most wolf–wolf killings ($n_{\text{April}} = 6$, range = 1–6; Fig. 1), yet it also was a month with a small number of observed aggressive interactions ($n_{\text{April}} = 5$, range = 2–22; Fig. 1). As a result, the highest IEI was observed in April (1.2), which was 1.6 times greater than any other month, and 2.3 times greater than the average IEI (0.52; Fig. 1). Because April appeared to be fundamentally different than all other months, we assessed how our previous regression analysis would be influenced by removing April from our analysis. After doing so, the number of observed aggressive interactions became a better predictor of wolf–wolf killings but was still not significantly correlated ($R^2 = 0.31$, $P = 0.07$; Fig. 2).

Table 2.—Sex, age, social status, and reproductive outcome of individual radiocollared Northern Range wolves killed during the denning season in Yellowstone National Park April 1995–March 2013.

Wolf ID	Age	Social status	Breeding status	Date of death	Pack size at death	Part of den attack?	Pregnancy status	Did pack reproduce?
4M	7.1	Alpha	Breeder	16 May 1996	3	Yes	Not applicable	No, part of den attack
19F	2.0	Subordinate	Breeder	22 Apr. 1997	9	Yes	Whelped 12 Apr. 1997. 4 pups, all died of exposure	Yes, dominant female and another subordinate female reproduced
40F	5.1	Alpha	Breeder	8 May 2000	8	No	Whelped 13 Apr. 2000	Yes, pack raised her pups and 2 litters from subordinate females
7F	8.1	Alpha	Breeder	5 May 2002	10	Yes	Whelped 8 Apr. 2002	Yes, pack raised her pups
206M	7.9	Alpha	Breeder	24 Mar. 2004	11	No	Not applicable	Yes, mate 152F still had pups
227M	4.9	Alpha	Breeder	27 Mar. 2005	11	No	Not applicable	No, pack disintegrates after his death, unknown fate of pregnant female
204M	7.0	Subordinate	Unknown	5 Apr. 2005	7	No	Not applicable	Yes, alpha female had pups
489M	5.0	Subordinate	Breeder	4 Apr. 2006	12	Yes	Not applicable	No, part of den attack
377M	5.0	Beta	Breeder	28 Apr. 2006	11	Yes	Not applicable	No, part of den attack
694F	3.0	Alpha	Breeder	14 Apr. 2009	2	Yes	Whelped 12 Apr. 2009, Cottonwood pack killed ≥ 2 pups	No
830F	2.9	Beta	Breeder	22 Mar. 2012	10	No	Pregnant with 6 pups	Yes, another subordinate female had pups
471F	9.0	Alpha	Breeder	10 Apr. 2012	7	No	Pregnant with 7 pups	No
759F	3.9	Alpha	Breeder	14 Mar. 2013	2	No	Pregnant with 1 pup	No

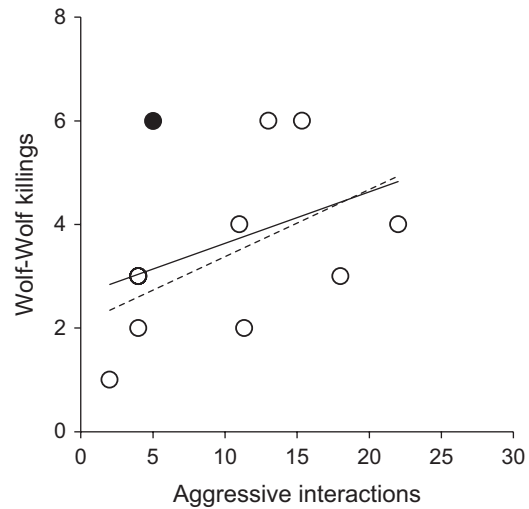


Fig. 2.—Monthly number of wolf–wolf (*Canis lupus*) killings of radiocollared wolves in relation to the number of observed aggressive interactions for that month. Interpack aggressive interactions were scaled to reflect changes in observation effort. Each observation indicates the number of wolf–wolf killings and aggressive interactions for each month of the year (pooled across years). The solid line represents a simple linear regression for all data ($R^2 = 0.15$; $P = 0.21$) and the dashed line represents a simple linear regression that excludes April (filled circle; $R^2 = 0.31$; $P = 0.07$).

Attacks on dens

Den attack #1.—In April 1996 (Table 1), when wolf density was low and wolves were being actively reintroduced, the March 1995-released Crystal Creek pack (3 wolves) denned within the core of their territory in late April 1996. We located all 3 collared wolves at their den for 2–3 weeks. The March 1996-released Druid Peak pack did not have an established territory and wandered widely clashing with at least 1 other territorial pack (Rose Creek, released in March 1995). In mid-May, the Druid Peak pack, which did not have any pregnant females and therefore did not localize at a den, discovered the denned Crystal Creek wolves and killed the breeding male (#4) and wounded the breeding female (#5). A search for pups and a den was unsuccessful, but the aforementioned observations strongly suggest that young were produced and lost. By July, the 2 remaining Crystal Creek wolves abandoned their former territory on the NR and established a new territory in the Interior of YNP, which did not yet have resident wolf packs. Although we recognize the uniqueness of the situation (i.e., reintroduction effort), the behavior of the wolves was still relevant.

Den attack #2.—In 1997, after active human intervention associated with reintroduction had ended (Table 1) another attack occurred. By mid-April, 3 females (#9 [dominant], 18, and 19) from the Rose Creek pack (9 wolves) denned, although each denned at a different location. Among these, #19 denned in an area considered territorial edge between the Rose Creek and Druid Peak (8 wolves) packs. On 22 April, #19 was attacked and killed by the Druid Peak pack (based on radiotracking), and her 4 pups perished at the den. Although 2 Druid Peak females (not including dominant female #40) produced pups in 1997, only 1 had denned by 22 April. Because the Rose Creek pack

had produced multiple litters, 9 pups (of 22) survived to the end of 1997, and the Rose Creek pack continued to maintain their territory following the death of #19 and her pups.

Den attack #3.—In May 2002, an attack occurred that highlights the potential impact that the timing of wolf–wolf killings may have on wolf population dynamics (Table 1). The Geode Creek pack (7 wolves) attacked the neighboring Leopold pack (19 wolves), killing the breeding and lactating female (#7) ~2.5 km away from her den and her ~4-week old pups. Although the Leopold pack was larger than the Geode Creek pack, not all of the Leopold wolves were likely present when they were attacked by the Geode Creek pack. The loss of the breeding female did not result in pup mortality, likely because the pups were old enough to survive without nursing. By winter, 4 of the 8 pups survived and the Leopold pack (16 wolves) maintained their territory.

Den attack #4.—Our most detailed interaction took place between 4–28 April 2006 (Supporting Information S2). Many of these wolves were radiocollared (6 of 12; Supporting Information S3), 1 of which was a GPS collar that collected 1 location/hour placed on the 2nd-ranking pregnant female (#527) that denned during the interaction. None of the individuals in the Unknown pack had functional radio collars.

On 4 April an “Unknown” pack was observed well within the territory of the Slough Creek pack. Both packs numbered 12 wolves and 2 of the Slough Creek females were visibly pregnant. Later we determined that 1 of the Unknown subordinate female wolves was also pregnant. Both packs were aware of each other through howling, but it appeared there were no aggressive interactions. Later a Slough Creek radiocollared adult male wolf (#489) was found dead and a necropsy indicated he had been killed by other wolves. We estimated the date of death as 4 April. The other packs near Slough Creek were also radiocollared and none of their signals were detected in the area; we assumed that the male Slough Creek wolf was killed by the Unknown pack.

On 12 April, both pregnant Slough Creek wolves denned communally. On 13 April, at the Slough Creek den with an estimated (based on radiocollars and observations) 6 Slough Creek females in the den, there was evidence of an aggressive interaction as 2 Unknown wolves were injured. Unknown wolves were observed near the Slough Creek den that morning. None of the Slough Creek wolves were observed.

From 13–24 April, at least 1 Unknown wolf was at the Slough Creek den during 91% of observation time (7,686 of 8,409 min). GPS radiocollar data indicated that 1 of the breeding females (#527) was inside the den 90% of the time (259 of 285 locations; Fig. 3). Diurnal data indicated that the 2 breeding females spent virtually all of their time inside the den, whereas 4 other female wolves spent some time in it. There were no documented visits to the den by Slough Creek male wolves. There were 35 approaches to the den by Unknown wolves: 30 of them were attempted entries into it.

On 25 April, the Slough Creek females abandoned the den and the pups were presumed dead. A search of the area after the wolves had left found no evidence of pups, but we did not excavate the den (National Park Service policy prohibits desecration

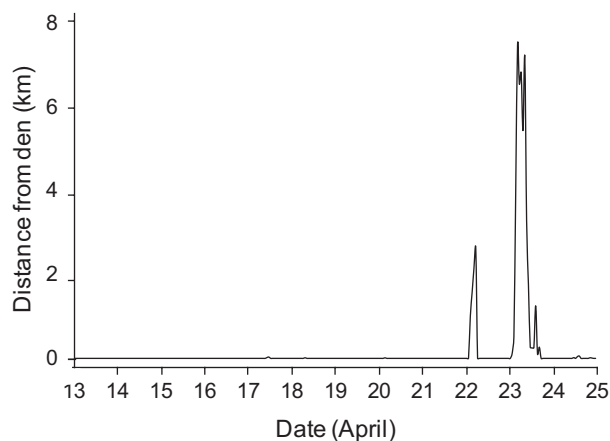


Fig. 3.—Distance from natal den of GPS-collared Slough Creek wolf (*Canis lupus*) (breeding female #527) from 13–24 April 2006. Wolf #527 had her pups on ~12 April and abandoned the den on ~25 April.

of natural features). The Slough Creek females later reunited with the Slough Creek male wolves.

On 24 April, the pregnant Unknown wolf denned 130 m from the Slough Creek den that was now abandoned (Supporting Information S4). On 28 April, an aggressive interaction occurred between the 2 packs and adult male wolf #377 from Slough Creek was killed and adult male #490 (dominant male of the pack) of Slough Creek was observed limping. After this interaction, the Unknown female abandoned her den. Later a search recovered no pups.

After the Slough Creek pack experienced a complete reproductive failure, their winter territory declined by 72% from 337 km² (2005–2006) to 93 km² (2006–2007; Fig. 4). Of note, the Slough Creek and Unknown packs probably interacted on at least 1 more occasion on 29 December 2006 as the dominant male (#490) of the Slough Creek pack was found dead, killed by other wolves near the edge of Slough Creek territory and the presumed edge of the Unknown pack’s territory.

Den attack #5.—In 2009, a newly formed pack of 2 wolves (694F Group), which included 1 uncollared male and female #694, denned between 2 larger packs (Cottonwood Creek [5 wolves] and Druid Peak [11 wolves]; Table 1). Wolf #694 denned on 9 April and located her den almost equidistant from where the Druid Peak pack would den on 10 April and where the Cottonwood Creek pack would den on 15 April. On 14 April, the 5 wolves of the Cottonwood Creek pack, including pregnant dominant female #527, repeatedly chased the uncollared male of the 694F Group away from the immediate area around the den and then killed #694 and at least 2 pups (~1 week old), consuming at least 1, at the den. If there were any other pups, they were also likely killed. The uncollared male lost the territory and became nomadic, although he was only observed a few more times after the interaction because he was not radiocollared.

Den attack #6.—In April 2012, 16 wolves from a pack in Yellowstone’s interior (Mollie’s pack) attacked a denning pack of 9 wolves (Lamar Canyon) living on the NR (Table 1). Radiotracking and observations of the pregnant female #832 indicated that she denned on 20 or 21 April. Mollie’s pack was

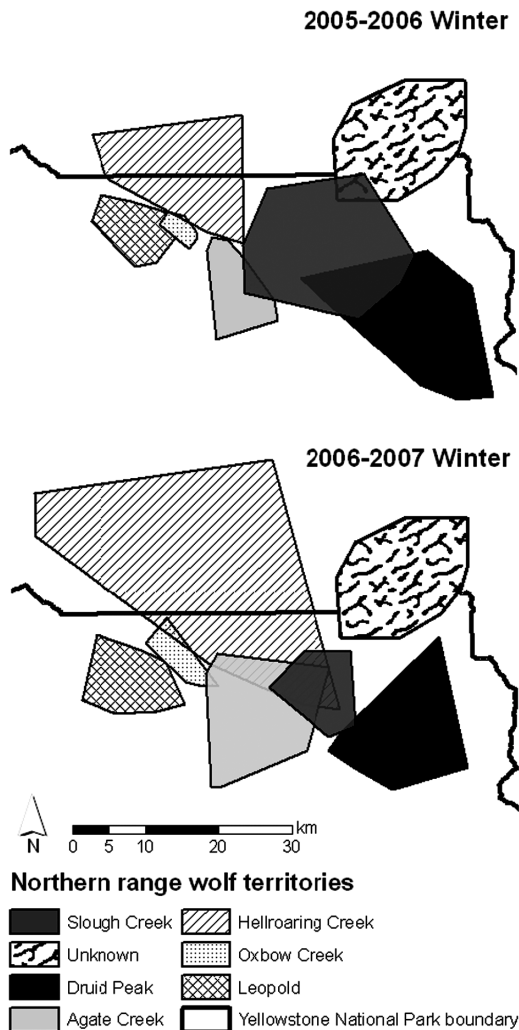


Fig. 4.—Winter territories of Northern Range wolf packs (*Canis lupus*) before (2005–2006) and after (2006–2007) the den attack that reduced the size of the Slough Creek pack. Territories are 95% minimum convex polygons of November–March aerial radiocollared wolf locations, except for the Unknown pack. No wolves in the Unknown pack were marked with functioning radiocollars, and we therefore display their estimated territory which is partly based on geography.

first observed at 0720h on 25 April well west of the Lamar Canyon den. By 1858h, they were observed within 600 m of the Lamar Canyon den. Radio tracking data indicated that 2 adult Lamar Canyon males were near the den (#754 and #755 both of high social rank), but forest cover prohibited any observation of the den area. The breeding female #832 was inside the den based on her radio signal. The Mollie's wolves went into the forest and out of sight where the den was located. Moments later #832 was observed being chased by all 16 Mollie's wolves. #832 fled south and Mollie's wolves could not continue to chase, perhaps because of proximity to the park road. They instead directed their chase at a 2-year-old female (uncollared) for a short distance, but then resumed searching the den area. #832 ventured back and joined with another Lamar Canyon wolf, a female yearling, and they intently watched the den area. At 2016h, Mollie's wolves left the area and #832 returned to the den. The 2 adult males were not observed during the entire

interaction, but it was presumed they were in the vicinity of the den. Although none of the 4 collared Lamar Canyon wolves were killed during the interaction, an uncollared male yearling, usually with the pack, was never observed after this encounter. On 7 July 4, pups were observed near the den indicating that none likely died during the encounter as average litter size for YNP wolves is 4.4 for a 6-year-old female (estimated from age-specific reproductive model in [Stahler et al. 2012](#)).

DISCUSSION

After reintroduction, and through colonization and population saturation, Yellowstone wolves interacted aggressively at a high rate. Various types of aggression were recorded, from howling to killing including behaving territorially without a territory. A seasonal pattern was evident: interpack killings peaked during April (denning) and October and December (beginning of nomadic season) but was also high in other months around the denning season ([Fig. 1](#)). Conversely, aggressive interactions were low during denning and throughout the pup-rearing season, but high during the breeding season months ([Fig. 1](#)). Therefore, we found a seasonal pattern to territorial behavior consistent with our prediction, but contrary to our prediction, aggression and mortality were not correlated ([Fig. 2](#)). Together these data suggest that wolves have evolved to attack competitors when they are most likely to impact their reproduction, with the highest success during the denning season when they attack a rival pack's den. When attacks on the den occur, typically pups die, which in some cases is that year's entire reproductive output. Loss of pups reduces pack size and may lead to loss of territory, or in some cases pack dissolution ([Table 1](#); [Cassidy 2013](#)). This is a different interpretation than the one presented by [Mech and Boitani \(2003\)](#), which states the most effective time to interfere with reproduction is during the few months around breeding season ([Mech and Boitani 2003:28](#)). This interpretation based on our detailed observations of free-ranging wolves provides a deeper understanding of their territoriality: a hypercompetitiveness where virtually all movements are some kind of territory patrol, with directed attacks preferentially at the den, then during the breeding season, both of which function to reduce a neighbors' competitiveness ([Mech and Boitani 2003](#)).

We acknowledge that this is one population at high density and that wolf behavior is plastic ([Packard 2003](#)). Nonetheless these findings, especially the prevalence of infanticide during a relatively short period of time (18 years), highlight how rare events may be important in the evolution of a behavior (e.g., territoriality). However, intraspecific mortality rates are very similar to other unexploited wolf populations in Alaska, Minnesota, and Isle Royale ([Mech 1994](#); [Mech et al. 1998](#); [Peterson et al. 1998](#)). This aggression underscores the importance of protected rearing space as wolves vigorously defend their territories, especially the territory cores where dens are located ([Packard 2003](#); [Trapp et al. 2008](#); [Unger et al. 2009](#)). Too, with opportunity, wolves readily attack and kill wolves at their dens, and this has not been widely reported on in the literature ([Theberge](#)

1998; Latham and Boutin 2011) and should be noted as an effective form of competition.

Other research in Yellowstone has shown pack size to be critical to territory acquisition and retention (Cassidy 2013). Therefore, a territory may be more important as rearing space (Wolff 1997; Jedrzejewski et al. 2007) than hunting grounds, which has been emphasized for wolves (Packard and Mech 1980; Mech and Boitani 2003:19–27). Other carnivores (e.g., cougars [*Puma concolor*]) function in a similar environment without being territorial and infanticide is common in protected (parks) populations (Logan and Sweanor 2001) suggesting territoriality protects offspring. Other support for our view comes from evidence that despite higher interaction rates during the nomadic season (winter when packs are typically cohesive), intraspecific killing is not greater. During winter, pups are traveling and functioning with the pack and harder to kill (80% of full size—MacNulty et al. 2009), and there is no opportunity to kill all of them, unlike during the denning season. Thus, killing during winter is more opportunistic.

Opportunistic killing is different than the interpretation articulated by Mech and Boitani (2003) who stated that the “territory holders” or “maturing or mature” wolves were targeted. If killing to reduce pack size is selected for, then killing pups when most vulnerable is most effective, and after that, packs should try to kill any competitor when possible. Our data, using observed fatal interactions only to eliminate collar bias (only 5 of 15 wolves [33%] observed killed had working radiocollars), indicate that “maturing or mature” wolves were not killed more than their availability (20%, 3 of 15 observed fatal interactions). Likely packs kill the 1st wolf they can catch, as pups make up 26% (4 of 15 interactions) of the observed mortalities and subordinate adults make up 53% (8 of 15).

We hypothesize that infanticide among wolves is not as rare as previously believed, just hard to detect, and is one of the driving forces behind wolf territoriality (Wolff 1997; Mech and Boitani 2003). For example, in 18 years of close monitoring, we have discovered 6 such events, all in northern Yellowstone where our monitoring is most intense (ground and air), and had our monitoring not been intensive, we would have missed several of the interactions. For example, on one radiotracking flight, we radiotracked both breeding Slough Creek females to the den and visually observed 6 wolves bedded around the den. The ground crews had identified these wolves as intruding Unknown pack wolves, whereas the air crew did not, which underscores the point that without detailed and continuous monitoring from the ground, the events we report herein might have gone unnoticed. Possibly additional attacks on dens throughout Yellowstone, particularly in the interior Yellowstone wolf population, were missed.

Attacks on a competitor’s den are feasible, and possibly common, because each year in YNP at least 1 pack does not reproduce, and many years there is more than 1 (Smith and Bangs 2009). Nonreproductive wolves are not tied to a den and are therefore able to travel together throughout their territory (nomadic), like they do in winter. Moreover, wolves that have not yet denned also still travel in this manner, and this may

select for birthing synchrony, like in ungulates, which would reduce the probability of suffering a den attack. In either situation, the attacking pack (which may be smaller than the denning pack) may therefore have a numerical advantage when attacking a den because rarely are all the denning wolves present, as many are often away hunting (Demma and Mech 2009). In winter, wolf packs commonly travel together and encounters between packs are more likely to involve all the wolves in each pack, with the larger pack more likely to win unless one pack has more old adults or adult males—the most aggressive individuals in a pack (Cassidy 2013). In the encounter between the Slough Creek and Unknown packs, the Unknown pack always outnumbered the Slough Creek wolves at the den: 2 females were typically in the den, sometimes with subordinate females, but the other Slough Creek wolves were not recorded all together around the den. In fact, the Slough Creek males avoided the den and never challenged the Unknown wolves probably because they were outnumbered. Only after the pack reunited when the pups had died did the Slough Creek pack challenge the Unknown pack.

Other studies on wolf denning ecology support the suggestion that wolf territoriality is at least partially evolved in response to protection from infanticide. Specifically, Trapp et al. (2008) and Unger et al. (2009) found dens centrally located within wolf territories, suggesting avoidance of edges and encounters with neighboring packs. Although Ciucci and Mech (1992) found dens randomly located throughout the territory, Trapp et al. (2008) suggested that this was due to analytical reasons (minimum convex polygon versus kernel estimator) rather than behavioral, leaving open the possibility that wolves choose den site locations to avoid attacks from neighbors. Most nondenning season attacks occur at the territory periphery (low risk because retreat to one’s own territory is relatively easy—Mech 1994), whereas attacks on dens are usually made at the core where they are typically located, which poses high risk to the trespassing pack (deep within a competitor’s territory). Den placement then is strategic to reduce attempts at infanticide from a competitor which we feel is the ultimate cause of wolf territoriality. These findings, taken together with our data and other reports of attacks on dens (Theberge 1998; Latham and Boutin 2011), suggests that wolf territoriality evolved as protective rearing space and secondarily to secure food (Mech and Boitani 2003).

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SUPPORTING INFORMATION

The Supporting Information documents are linked to this manuscript and are available at Journal of Mammalogy online (jmmam.oxfordjournals.org). The materials consist of data provided by the author that are published to benefit the reader. The posted materials are not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the author.

SUPPORTING INFORMATION S1.—Detailed account of Den Attack #4.

SUPPORTING INFORMATION S2.—Timeline of significant events while the Unknown pack was present in Yellowstone National Park from April through December 2006. Location of events references Fig. 3.

SUPPORTING INFORMATION S3.—Pack structure for Slough Creek and Unknown packs during April 2006.

SUPPORTING INFORMATION S4.—Map of significant events while the Unknown pack was present in Yellowstone National Park. Numbers reference events described in [Supporting Information S2](#).

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