Brief Communication

Influence of wolf predation on population momentum of the Nushagak Peninsula caribou herd, southwestern Alaska

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Abstract: We investigated wolf predation as a potential driver of population change in the Nushagak Peninsula caribou herd, southwestern Alaska. We investigated the time budgets of three wolf packs using the peninsula from 2007 through 2012, and thus potentially preying on caribou there, in order to make inferences on their likelihood of serving as an important population modifier for the Nushagak Peninsula caribou herd. We found that only one pack regularly used the peninsula. The pack using the peninsula spent an average of 35% of its time there. Its use of the peninsula was disproportionately high in late summer and fall, disproportionately low in winter, and proportional during the caribou calving season in early summer. Overall wolf use of the Nushagak Peninsula increased in direct response to increasing caribou abundance but was not a primary population driver.

Key words: *Canis lupus*; caribou; predation; predator control; *Rangifer tarandus*; wolf.

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Introduction

The Nushagak Peninsula caribou (*Rangifer tarandus*) herd (NPCH) was established by relocating caribou to the Nushagak Peninsula (NP) from the Alaska Peninsula in 1988 after an absence of >100 years (Hinkes & Van Daele, 1996). The NPCH has been non-migratory since establishment. The population increased from an initial stocking of 146 to a peak of ~1,400 in 1997, then declined to ~500 in 2007, at which time this study began (Aderman, 2013).

There are a number of potential causal or contributing factors to this population decline, including predation by wolves (*Canis lupus*). This possibility was regularly voiced by state and federal citizen wildlife advisory groups, and predator control was often suggested as a solution to the population decline. It is reasonable to hypothesize that wolf predation drove the caribou population decline, as wolf predation has been described by many investigators as the leading source of caribou mortality, and it is commonly suspected in population declines (McLoughlin *et al.,* 2003; Jenkins & Barten, 2005; Farnell & McDonald, 1988; Gunn *et al.,* 2006; Kojola *et al.,* 2004; Hayes *et al.,* 2003). However, in many cases where wolf predation was suspected as a driver of population declines, evidence was lacking (e.g., Hayes *et al.,* 2003; Boertje *et al.,* 2017).

We undertook this study in response to the concerns of the role that wolves play in modifying NPCH population size. Specifically, our objectives were 1) determine the number and composition of wolf packs which preyed on the NPCH herd, 2) determine the seasonality and proportion of time throughout the year that wolves spent in potential contact with the NPCH, and 3) relate wolf use of the NP to NPCH population change.

Study area

The study area covered the likely ranges of wolves that have the potential to prey on the NPCH. This area included the NP, plus the headlands of the NP to a distance of approximately 50 km (Fig. 1). The area occurs within the Togiak National Wildlife Refuge and Alaska Game Management Unit 17. The NP, located at approximately 58.6° N latitude, 159.0° W longitude, is a ~24 km wide peninsula of treeless lowland tundra extending approximately ~55 km into Bristol Bay of the Bering Sea. Plant communities include a mixture of graminoid-dominated wetlands and dwarf shrub heath and lichen communities.

The headlands of the NP include a greater variety of landforms, including the southern extent of the Ahklun Mountains, which is composed of rolling hills up to mountains of 1,000 m elevation. The mountainous terrain is primarily vegetated with dwarf shrub plant communities above alder (*Alnus*) slopes at the bases. Lake shore and riparian corridors include mixtures of willow (*Salix*)-dominated tall shrub communities and deciduous forests. Approximately 20% of the NP headlands is forested with white spruce (*Picea glauca*). These communities provide habitat to moose (*Alces alces*). In March 2006, a total-count population estimate found a minimum of 165 moose in the NP headlands (Togiak Refuge, unpublished data). Brown bears (*Ursus arctos*) are common throughout all portions of the study area. Brown bear population density for Togiak Refuge in its entirety, including the NP, was estimated in 2003-2004 to be 40.4 bears/1,000 km^2, 95% CI = 34.4-54.5 (Walsh *et al.*, 2010).

The study area climate is sub-arctic maritime. Temperatures range from average daily low and high of -11.7 and -5.8 ° C in January, the coldest month, to 9.2 and 15.8° C in July, the warmest month at the nearest weather station, Dillingham, Alaska (climate data averaged 1981-2010, National Oceanic and Atmospheric Administration, 2018). Annual precipitation averages 65.5 cm and snowfall averages 208 cm. There are no roads or human infrastructure within the study area with the exception of the village of Manokotak, a community of approximately 500 individuals located on the Igushik River north of the NP, and a commercial fishing camp used during the summer at the outlet of the Igushik River. The majority of human activities in the study area consist of subsistence hunting and fishing, and access is provided primarily by snowmobile in winter.

Methods

Wolves were captured during spring and fall by darting from helicopters with doses of 572 mg of Telazol dissolved in 2.6 ml of sterile water and delivered with 3 cc Palmer™ darts with 1.9 cm barbed needles. Wolves were sexed, weighed, and aged by tooth wear (Gipson *et al.*, 2000). Wolves were instrumented with either conventional VHF radio collars (Lotek™ model LMRT-3 VHF radio collar with mortality sensor) or remote-downloadable GPS collars (Lotek™ model GPS4400S collar with mortality sensor). Animal care and hand-

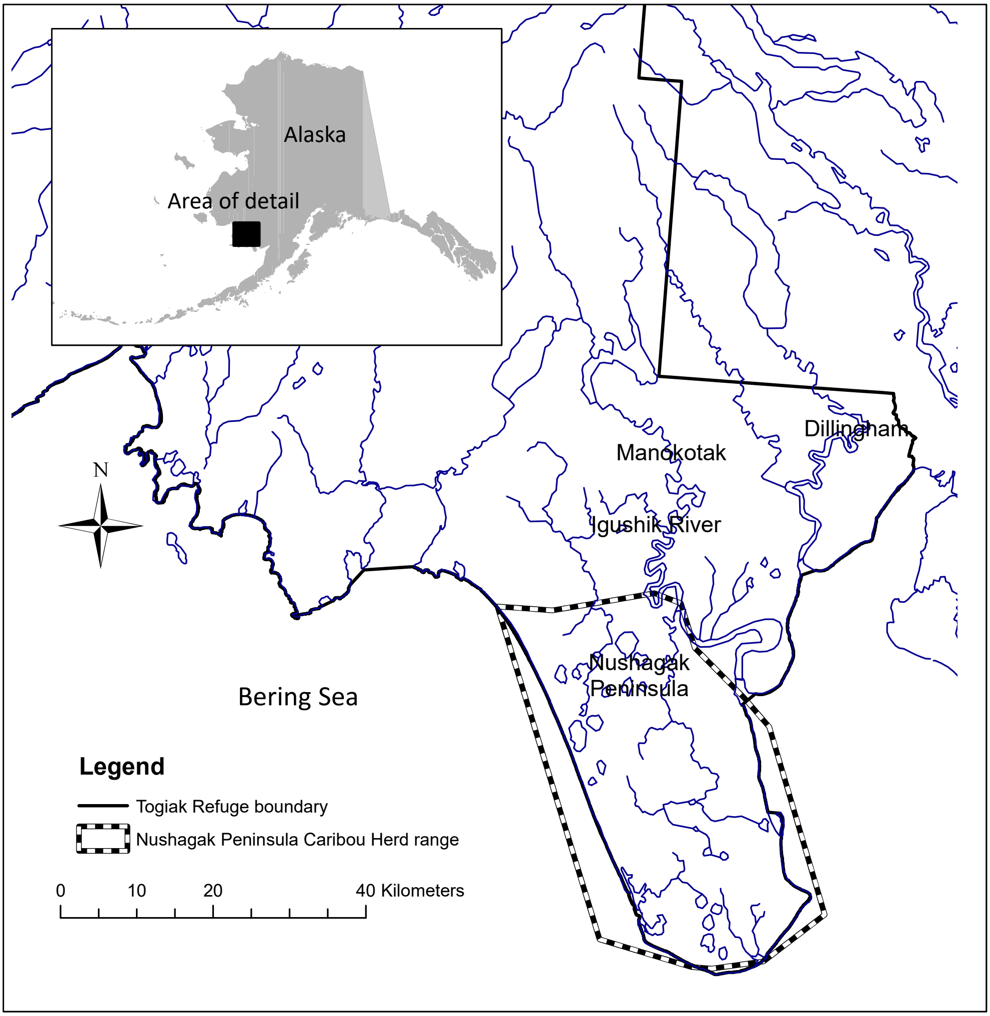

Figure 1. Study area, including Nushagak Peninsula plus adjacent headlands to a distance of approximately 50km, Togiak National Wildlife Refuge, southwestern Alaska.

ling was consistent with the Animal Welfare Act as Amended, 7 USC, 2131-2156 under Alaska Department of Fish and Game Animal Care and Use Committee Assurance 07-04.

GPS collars collected locations every three hours throughout the year. Conventional collars were re-located approximately once monthly during aerial surveys, at which time wolf locations were recorded, as well as activity, habitat, pack composition, and GPS collar location data were remotely downloaded. Spatial data were analyzed with ArcMap 10.1 (Environmental Systems Research Institute, 2012). We determined pup production by locating dens based on wolf telemetry data during May-June. Number of pups produced was determined through making visual observations from ground blinds near den locations during July, and aerial surveys during August.

Because the NPCH did not migrate from the NP, we assumed that when wolves were away from the NP, there was minimal wolf predation potential, and that when wolves were present on the NP, they were likely preying upon caribou. (This necessary oversimplification has the potential to overestimate the reliance of wolves on caribou in this system, and thus we make no assumptions on other wolf diet components while on the NP.) As such, wolf time budget within and out of potential contact with NPCH was determined by calculating the proportion of wolf locations, by season, within and outside the herd range (HR) of the NPCH. The HR was geographically determined by delineating the distribution of 95% of 7,012 caribou locations (Fig. 1) collected monthly 1988—2007 during radio telemetry flights (Aderman, 2013). Wolf peninsula-days were defined as any day in which at least one wolf location occurred within the HR. Seasons were defined as Winter: 1 December – 15 May; Early Denning/Caribou Calving: 16 May – 30 June; Late Denning: 1 July – 15 August; Late Summer: 16 August – 15 September; and Fall (caribou rut/post rut): 16 September – 30 November. A chi-square goodness-of-fit test was used to determine whether there was a significant difference in the expected and observed times that wolves occurred in the HR, based on time per season. If significant differences were found, Bonferroni family of confidence intervals was used to determine which seasons were different (Byers *et al.*, 1984). An index to the potential level of wolf predation on NPCH was developed by calculating wolf peninsula-days per season as:

$$PD_{wolf} = N_{wolf} * (P_{cw} * D)$$

where N_{wolf} was the number of wolves in packs using the HR in a given season, P_{cw} was proportion of time that radio collared members of these packs used the NP, and D was the number of days in the season. Annual indices were calculated by summing the seasonal numbers of wolf peninsula-days. We used linear regression to determine trends over time in annual and seasonal wolf use of the NP.

We estimated caribou population size approximately twice annually from small fixed-wing aircraft using transect-based minimum population counts in late winter and by photograph counts taken after post-calving aggregations in summer (Aderman, 2013). We estimated composition and calf production in most years in early October via helicopter surveys. We determined relationships between wolf occurrence in the HR and NPCH population size by regressing caribou population counts with total wolf peninsula-days. We regressed winter caribou counts with the sum of wolf peninsula-days in Fall and Winter seasons, and summer caribou counts with the sum of wolf peninsula-days in Early Denning, Late Denning, and Late Summer seasons.

Results

We captured a total of 20 individual wolves, for a total of 35 capture events, including recaptures to replace collars. Wolves were surveyed via 87 radiotracking flights, for a total of ~35,000 individual locations. Two packs were identified in spring 2007 when the study began. A third pack formed in 2008 when a young adult female from one of the packs dispersed to an area at the border of the existing pack territories, found a mate, and established a pack territory. No additional packs were found within the study area. Of the three wolf packs, only one (referred to as the Ualik Lake Pack) used the NP, and so is used as the basis for measuring the effects of wolf predation on the NPCH.

Known pack size in the Ualik Lake Pack varied from 5-15 individuals, and averaged 12 in Fall. Pack sizes were highest in spring, after pups were produced, and lowest in winter, when mortality and dispersion reduced numbers. It is possible that the 2007 count of five was an underestimate, as this was based on a single observation, while all subsequent counts were based on multiple observations during telemetry survey flights.

NP use was not proportional seasonally (Fig.

Table 1. Simultaneous confidence intervals for wolf seasonal use of the Nushagak Peninsula, Togiak National Wildlife Refuge, southwestern Alaska, 2007 – 2012. Time spent on the Nushagak Peninsula was significantly ($P < 0.01$) higher than expected in Late Denning, Late Summer, and Fall, lower than expected in Winter, and proportional in the Early Denning season.

Season	Expected proportion of time	Actual proportion of time P_i	Bonferroni intervals for P_i		Direction of difference
			Lower limit	Upper limit	
Winter	0.455	0.139	0.138	0.139	Lower
Early denning	0.126	0.126	0.125	0.127	As expected
Late denning	0.126	0.234	0.234	0.235	Higher
Late summer	0.085	0.174	0.174	0.175	Higher
Fall	0.208	0.327	0.326	0.327	Higher

2, Table S1). Wolves spent 11% of their time on the NP during Winter, and 70% of their time there in Late Summer. During the Early Denning/Caribou Calving season, wolves used the NP 32% of the time.

Our seasonal division of the year was not equal, with Winter totaling 45% of the year (166 d), while Late Summer only accounting for 8% of the year (31 d). Accounting for this unequal season length, the time that wolves spent on the NP was not proportional to the amount of time per season ($X^2 = 767.4$, d.f. = 4, $P < 0.001$). Use of the NP in Winter was significantly lower ($P < 0.01$) than expected, while time on the NP in Late Denning, Late Summer, and Fall seasons was significantly higher ($P < 0.01$) than expected (Table 1, Fig. 2). Use of the NP was proportional to its availability

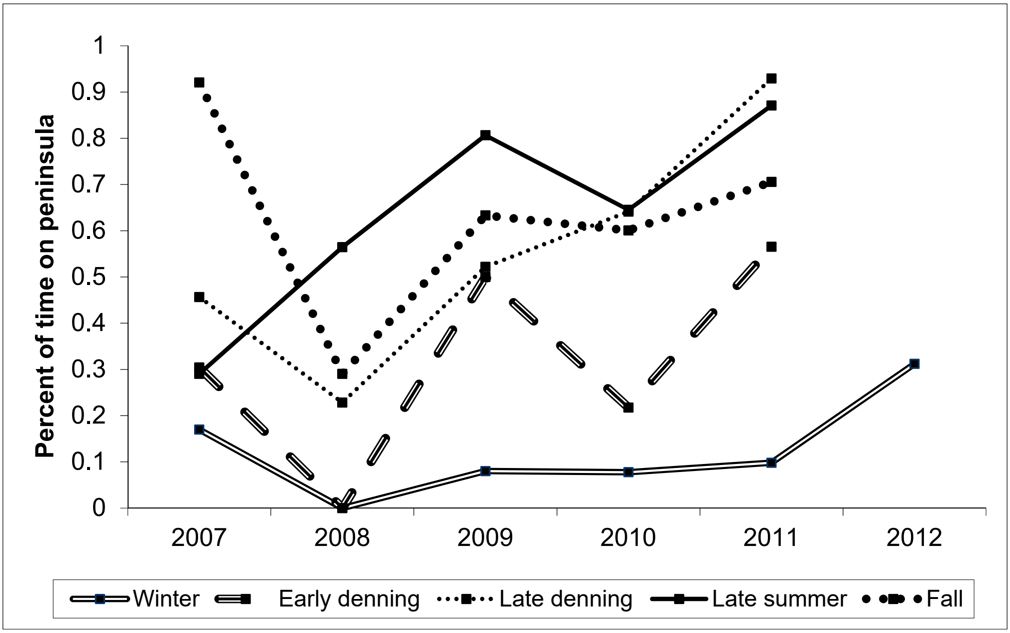

Figure 2. Proportion of time by season from 2007 – 2012 that Ualik Lake Pack wolves occurred on the Nushagak Peninsula, Togiak National Wildlife Refuge, southwestern Alaska.

in the Early Denning/Caribou Calving season only. Thus, wolves avoided the NP in winter (perhaps to avoid hunters on snowmobiles), preferred it during mid-summer through fall, and used both it and the headlands to the north proportionately during caribou calving seasons. During the course of this study, we incidentally observed wolves preying on or eating a total of 11 caribou and 23 moose. All depredated caribou were on the NP, and all moose were off.

Wolf use of the NP was not constant over time. There was an increasing trend over the course of the study (r^2 = 0.64, P = 0.005, Fig. 3). Simultaneously, caribou population estimates during the course of this study reversed the trajectory of the preceding decade and demonstrated a clear increasing trend (r^2 = 0.91, $P < 0.001$, Fig. 3). There was a significant positive correlation between wolf use of the NP and caribou population size (r^2 = 0.743, $P < 0.003$, Fig. 3).

Discussion

Correlative studies such as ours are not cause-effect experiments; as such, it can be difficult to discern the independent from the response variable. However, logic argues that increased wolf use of the NP should not have caused the caribou population to rise, but conversely, it is reasonable to believe that the rising caribou population caused wolves to spend more time capitalizing on a more productive food source. If so, caribou abundance likely drove wolf prey selection, and thus demonstrated a bottom-up, functional response rather than top-down predator-prey relationship.

Understanding the relationship between wolves and caribou on the NP is complicated by the presence of moose within the range of the wolves. In some cases, having an alternative prey source results in wolf predation depressing and maintaining caribou population levels at low levels (Seip, 1991), particularly in non-migratory caribou populations. However, in this case, the presence of moose may have moderated the predation effects on NPCH. Wolves did not spend a disproportionately high amount of time on the NP during the caribou calving season, assumedly because they were equally focused on moose calving (which was concurrent with caribou calving), when viewed across all years. However, there

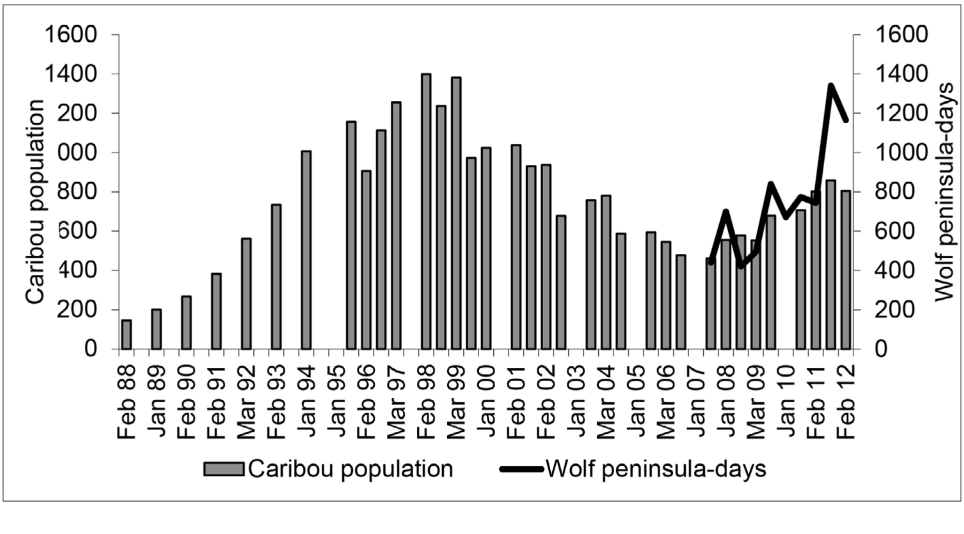

Figure 3. Nushagak Peninsula caribou herd population estimates, 1988-2012, and total estimated time spent by wolves on the Nushagak Peninsula, 2007-2012, Togiak National Wildlife Refuge, southwestern Alaska.

was an increase in the proportion of time that wolves spent on the NP during caribou calving season over the course of this study; likely a response to increasingly abundant caribou calves. We suspect that the reason that wolf use of the NP was disproportionately high during late summer and fall is that they were focused on preying on bull caribou then. Mech et al. (1998) found that bull caribou was the predominant prey type taken by wolves in Denali National Park August through October. They attributed this to bull caribou being in poor nutritional condition and often injured during and after the rut. During the course of this study, we incidentally observed wolves preying on or eating a total of 11 caribou, including five bulls (45%), three cows (27%), one calf (9%), and two undetermined (18%). All bull mortalities were observed during Fall. However, cow mortality did not follow this same pattern. During the course of a radio telemetry study of NP adult caribou cows, a total of 60 natural (not related to human hunting) mortalities were observed from 1990 through 2013 (Aderman, 2013). There were no seasonal differences in mortality rate of adult female caribou ($X2 = 7.75$, d.f. = 4, $P > 0.1$) for this entire period of time, nor were there seasonal differences during just the time period of the current study ($X2 = 5.94$, d.f. = 4, $P > 0.1$).

It is thought that high caribou population density is not possible with wolf predation unless 1) the caribou population has much greater productivity than the wolf population, or 2) wolf predation is limited by factors other than availability of caribou, such as disease, wolf control, or availability of other prey species, or 3) caribou have an effective wolf avoidance strategy, such as use of escape terrain or migrations (Seip, 1995). In the case of NPCH, increasing population density was possible despite wolf predation due to all three of these reasons, but, we suspect, especially the second. A primary limit to wolf predation is the geography of the NP. Approximately 75% of the NP is bordered by the ocean, a barrier to access by wolves. The ~25% of the NP border adjacent to the mainland is <40km wide, a sufficiently narrow entrance point that it could be effectively defended against other wolf access by the Ualik Lake Pack. The Ualik Lake Pack was relatively large and relatively stable in number throughout the five years of this study, and may have served as a formidable shield against incursions by other established packs and by lone wolves. The pack also spent an increasing amount of time in contact with the caribou population as the caribou population grew, thus increasing both its level of predation and protection of the caribou from outside predation.

The principal reason for conducting this study was to address whether wolf population control was necessary to address the population decline in the NPCH. Had predator control been instituted at the onset of this study as requested by local management committees, it is reasonable to believe that the caribou population would have increased as it did, and it is also reasonable to believe that an incorrect conclusion would have been reached that wolf control was the casual reason for the caribou population response. Thus, this case illustrates the importance of careful thought and sufficient data on both ungulates and predators before undertaking predator control operations.

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Supplemental materials Table 1. Wolf peninsula-days by season on and off Nushagak Peninsula, Togiak National Wildlife Refuge, southwestern Alaska, from 2007 through 2012.

Wolf peninsula-days													
		Winter 1 Dec-15 May		Early denning/ caribou calving 16 May-30 Jun		Late denning 1 Jul-15 Aug		Late summer 16 Aug-15 Sep		Fall 16 Sep - 30 Nov		Total year	
Year	Wolf	On	Off	On	Off	On	Off	On	Off	On	Off	On	Off
2007	W0703	9	44	14	32	21	25	9	22	58	5	111	128
2008	W0702									2	66	2	66
	W0703	0	37	0	33					25	42	25	112
	W0801	0	36	0	46	21	25	18	13	24	52	63	172
	W0802	0	36	0	46	0	46	17	14	29	9	46	151
	W0803	0	15							12	56	12	71
2009	W0702	0	12									0	12
	W0703	16	150	36	10	34	12	27	4	53	23	166	199
	W0801	13	153	10	36	14	32	23	8	57	19	117	248
	W0803	11	145									11	145
	W0905									16	31	16	31
2010	W0703	13	153	24	22	36	10	25	6	42	34	140	225
	W0801	13	153	3	43	18	28	19	12	41	35	94	271
	W0905	0	80									0	80
	W1003	4	35	0	46	38	8	27	4	40	0	109	93
	W1004	8	31	13	33	26	20	9	22	38	38	94	144
2011	W0703	12	154	22	24	43	3	26	5	19	14	122	200
	W0801	13	153	8	38	36	10	23	8	16	16	96	225
	W1004	25	141	46	0	46	0	31	0	32	0	180	141
	W1102	4	49	28	18	46	0	28	3	24	8	130	78
2012	W0703	2	54									2	54
	W0801	3	105									3	105
	W1004	78	24									78	24
Total wolf days		224	1760	204	427	379	219	282	121	528	448	1617	2975
% time on Peninsula		0.11		0.32		0.63		0.70		0.54		0.35	