



Seasonality of intraspecific mortality by gray wolves

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Of 41 adult wolf-killed gray wolves (*Canis lupus*) and 10 probably or possibly killed by wolves from 1968 through 2014 in the Superior National Forest (SNF) in northeastern Minnesota, most were killed in months leading up to and immediately following the breeding season, which was primarily February. This finding is similar to a published sample from Denali National Park, and the seasonality of intraspecific mortality generally parallels the known seasonality of testosterone levels, scent-marking, howling frequency, and general interpack aggression. Males and females were killed in the same proportion as in the population of radiocollared wolves. The annual rate of wolf-killed wolves was not related to the annual wolf density. Our findings tend to support intraspecific mortality of adult wolves as a means to reduce breeding competition and to maintain territories.

Key words: breeding, *Canis lupus*, howling, intraspecific strife, mortality, scent-marking, territoriality, testosterone, wolves

A primary cause of nonanthropogenic adult wolf (*Canis lupus*) mortality is other wolves (summarized by [Mech and Boitani 2003](#)), and much new information has been documented about such mortality ([Cassidy et al. 2015, 2016, 2017](#); [Smith et al. 2015a](#)). Explanations for intraspecific strife among wolves have included territorial defense ([Murie 1944](#); [Mech 1970](#); [Mech and Boitani 2003](#); [Stahler et al. 2013](#)), because most wolf killing by other wolves both in northeastern Minnesota and Denali National Park, Alaska, has occurred along edges of wolf-pack territories or in adjacent territories ([Mech 1994](#); [Mech et al. 1998](#)). Other explanations have included genetic or breeding competition ([Mech 1977](#); [Messier 1985](#); [Mech and Boitani 2003](#); [Cassidy et al. 2017](#)), and offspring defense ([Smith et al. 2015a](#); [Cassidy et al. 2015](#)). These explanations are not mutually exclusive.

[Mech and Boitani \(2003:28\)](#) stated that wolf killings by other wolves are “concentrated in the few months before and after the breeding season,” but they documented this only by citing unpublished data. [Smith et al. \(2015a:1174\)](#) indicated that [Mech and Boitani \(2003\)](#) interpreted that finding as “a form of interference competition,” and [Smith et al. \(2015a\)](#) suggested that the [Mech and Boitani \(2003\)](#) finding might have resulted from more intensive monitoring around the breeding season. In Yellowstone National Park (YNP), [Smith et al. \(2015a\)](#) found spikes in wolf–wolf killings of adults not only around the breeding season but also during the denning season.

Because information on the seasonality of intraspecific mortality among wolves is relatively rare, we analyzed data about wolf–wolf killings from our own studies and the literature. Our goals were to 1) determine whether the suggestion by [Mech and Boitani \(2003\)](#) that intraspecific mortality is concentrated around the breeding season would be confirmed, and 2) compare these additional data on wolf–wolf killings to YNP’s seasonality of wolf aggression, including spikes in wolf–wolf killing of adults during the denning season. Although an important focus of [Smith et al. \(2015a\)](#) was a relationship during the denning season between fewer overall aggressive encounters (although only pack–pack interactions were considered) and increased adult wolf–wolf killings and infanticide, we attempted here only to assess the seasonality of adult wolves killing other adults. We had no other data on interpack aggressiveness.

MATERIALS AND METHODS

Study area.—Our study area consisted of 2,060 km² of the Superior National Forest (SNF) east, northeast, and southeast of Ely, Minnesota (48°N, 92°W) just south of the Ontario, Canada border. A detailed description of the vegetation, topography, and legal history of the wolf population through 2007 was given by [Mech \(2009\)](#). Wolves were off the federal endangered species list and managed by the state, including public harvesting, during 2012–2014 but were classified as threatened

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before and since. During our study, wolf density varied between 17 and 47/1,000 km² (Mech and Fieberg 2014). The breeding season for wolves in our study area spanned at least from 28 January to 4 March (Mech and Knick 1978).

Methods.—We livetrapped wolves with modified foot-hold traps from 1968 to 2014, mostly June through October, drugged the animals intramuscularly with anesthetics via syringe-pole, and radiocollared them. Anesthetics used were the following: phencyclidine hydrochloride and promazine hydrochloride; ketamine hydrochloride and promazine hydrochloride; and tiletamine hydrochloride, zolazepam hydrochloride, and xylazine, reversed with yohimbine or tolazoline (Barber-Meyer and Mech 2014). We weighed, measured, collected biological samples, and radiocollared the wolves, then injected them with prophylactic antibiotics, and released them. We followed the guidelines of the American Society of Mammalogists for use of wild mammals in research (Sikes et al. 2016) under U.S. Fish and Wildlife Service permits PRT831774 and TE3886A-0 and the approval of the U.S. Geological Survey, Northern Prairie Wildlife Research Center Animal Care and Use Committee.

Prior to 2000, we assumed that all non-pup wolves were at least 1 year old unless tooth-wear information at capture allowed us to retroactively assign a more precise age (Mech et al. 2016). From 2000 on, we compared the tooth wear to a tooth-wear chart of known-age wolves to assign ages to all non-pups (Gipson et al. 2000).

Generally, we aerially located the collared wolves weekly year-round and observed them mostly in winter but occasionally other times. We determined that a wolf might be dead when its location did not change for several consecutive tracking sessions (prior to the development of mortality switches in telemetry collars in 1987) or when a radio signal indicated the collar did not move for at least 4 h. We then investigated the remains from the ground as soon as possible to determine cause of death, usually within 1–5 days (Mech 1994). To minimize possible capture effects on wolf fates, we only used for this study wolves confirmed by telemetry to be active at least 14 days post-capture.

We judged that wolves were killed by other wolves by examining the carcass and the surrounding area and by excluding (as carcass remains allowed) other mortality sources (e.g., vehicle strike, shooting, starvation, disease, drowning, killed by prey). Wolf-killed wolf carcasses exhibited numerous bite marks (and blood on their fur) consistent with wolf canines on the face, neck, shoulders, rump, groin, or legs. We concluded some wolves were eaten by other wolves by fresh blood in the surrounding area and numerous wolf tracks (more than what the dead wolf would have made). Other factors that helped when the carcass evidence was only suggestive (depending on the amount and condition of the remains and time since mortality) were locations of other radiocollared wolves and evidence in the surrounding area (e.g., broken branches suggestive of a struggle, blood on vegetation and ground, etc.). Probable kills were those in which such evidence was present but not definitive (e.g., fewer bite marks but no other apparent source of mortality), and possible kills showed weaker but suggestive

evidence (e.g., insufficient carcass remains or deteriorated condition of surrounding area).

Because of mortalities and dispersals, and monthly captures, the number of wolves monitored varied by month. We addressed the potential bias that more intensive monitoring around the breeding season could result in detection of more wolf-killed wolves at that time by calculating wolf-killed mortality as a monthly rate. We tallied wolf-months of monitoring for each month throughout the study (1 wolf monitored weekly for 1 month tallied as 1 wolf-month) for all wolves radiomonitored. Our monthly wolf-killed mortality rate thus was the number of wolves killed by wolves in a given month divided by the number of wolf-months (e.g., radiocollared wolves at risk per month) monitored for that month (Ballard et al. 1987). We also examined the rate of mortality due to unknown causes for each month, hypothesizing that if misinterpretation of cause of death was the reason for a low wolf-killed mortality rate for any given month, a higher rate of death by unknown causes might be found during those months.

Using raw data (not normalized by wolf availability) of wolf-killed wolves from Denali National Park (Mech et al. 1998) and miscellaneous reports, we examined monthly distribution of wolf-killed wolves in areas other than the SNF. We also reviewed literature involving observations around wolf dens to obtain some perspective on frequency of wolf raids on dens, including possible wolf–wolf killings of adults during the denning season (Smith et al. 2015a).

We used a 2 × 2 contingency table in Statistix 9 to test for sex ratio differences in wolf-killed wolves and in wolf-killed wolves before (September–January in the SNF, and October–February in Denali) and after (March–August in the SNF, and April–September in Denali) the breeding season (February for the SNF, and March in Denali). We used simple linear regression to test whether the annual rate of wolf-killed wolves and probable wolf-killed wolves in the SNF increased linearly with wolf density (Mech and Boitani 2003) at the beginning of the same year and of the previous year. Finally, we used Pearson's test to determine the correlation between YNP interpack aggression and wolf–wolf mortality and our monthly wolf–wolf mortality rate. We evaluated results at $\alpha = 0.05$.

RESULTS

During primarily June through October 1968–2014, we made 914 captures of 671 wolves (329 males, 342 females) that we radiocollared in the SNF and for which we monitored survival and mortality for at least 14 days. At least 41 of those wolves were killed by wolves, and 10 more were probably or possibly killed by wolves (Table 1; Mech and Barber-Meyer 2017). Most SNF wolf-killed wolves were killed during October through March, with the fewest during September and the April–July denning period (Fig. 1). The rate of SNF wolf-killed mortality during February, the primary breeding season, was relatively low, although, as with all our monthly rate estimates, that could be because of the small monthly sample. The fewest SNF

Table 1.—Monthly distribution of wolf-killed wolves (*Canis lupus*), wolves whose causes of death were unknown, and number of wolf-months during which wolves were monitored in the Superior National Forest of northeastern Minnesota, 1968–2014.^a

Wolf-killed				Cause of death unknown	Wolf-months available	Ratio of deaths to wolf-months ^c		
Month	Definite	Probable ^b	Total			Wolf-killed ^d	Unknown	Wolf-killed and unknown
January	5	1	6	5	938	0.0064	0.0053	0.0117
February	3	0	3	3	886	0.0034	0.0034	0.0068
March	7	0	7	3	840	0.0083	0.0036	0.0119
April	1	0	1	2	795	0.0013	0.0025	0.0038
May	0	2	2	3	752	0.0027	0.0040	0.0066
June	1	0	1	3	757	0.0013	0.0040	0.0053
July	1	0	1	5	838	0.0012	0.0060	0.0072
August	3	1	4	7	924	0.0043	0.0076	0.0119
September	1	0	1	8	988	0.0010	0.0081	0.0091
October	7	1	8	7	1,061	0.0075	0.0066	0.0141
November	3	1	4	11	1,079	0.0037	0.0102	0.0139
December	9	4	13	5	998	0.0130	0.0050	0.0180
Total	41	10	51	62				

^aIncludes those in Mech (1994).

^bIncludes 5 possible wolf kills.

^cAlthough these are rates, conceivably the smaller sample in spring could present a slight bias.

^dIncludes probable and possible.

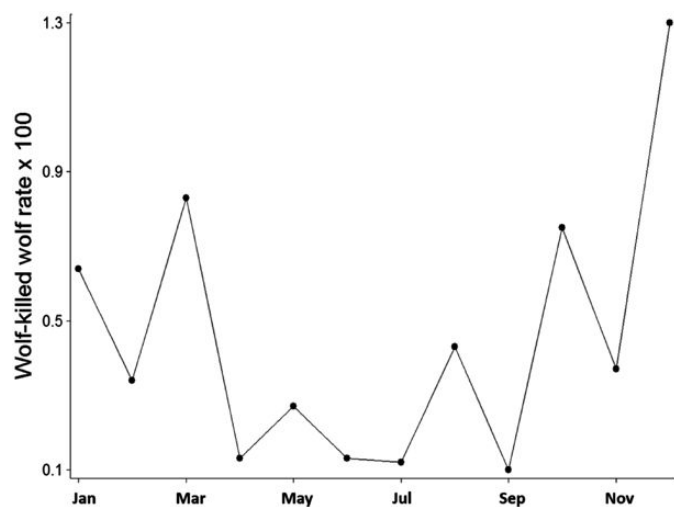


Fig. 1.—Monthly rate of wolf-killed wolves (*Canis lupus*) in the Superior National Forest of northeastern Minnesota, 1968–2014. The main denning season is April–June. Breeding season is approximately 63 days earlier (mainly February). Y-axis ratios are times 100.

wolves dying of unknown causes occurred during February through June (Table 1; Fig. 2).

The SNF monthly rate of wolf-killed wolves generally decreased after January, bottoming out during summer, and increased during early winter as the breeding season approached. The monthly wolf-killed mortality rate at SNF also moderately correlated with both the YNP monthly rate of wolf-pack aggression with other packs and the wolf-killed mortality rate at YNP (Smith et al. 2015a; both $r = 0.57$, $P = 0.05$).

In Denali National Park, the Mech et al. (1998) sample included 170 captures of 147 wolves (72 males, 75 females), and none of 23 wolf-killed wolves there was killed during the May–July denning period (Fig. 3). In Algonquin Provincial

Park, where 26 natural deaths were recorded, none was found during April or May (Theberge and Theberge 2004). Similarly, in 7 miscellaneous reports of 18 wolf-killed wolves, only 2 wolves were killed between March and October, 1 in June and 1 in July (Table 2), and during at least 6,450 h of observations around wolf dens in 3 study areas, no wolf killing of other wolves was observed associated with the dens, although more than one-half of those observation hours were on Ellesmere, where density is lower (Table 3).

The sex ratio of our SNF wolf-killed wolves tended toward males (30 males:21 females) but was not significantly different from that of all our radiocollared wolves (Pearson's $\chi^2_1 = 1.82$; $P = 0.18$). The sex ratio of Denali wolf-killed wolves was 16 females:7 males but was also not significantly different from that of all the collared wolves (Pearson's $\chi^2_1 = 2.75$; $P = 0.10$). Neither was the sex ratio of either wolf-killed sample significantly different before or after the breeding season (SNF, Pearson's $\chi^2_1 = 0.17$, $P = 0.68$; Denali, Fisher 2-tailed exact test, $P = 0.24$).

Wolves of all ages were killed by other wolves, but only 1 of the 51 SNF wolf-killed wolves was a pup (7–8 months old). This is due, at least in part, because we only collared pups at least 5 months old (so our sample is largely adults). Similarly, in Denali, few wolves were collared before 9 months of age, so information about proportion of pups killed by wolves could be highly biased.

Of 38 summers of den watching (6,450 h) reported from multiple study areas, 4 included cases of apparently unfamiliar wolves being chased from within 0.5 km of the den area, but no case of wolves killing other wolves or attacking pups around dens was reported (Table 4). However, 10 summers were for a pack on Ellesmere where wolf density is low, so encounter rates and wolf–wolf mortalities would be lower, although we know of 2 unpublished records from this study area (D. R. MacNulty,

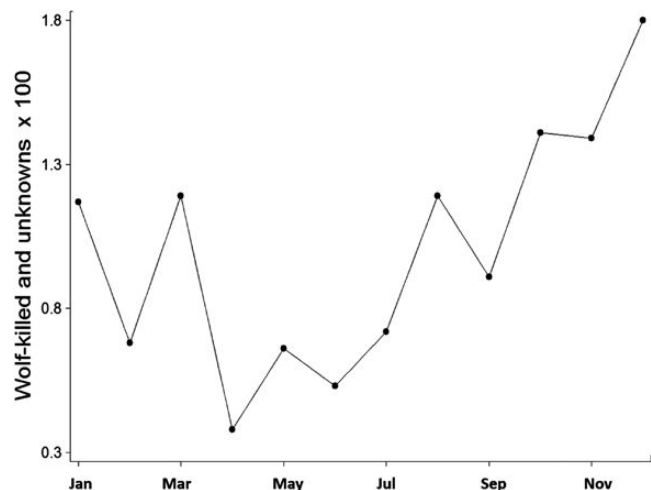


Fig. 2.—Monthly rate of wolf-killed wolves (*Canis lupus*) combined with all cause-of-death-unknown mortalities in the Superior National Forest of northeastern Minnesota, 1968–2014. The main denning season is April–June. Breeding season is approximately 63 days earlier (mainly February). Y-axis ratios are times 100.

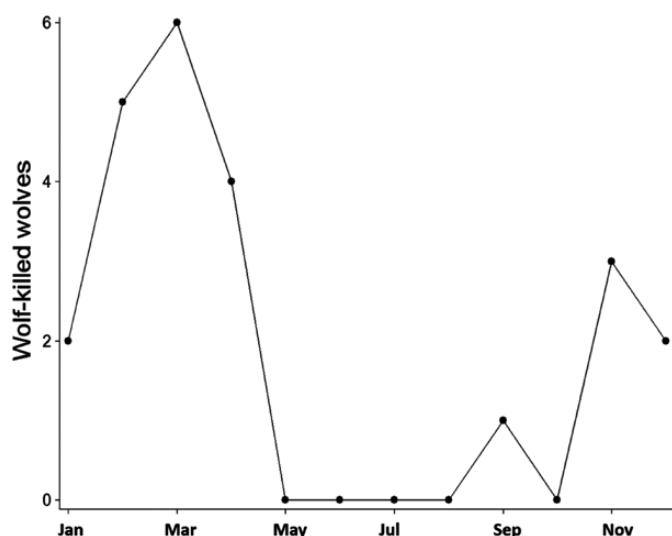


Fig. 3.—Monthly number of wolf-killed wolves (*Canis lupus*) in Denali National Park, 1986–1993. The main denning season is May–July. Breeding season is approximately 63 days earlier (mainly March).

Utah State University, pers. comm.). Nineteen summers were from 3 packs in Denali.

The annual rate of wolf-killed or probable wolf-killed wolves in the SNF during 1968–2014 was not linearly related to our annual wolf density the same year ($P = 0.74$) or the previous year ($P = 0.69$).

DISCUSSION

Although our data from throughout the year included a total of 51 wolf-killed wolf mortalities, our monthly samples were small enough that sampling error could weaken conclusions about any specific month. However, the general seasonal trend should be less subject to sampling error.

Our data and the literature accord with the YNP findings that general wolf aggressiveness (as indexed by wolf–wolf mortalities) increases as the breeding season approaches and diminishes after it (Smith et al. 2015a:figure 1) and that wolf-killed mortalities of adults are “concentrated in the few months before and after the breeding season” (Mech and Boitani 2003:28). Our raw data support those conclusions, as do our normalized data (monthly rates of wolf-killed wolves). In addition, the seasonal distribution of wolves dying of unknown causes at SNF (Table 1; Fig. 2) also assures that our lack of wolf-killed wolves during denning season did not result from seasonal biases in effort (Smith et al. 2015a) or failure to determine cause of death due to, for example, more rapid decomposition during wet spring months. These findings about seasonality of aggression are similar to those for coyotes (*Canis latrans*), except that coyotes usually do not kill each other (Gese 2001). Other large carnivores, including pumas (*Puma concolor*) and African hunting dogs (*Lycaon pictus*), do kill adult conspecifics (Creel and Creel 1998; Quigley and Hornocker 2010). However, we could find no information about the seasonality of such mortality.

Seasonality of wolf intraspecific mortality in the SNF may broadly correlate with periods of peak dispersal (February to April and October–November—Gese and Mech 1991). Thus, some intraspecific mortality could be a function of more unrelated wolves afield. If so, we would expect more dispersing wolves to be killed during these periods than breeding wolves because dispersers would be trespassing through defended territories. We did not assess individual pack status of wolves killed in the SNF. In YNP, no radiocollared pups were killed by wolves, and dominant wolves or breeders were killed most often (53%) among the radiocollared sample (Smith et al. 2015a:1177). However, “‘maturing or mature’ wolves were not killed more than their availability” (Smith et al. 2015a:1181).

Our findings differ in 2 respects from findings at YNP. First, we did not detect a spike in wolf–wolf killings of adults during the denning season (but note that the April spike in YNP is dependent on only 2 more wolf-killed wolves than in February and March—Smith et al. 2015a). Some of the wolf–wolf killing during March at SNF could have been during the denning season although, other than 1 mating observed in late January, we have no evidence of denning in our area in March (other wolf populations in Minnesota do—Fritts and Mech 1981; Fuller 1989a). Second, the decline in intraspecific mortality at SNF from December to January and low rate in February is perplexing if breeding competition is a driving mechanism behind intraspecific mortality. That could be due to sampling error, or it may be that it is most efficient to kill potential competitive breeders in the months leading up to the breeding season and to focus on breeding (rather than on killing) during the main breeding season. If it was sampling error, that could explain why this pattern was not detected in either Denali or YNP.

The main difference, then, involves the YNP wolves killing other adult wolves during April and May, 6 kills associated with den attacks, including infanticide in 4, plus 2 other kills (Smith et al. 2015a:figure 1). Although the literature documents several cases of unfamiliar wolves being chased from near dens

Table 2.—Monthly distribution of wolf-killed wolves (*Canis lupus*) in miscellaneous reports.

Month	No.	Location	Dates	Reference
January	1	W. Canada	1943–1946	Cowan (1947) ^a
June	1	Alaska		Mahrenke (1971)
January	1	Minnesota	1969–1972	Van Ballenberghe and Erickson (1973)
January	1	Minnesota	1972–1975	Fritts and Mech (1981) ^b
March	3	Minnesota	1972–1975	Fritts and Mech (1981) ^b
October– December	9	Minnesota	1990–1986	Fuller (1989b) ^b
February	1	Alberta	1978–1981	Carbyn et al. (1993)
July ^c	1	N. Canada	1986–2010 ^d	Mech (1993)

^aBadly wounded; then shot.^bBased on year-around radiomonitoring.^c1992. Year given in Mech (1993) was erroneous.^dJuly and August only.**Table 3.**—Numbers of wolf-killed and probable or possible wolf-killed wolves (*Canis lupus*) of various ages in the Superior National Forest, 1968–2014.

Age at death (years)	Number killed			
	Known age	Known minimum age	Estimated age	Total
Pup	1	0	0	1
1	2	8	1	11
2	2	10	0	12
3	0	4	2	6
4	2	3	3	8
5	0	1	1	2
6	1	0	0	1
7	0	1	1	2
8	1	0	2	3
9	0	1	1	2
10	0	0	1	1
11	1	0	1	2

or rendezvous sites (Table 3), there is only 1 other documentation of possible infanticide by wolves (Latham and Boutin 2011) and 2 unpublished records mentioned above. The great difficulty and low probability of observing wolf raids on other packs' dens and the lack of young pups radiocollared or otherwise tagged could explain why infanticide has been witnessed so rarely in wolves. Unless older wolves are killed at or near den sites, infanticidal attacks would be nearly impossible to detect in the wild, especially in dense forests.

In contrast, discovery of adult wolf mortality during denning seasons, if it occurs very often, should be discernible. Much radiomonitoring of wolves has been conducted, for example, 200 packs for 2–8 years in Alaska and Yukon through 1990 (Stephenson et al. 1995) and 795 wolf-months in the SNF during April, 752 in May, and 757 in June (Table 1). Thus, if wolf–wolf killing of adults during April through June were common, more cases should have been found. It might be difficult to detect such cases because of differences in study design, study sites, monitoring intensity, or wolf population characteristics. In YNP, only 1 adult was killed at a den in April; the rest associated with den raids were found up to several kilometers away. Only through intense monitoring were the deaths known to be associated with a den raid (K. A. Cassidy, Yellowstone Center

for Resources, pers. comm.). Still, in both the SNF (Table 1) and Denali (Mech et al. 1998), fewer, rather than more, deaths from any cause generally occurred during denning months and mid-late summer.

Possible explanations for the larger number of wolf–wolf deaths of adults associated with den attacks in YNP compared to elsewhere include: 1) greater competition for prey, 2) higher wolf density, 3) closer den proximity, 4) habitat differences at den sites (Sazatornil et al. 2016), 5) larger packs, 6) disparity in denning times for adjacent packs (K. A. Cassidy, Yellowstone Center for Resources, pers. comm.), and 7) greater genetic disparity among the founding wolf population (Mech, in Reid 2016).

Competition for prey can be ruled out for at least the first 3 cases around dens because the prey biomass was the highest of any of more than 30 previous wolf-prey systems studied (Mech and Barber-Meyer 2015).

Evidence for high wolf density being an explanation is equivocal. Against it is our SNF finding of no linear relationship between rate of wolf-killed wolves and wolf density, at least with densities up to 47/100 km². Four of the 6 April–May raids in YNP occurred when wolf densities were some of their lowest, both where the killings occurred and in the entire park (20–40/1,000 km² and 4–11/1,000 km², respectively), and the prey biomass highest (Smith et al. 2015a, 2015b). Wolf densities at the time of these raids were similar to those in the SNF (above), although higher than at Denali (Mech et al. 1998). Additional evidence are the reports of wolf–wolf killings (1/20 radiocollared wolves) in colonizing populations at low densities of 10–30 wolves/1,000 km² (Fritts and Mech 1981; Wydeven et al. 1995). On the other hand, wolf–wolf aggression and wolf mortality (from all causes) at YNP increased when wolf density exceeded 55–60 wolves/1,000 km² (Cubaynes et al. 2014).

Close dens in YNP might explain the den raids and April–May wolf–wolf killings of adults. However, some dens in SNF are as close as 6.5 km apart, less than an hour's wolf travel time between them. In addition, during 3 years when 4 pairs of dens at SNF (75% of packs generally monitored, $n = 8/12$) were only 6.5–8.0 km apart (mean 7.74 km), our annual rate of wolf–wolf killings (0.0035) was below the annual average (0.0048) for our study area. This observation does not disprove

Table 4.—Summary of reported observations of active wolf (*Canis lupus*) dens or rendezvous sites and intraspecific strife (apart from data in this article or in [Smith et al. 2015a](#)).

Pack years of observation	Hours of observation	Intraspecific strife near den or rendezvous site	Area	Reference
2	≥ 195	Unknown wolf chased from den area, May	Denali Park, Alaska	Murie (1944)
19	1,590	3 packs; no den attack ^a	Denali Park, Alaska	Haber (1977)
7	≥ 1,180	Breeding female chased female of unknown pair at den but socialized with male ^b	Baffin Island, Canada	Clark (1971)
10	3,500	Breeding female and daughter chased 2–4 unknown wolves when 0.5 km from den, July	Ellesmere Island, Canada	Mech, unpublished
		Breeding pair chased unknown wolf duo ^c when 0.5 km from den, July	Ellesmere Island, Canada	Mech, unpublished
		Possible adult kill	Algonquin Park, Canada	Theberge (1998)

^a15 cases of interpack aggression, January–April (May–July is denning season in Denali).

^bSuggests this male was related to the breeding female.

^cConsidered immature or nonresident wolves because no scent-marking for several miles.

the den-proximity hypothesis but fails to support it. Also of note, differences in habitats may make dens at SNF (generally denser forest cover and understory) more secure than dens at YNP (potentially more exposed—[Sazatornil et al. 2016](#)).

Yellowstone has hosted some uncommonly large wolf packs ([Barber-Meyer et al. 2016](#)), including the Druid Peak Pack of 37 wolves in 2001 ([Smith et al. 2002](#)). Such large packs might affect intraspecific strife because more nonbreeders would be available ([Ausband et al. 2016](#)) to visit other dens. Generally in spring, wolves at SNF and Denali tend not to travel as full packs but rather as singles or dyads ([Murie 1944](#); [Mech et al. 1998](#); [Demma et al. 2007](#); [Barber-Meyer and Mech 2015](#)). However, during the 5 den raids at YNP with sufficient information, several wolves from at least 1 of the interacting packs were present. With more wolves involved, more would be available to kill or be killed. Also, it may be that with generally smaller packs than YNP ([Barber-Meyer et al. 2016](#)), breeding females at SNF forage away from dens, so are more often absent during a den raid. Additional research would be needed to confirm if this is the case. Wolves at YNP also might travel in larger groups in April, at least compared to the SNF, because they primarily hunt riskier prey ([Barber-Meyer et al. 2016](#)). The main prey in YNP are elk (*Cervus canadensis*) and bison (*Bison bison*), and the optimum success of wolves killing elk is with at least 3–4 wolves ([MacNulty et al. 2012](#)) and for capturing bison about 11 wolves ([MacNulty et al. 2014](#)).

Genetic disparity of the YNP wolf founders also might be a cause of some of the wolf-den raids. Most recolonizing wolf populations proliferate via dispersers from existing populations ([Fritts and Mech 1981](#); [Ream et al. 1991](#); [Wydeven et al. 1995](#)), so most extant populations include related packs ([Lehman et al. 1992](#)). However, the YNP wolf population was reintroduced with wolves from 3 populations, primarily from British Columbia and Alberta some 370 km apart ([Bangs et al. 1998](#)), so were probably distantly related. Den attacks 1 and 2 ([Smith et al. 2015a](#)) both involved British Columbian wolves killing Albertan wolves.

However, wolves also sometimes kill close relatives, with at least 1 record in YNP ([McIntyre and Smith 2000](#)) and others from Isle Royale, where most wolves are highly related ([Peterson and Page 1988](#); [Raikonen et al. 2009](#)). Furthermore, if genetic

disparity were an important cause of wolf strife, wolf aggression would be greatest immediately after wolves were reintroduced (March 1996 to March 1998), but only 2 conflicts were recorded then (K. A. Cassidy, Yellowstone Center for Resources, pers. comm.). Genetic disparity may be more important to wolf aggression when there is greater competition for resources, but such disparities might become trivial because of possible mixing over time, and in YNP the greatest genetic disparity occurred when wolf densities were lowest and prey densities highest. Thus, genetic differences as a cause for wolves killing adult wolves during denning season remains a hypothesis best tested with long-term pedigree data that can address confounding factors.

All the den raids at YNP involved a pack not yet denning attacking a denning pack ([Smith et al. 2015a](#)). In attack 1, the British Columbian pack did not den that year, but in all the other attacks the attacking pack denned later than the attacked pack. This disparity in times of denning might be attributable to the different sources of wolves reintroduced to YNP, for the breeding (and thus whelping) season is later for wolves of higher latitude ([Mech 2002](#)). The YNP wolves from British Columbia (56°N) in the [Smith et al. \(2015a\)](#) den attack 2 denned 7–16 days later than the pack from Alberta (53°N) that they attacked. The dominant female in den attack 3 was a descendent of British Columbian wolves and denned 14 days later than the Albertan pack that her pack attacked.

All the above explanations for why wolf raids on denning wolves including infanticide and killing of adults occurred in YNP but were rarely reported elsewhere are speculative. The hypothesis with the most support is the disparity in denning dates between attacking wolves and those attacked ([Smith et al. 2015a:1181](#); K. A. Cassidy, Yellowstone Center for Resources, pers. comm.). Attempts to determine the adaptive value of intraspecific strife among adult wolves should consider that most wolf–wolf killing of adults appears to occur in fall through late winter, with the notable exception of April in YNP (Figs. 1 and 3; [Smith et al. 2015a:figure 1](#)).

Because the monthly samples from SNF, Denali, and YNP are small, and the months of wolf whelping vary among the areas ([Mech 2002](#)), care must be taken in comparing data for individual months across study areas. Nevertheless, data from all 3 areas accord that wolf–wolf killings of adults generally increase during some part of the fall and decrease again during summer, with less

clear trends during other times of the year. The greatest decreases in the SNF are from December to January (an unexpected decline immediately prior to the main breeding season in February) and from March to April (a decline during the main onset of denning) that could be real or could be due to sampling error. In Denali, the largest decline is after April, right after the breeding season (March). In YNP, wolf aggression also spiked during the breeding season, based on a large sample (121) of pack–pack aggressions (Cassidy et al. 2015), and when the spring killings associated with den attacks were removed, aggressive interactions each month and wolf–wolf killings of adults were weakly correlated ($R^2 = 0.31$, $P = 0.07$ —Smith et al. 2015a).

Monthly variations notwithstanding, the seasonal trend in wolf–wolf killings of adults in SNF generally (except February which could be due to sampling error) parallels that of interpack aggression (Smith et al. 2015a), testosterone levels in both males (Asa et al. 1986) and females (Asa et al. 1990), scent-marking (Peters and Mech 1975), and howling (McIntyre et al. 2017), all of which tend to peak around the breeding season. Similarly, wolf–wolf killings of adults in YNP generally track these trends except for April. Although males are more aggressive and are especially important to winning interpack fights (Cassidy et al. 2015, 2016, 2017), similar numbers of both sexes were killed by conspecifics in the SNF and Denali. That testosterone and aggression peak around the breeding season accords with our findings and those of Mech and Boitani (2003) that wolf–wolf killings of adults generally are concentrated around the breeding season. The low number of wolf–wolf killings at SNF during February and the steep decline from December to January, if not due to sampling error, would tend to contradict this (Fig. 1).

In summary, our results support the generalization that wolf–wolf killings of adults peak around the breeding season (Mech and Boitani 2003), paralleling and supporting the findings of Smith et al. (2015a) at YNP except for the additional spike of wolf–wolf killings of adults in April. Our results do not refute the hypothesis of Smith et al. (2015a) that infanticide may be one of the driving forces behind wolf territoriality. How common these raids and infanticides are across other wolf populations remains to be determined. Unless adults, especially collared animals, are killed at the site, such raids are difficult to document. Rather than being unique, YNP may simply be a highly observable representative of this phenomenon.

Wolves are extremely competitive even within litters and with close relatives, and kill other wolves of every age year-around. Such intraspecific strife is common among territorial mammals (references in Cassidy et al. 2015) and could function not just as territorial defense, as indicated by the locations of adult killings along and outside territory edges (Mech 1994; Mech et al. 1998), but also as genetic and breeding competition and competition for resources. These findings support the view that “. . . intraspecific strife primarily represents territorial competition that reduces competing breeders and increases opportunities for packs to expand their territories, while indirectly tending to hold each pack in its territory” (Mech and Boitani 2003:28).

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