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Wolf (*Canis lupus*) Winter Density and Territory Size in a Low Biomass Moose (*Alces alces*) System

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ABSTRACT. We investigated the winter density and territory size of wolves (*Canis lupus*) on the Yukon Flats, Alaska, where moose (*Alces alces*) was the sole ungulate prey, occurring at a low density and representing a biomass of ungulate food lower than previously studied in North America. Using locations (GPS coordinates) from collars deployed on seven wolves, we estimated territory sizes with adaptive kernel and minimum convex polygon methods. We then estimated wolf density from a population area defined by these territory sizes and counts of wolves in five marked packs. From November 2009 to April 2010, we obtained 6263 GPS locations. Pack size ranged from two to 10 wolves, with average size of 5.0 in November 2009 and 4.8 in March 2010. Average winter territory size for the five packs was 1433 km^2 with the 95% adaptive kernel method and 1608 km^2 with the minimum convex polygon method. Density (wolves/1000 km^2) was 3.6 in November and 3.4 in March with the 95% adaptive kernel method and 3.4 in November and 3.3 in March with the minimum convex polygon method. Territories were large and estimates produced by the two methods differed by 11%. Densities were low, and the two analysis methods yielded densities that differed from each other by 3% to 6%. Low wolf density corresponded with low biomass of ungulate food, suggesting that moose availability on the Yukon Flats likely limited wolf density.

Key words: Alaska; biomass; density; GPS; moose (*Alces alces*); territory; wolf (*Canis lupus)*

RÉSUMÉ. Nous avons étudié la densité hivernale et la taille du territoire du loup (*Canis lupus*) aux Yukon Flats, en Alaska, où l'orignal (*Alces alces*) était la seule proie ongulée. Il s'y trouvait en faible densité et représentait une biomasse de nourriture ongulée inférieure à celle étudiée ailleurs en Amérique du Nord. Grâce aux positions (coordonnées de GPS) prélevées à partir de colliers posés sur sept loups, nous avons estimé la taille des territoires au moyen de la méthode d'estimation adaptative à noyaux et de la méthode du polygone convexe minimal. Ensuite, nous avons estimé la densité du loup à partir d'une zone de population définie par la taille de ces territoires et par les dénombrements de loups de cinq meutes marquées. De novembre 2009 à avril 2010, nous avons obtenu 6 263 positions GPS. La taille des meutes variait de deux à dix loups, pour une taille moyenne de 5,0 loups en novembre 2009 et de 4,8 en mars 2010. La taille moyenne du territoire hivernal de cinq meutes était de 1 433 km^2 dans le cas de la méthode adaptative à noyaux de 95 % et de 1 608 km^2 dans le cas de la méthode du polygone convexe minimal. La densité (loups/1000 km^2) était de 3,6 en novembre et de 3,4 en mars avec la méthode adaptative à noyaux de 95 %, puis de 3,4 en novembre et de 3,3 en mars avec la méthode du polygone convexe minimal. Les territoires étaient vastes et les estimations obtenues à l'aide des deux méthodes différaient de 11 %. Les densités étaient faibles, et les deux méthodes d'analyse ont donné des densités qui différaient l'une de l'autre dans une mesure 3 % à 6 %. La faible densité des loups correspondait à la faible biomasse de nourriture ongulée, ce qui laisse supposer que la disponibilité de l'orignal aux Yukon Flats limitait vraisemblablement la densité du loup.

Mots clés : Alaska; biomasse densité; GPS; orignal (*Alces alces*); territoire; loup (*Canis lupus)*

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INTRODUCTION

Wolves (*Canis lupus*) are efficient, coursing predators whose ability to maintain kill rates at the level needed to meet nutritional requirements allows them to persist down to low ungulate densities (0.11 moose/km^2) or biomass of food (0.66 ungulate biomass index, or UBI/km^2; Lake et al., 2013). Low ungulate biomass (< 4 UBI/km^2) can affect wolf populations in two ways. First, wolves may enlarge their territories (≥ 800 km^2; Hayes, 1995; Mech et al., 1998; Fuller et al., 2003; Burch et al., 2005) in order to ensure an adequate supply of vulnerable prey (Peterson, 1977). Second, wolf populations may become smaller (Fuller, 1989; Fuller et al., 2003; Cariappa et al., 2011; McRoberts and Mech, 2014). The combined effect is that wolf density (i.e., wolf numbers divided by area occupied) is lowest in systems of low ungulate biomass (Fuller et al., 2003; Cariappa et al., 2011; McRoberts and Mech, 2014). Examples of these

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systems include northern regions, such as parts of interior Alaska and Yukon, where densities of wolves are among the lowest in North America (2–4 wolves/1000 km^2; Gasaway et al., 1992; Messier, 1994; Fuller et al., 2003).

The most common method to assess wolf density in these regions is by aerial surveys: the number of wolves is determined by counting wolves or wolf tracks, and density is the total count divided by the area surveyed (Stephenson, 1978; Gasaway et al., 1992; Hayes and Harestad, 2000; ADFG, 2009; Keech et al., 2011). However, these surveys have limitations because wolf territory size is not known, and territories of packs on the periphery of the survey area may overlap its boundaries, thereby inflating density. Alternative methods use locations of packs and calculate density using the territory size rather than the areas surveyed (Fuller and Snow, 1988; Burch et al., 2005; Adams et al., 2008), but these methods are more costly and require frequent telemetry flights to obtain locations. Consequently, studies that use these methods take place less often in northern regions, and when they do, it is problematic to achieve a sampling intensity that will accurately estimate territory size (Mech et al., 1998; Burch et al., 2005; Adams et al., 2008). Ballard et al. (1998) recommended an average of 98 locations to describe 90% of a winter territory where territory sizes are large. Achieving this sampling intensity requires multiple weekly telemetry flights during the winter months, which is challenging in practice with very high frequency (VHF) collars (Mech et al., 1998; Burch et al., 2005; Adams et al., 2008). With the advent of global positioning system (GPS) collars, it has become straightforward to acquire location coordinates at regular intervals (Mills et al., 2006; Tomkiewicz et al., 2010) that greatly exceed the minimum sampling intensity recommendations of Ballard et al. (1998). Use of such technology provides the opportunity to estimate wolf density and territory size more accurately.

Another consideration for estimating wolf density and territory size is the method used to analyze the locations. Mills et al. (2006) compared the performance of the minimum convex polygon and adaptive kernel methods for estimating wolf territory size. Their study demonstrated that the adaptive kernel method was robust across a range of sampling intensities, but the minimum convex polygon method was not. Mills et al. (2006) concluded that the adaptive kernel method should be the standard for measuring animal home ranges. However, estimates of territory size from systems of low prey biomass in Alaska and Yukon were based on the minimum convex polygon method (Hayes, 1995; Mech et al., 1998; Burch et al., 2005) and in some instances may represent only general estimates (Mech et al., 1998).

We had the opportunity to study winter wolf density and territory size in a landscape where wolves persisted with less available biomass of ungulate food than had previously been documented (0.66 UBI/km^2; Fuller et al., 2003). Our goal was to use locations from GPS collars to estimate winter density and territory size and to compare these estimates with corresponding estimates from other systems with lower prey biomass. Secondarily, we contrasted estimates of territory size and density made using the minimum convex polygon method with estimates produced using the adaptive kernel method.

METHODS

Study Area

The Yukon Flats (Alaska Game Management Unit 25, Yukon Flats National Wildlife Refuge) is a broad, relatively flat region of eastern interior Alaska that spans the Arctic Circle, stretching approximately 325 km from west to east. It is situated between the White Mountains to the south and the Brooks Range to the north and is bisected by the Yukon River. The heterogeneous landscape of this region includes many wetlands, meadows of graminoids (*Arctagrostis* spp., *Beckmannia eruciformis*, *Bromus* spp., *Calamagrostis* spp., *Eriophorum* spp., *Glyceria* spp., *Hordeum jubatum*, *Poa glauca*, *Triglochin* spp.), sedges (*Carex* spp.), and floating mats of bog vegetation (*Menyanthes trifoliata*, *Potentilla palustris*, *Caltha palustris*, *Equisetum* spp.). Forest stands consist of black spruce (*Picea mariana*), white spruce (*P. glauca*), balsam poplar (*Populus balsamifera*), quaking aspen (*P. tremuloides*), and paper birch (*Betula papyrifera*). Shrub stands of willow (*Salix* spp.) and alder (*Alnus* sp.) are interspersed, particularly around riparian corridors. Upland habitats (91 to 912 m) are dominated by alder, willow, dwarf birch (*B. nana*), Labrador tea (*Ledum decumbens*), crowberry (*Empetrum nigrum*), and blueberry (*Vaccinium uliginosum*).

The major prey for wolves is moose, and moose densities had been low (< 0.2 moose/km^2) at least since the 1960s (Bentley, 1961; Gasaway et al., 1992; Bertram and Vivion, 2002; Caikoski, 2010; Lake et al., 2013). Density in a 2010 survey was 0.11 moose/km^2 (Lake et al., 2013). This density corresponded to an ungulate biomass index of 0.66 UBI/km^2, which reflected a conversion of moose density•6 (Fuller et al., 2003). A biomass conversion factor of 6 was applied to moose density to make results comparable with systems that contained multiple prey species at varying densities and body sizes, such as white-tailed deer (*Odocoileus virginianus*; conversion = 1) or bison (*Bison bison*; conversion = 8; Fuller et al., 2003). The resulting ungulate biomass index was more representative of food availability to wolf populations. Minor prey species for wolves during winter were beaver (*Castor canadensis*) and snowshoe hare (*Lepus americanus*; Lake et al., 2013). During summer, salmon (*Oncorhynchus* spp.) and ducks (Anatidae) and their eggs were present.

Black bear (*Ursus americanus*) densities were high (155 or more independent bears/1000 km^2) in a 2010 survey that covered 1373 km^2 (Caikoski, 2011). Grizzly bears *(Ursus arctos*) were also present and thought to be at low densities (Bertram and Vivion, 2002).

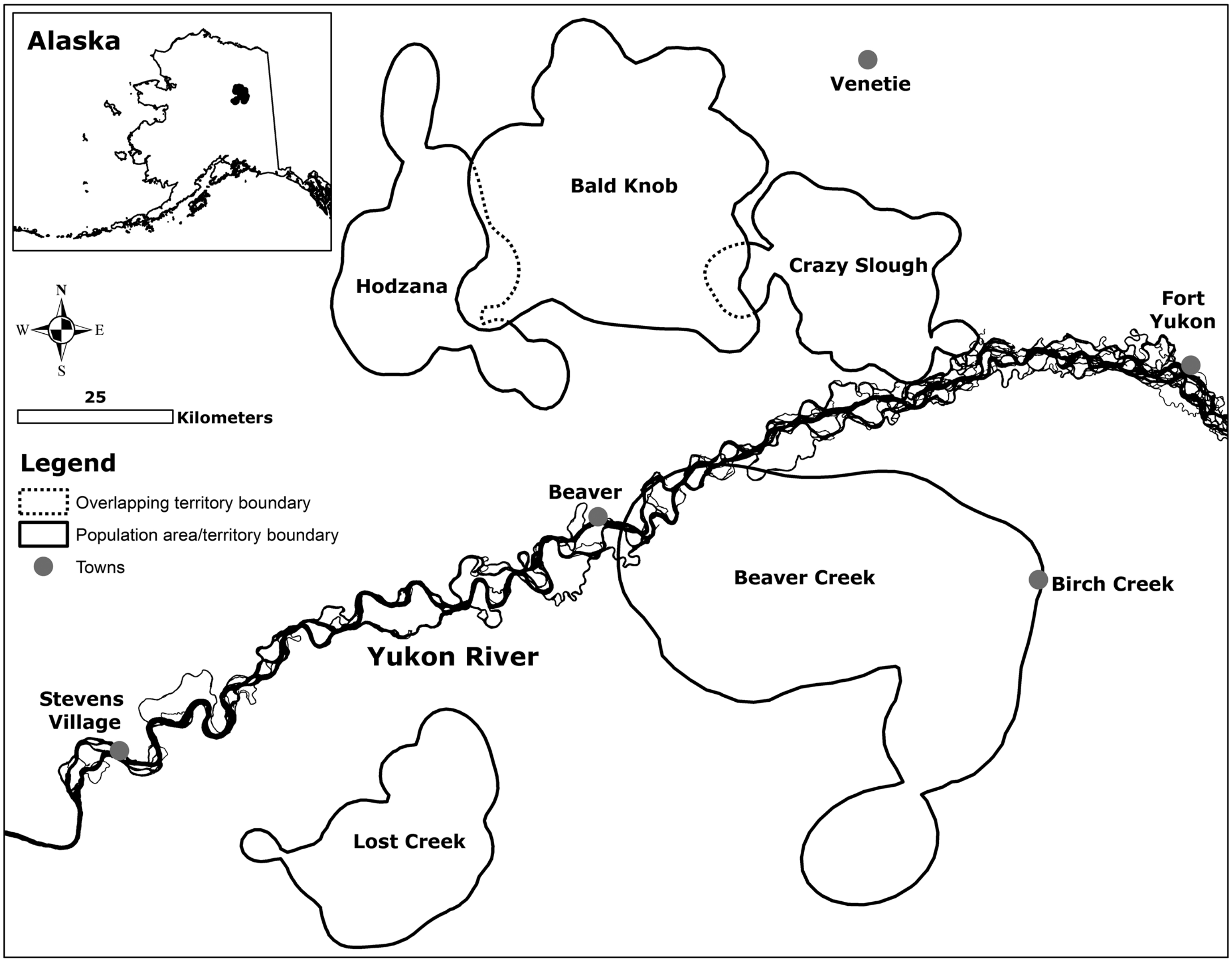

FIG. 1. Wolf pack territories and population area during winter (November 2009 – April 2010) on the Yukon Flats, Alaska. Boundaries were developed with 95% adaptive kernels. The dotted lines represent territorial boundaries of the Hodzana and Crazy Slough packs that overlap the Bald Knob territory. The remaining packs had no overlapping boundaries.

Data Collection

We placed seven GPS collars (Telonics model TGW-3580) on wolves in five packs on 2 – 3 November 2009. The five packs that we marked with collars represented 21% (5/24 packs) of the packs observed in a spring 2009 aerial survey (Caikoski, 2009). All collars were removed on 11 – 12 April 2010. Collars were programmed to record eight locations per day. All captures (U.S. Fish and Wildlife Service Region 7 Animal Care Protocol no. 2008022) were conducted by shooting a dart from a Robinson R-44 helicopter, and we remotely delivered (Palmer Cap-chur™) 540 or 572 mg of tiletamine HCL and zolazepam HCL (Telazol®; Fort Dodge Animal Health, Ford Dodge, IA; Ballard et al., 1991) to chemically immobilize wolves. We used tooth wear and staining and body size to differentiate young-of-the-year, yearlings, and adults (Gipson et al., 2000).

Territory Size Estimation

We used GPS locations from a single collar in each pack to estimate winter territory size (early November 2009 to mid-April 2010; Fig. 1, Table 1). Although we marked more than one wolf in two packs, only a single collar in each pack functioned throughout the winter months. We assumed that locations from a single collar reflected the location of the pack during winter. We believed this assumption to be reasonable because wolf packs were cohesive during the winter months (Peterson et al., 1984; Fuller and Snow, 1988), often traveling and feeding together (Metz et al., 2011).

We used two methods to estimate territory size. First, we surrounded the outermost locations for each pack with a minimum convex polygon (Fuller, 1989; Ballard et al., 1998; Burch et al., 2005; Mills et al., 2006). Second, we estimated 95% adaptive kernel territory size by following the guidelines of Mills et al. (2006). We used the Home Range extension of Rodgers and Carr (1998) to estimate territory sizes for each pack (Table 1). For adaptive kernel territory size, our objective was to produce a single polygon for each pack, and we followed the guidance of Mills et al. (2006) and Kie et al. (2010) and incrementally decreased (or increased) the bandwith parameter by 0.1 until a single polygon resulted. This method was repeatable and consistent, had a lower probability of Type 1 errors than least-squares cross-validation and reference bandwidths (Kie, 2013), exhibited only moderate bias compared to true home ranges (Kie, 2013), and has been applied by others (Mills et al., 2006; Berger and Gese, 2007; Jacques et al., 2009). We used the default resolution (70), which Rodgers and Carr (1998) described as a compromise between accuracy of low resolutions and processing speed.

Density Estimation

We estimated November and March wolf density following the radiotelemetry method advocated by Fuller and Snow (1988) and Burch et al. (2005), using the highest count of wolves in instrumented packs as the numerator and the population area during winter as the denominator. Burch et al. (2005) advocated using more than six packs to estimate wolf density, but noted that with intense sampling to delineate territories, such as that provided by GPS collars, fewer packs can be used. We defined the population area as the sum of pack territories. From this population area, we deducted portions of Hodzana and Crazy Slough territories that overlapped with Bald Knob territory (Fig. 1). We calculated separate population areas using 95% adaptive kernel and minimum convex polygon methods (Table 2). Aerial counts were obtained by tracking wolves from fixed-wing aircraft in early November ($\geq$ 2 counts per pack) and late March (> 5 counts per pack). The total number of wolves reflected the sum of wolves observed in five packs.

RESULTS

We obtained a total of 6263 locations of the five wolf packs from early November 2009 to mid-April 2010 (Table 1). Location fix success was high during this period (mean = 98%). Pack sizes ranged from two to 10 wolves in early November 2009, with a mean of five (Table 1). March 2010 pack sizes ranged from two to eight, with a mean of 4.8 wolves.

The bandwidth parameter for adaptive kernel territory sizes ranged from 0.5 to 0.9 of the reference bandwidth. During winter, mean territory size was 1433 km^2 (range 809–2681) with the 95% adaptive kernel method and 1608 km^2 (range 880–2653) with the minimum convex polygon method (Table 1).

Table 2 shows density estimates for November 2009 and March 2010. The total number of wolves was 25 in November and 24 in March. Using the 95% adaptive kernel method, the estimated population area was 6997 km^2, resulting in a wolf density of 3.6/1000 km^2 in November and 3.4/1000 km^2 in March. Using the minimum convex polygon method, the population area was 7374 km^2, resulting in wolf density of 3.4/1000 km^2 in November and 3.3/1000 km^2 in March.

DISCUSSION

Low wolf density corresponded to low ungulate biomass on the Yukon Flats, and this association is consistent with the observation that wolf populations throughout North America were likely limited by ungulate availability at low biomass (Fuller, 1989; Fuller et al., 2003; Cariappa et al., 2011; McRoberts and Mech, 2014). Thus, we suggest that moose availability on the Yukon Flats probably limited wolf density. Low density of Yukon Flats wolves in our study resulted from smaller-than-average pack sizes and large territories. Pack size averaged 5.0 in November and 4.8 in March, compared to an average of 6.5 from 11 studies in which moose was the principal prey (Fuller et al., 2003). Average 95% adaptive kernel territory size (1433 km^2) was larger than averages of 198 km^2 (n = 8 territories) from Mills et al. (2006) and 556 km^2 (n = 9 territories) from Rich et al. (2012). Those two studies used kernel methods and analyzed locations from GPS collars, though comparable ungulate biomass was not reported. Where comparable ungulate biomass was reported (Fuller et al., 2003), territory sizes generally reflected a continuum of declining values with increasing ungulate biomass. At the lower end of this continuum, some territories were one-tenth the size of those exhibited by wolves on the Yukon Flats. At the upper end, territories were similar in size to those on the Yukon Flats. However, these comparisons were complicated by territory sizes calculated by the minimum convex polygon method, for which sampling intensity may have been inadequate and from which extraterritorial forays may have been eliminated. Accordingly, we advocate the use of comparable territory sizes in future research and suggest that our results may represent a baseline for territory size at low ungulate biomass. We note that territory sizes in our study were based on winter locations only and might have increased if we had obtained year-round locations. However, this result would not have affected our conclusion that territory size was large or density was low, since larger territories would have decreased density.

This study benefited from the use of GPS collars, which provided a sampling intensity that exceeded recommendations for estimating territory size and density (Fuller and Snow, 1988; Ballard et al., 1998; Burch et al., 2005; Mills et al., 2006). Additionally, we used a 95% adaptive kernel method, which was more robust than the minimum convex polygon method (Mills et al., 2006); we did not subjectively eliminate extraterritorial forays (Peterson et al., 1984; Ballard et al., 1998; Adams et al., 2008); and we used a repeatable and consistent method to select the adaptive kernel bandwidth parameter (Mills et al., 2006; Kie, 2013). In our study, comparison between adaptive kernel and minimum

TABLE 1. Winter pack and territory sizes of five wolf packs on the Yukon Flats, Alaska (November 2009 – April 2010). Pack sizes from November and territories calculated by two methods are shown. The bottom row gives mean values for the five packs.

Pack	Pack size	# locations	95% Adaptive kernel territory (km^2)	Minimum convex polygon territory (km^2)
Bald Knob	4	1244	1821	2533
Beaver Creek	10	1249	2681	2653
Crazy Slough	4	1257	842	957
Hodzana	5	1259	1013	1017
Lost Creek	2	1254	809	880
Mean	5	1253	1433	1608

TABLE 2. Density of wolves on the Yukon Flats, Alaska, in November 2009 and March 2010.

Month	Estimation method	Population area (km^2)	# wolves	Density (wolves/1000 km^2)
November	95% Adaptive kernel	6997	25	3.6
	Minimum convex polygon	7374	25	3.4
March	95% Adaptive kernel	6997	24	3.4
	Minimum convex polygon	7374	24	3.3

convex polygon methods revealed an average difference of 11% in estimates of territory size. The minimum convex polygon method gave the larger territory size, and correspondingly, the lower density (3% lower in March and 6% lower in November). The 11% difference between methods that we observed in territory size was similar to the 13% difference reported by Mills et al. (2006). Thus, our study adds to a body of evidence that suggests adequate sampling intensity may reduce (but not eliminate) potential impacts of method (Mills et al., 2006) on wolf territory size. We encourage researchers to evaluate this factor in their studies, as our sample size of packs was lower than Mills et al. (2006; $n = 8$).

The low density of wolves found in this study is similar to findings of previous aerial surveys on the Yukon Flats (Gasaway et al., 1992; Caikoski, 2009). However, the range of spring densities from recent aerial surveys (4.4 – 5.3 wolves/1000 km^2 in 2006 and 2009; Caikoski, 2009) was 23% – 38% greater than density derived through telemetry methods (3.3 – 3.4 wolves/1000 km^2). This result could reflect either sampling variation associated with the small sample used to estimate density with telemetry methods (only five wolf packs), or annual variation, since no aerial survey was conducted in 2010 because of poor snow conditions. However, tracks of wolves that led outside the boundary have regularly been noted during aerial surveys (ADFG, 2009; J. Caikoski, unpubl. data), and we speculate that greater density from aerial surveys was most likely the result of wolf pack observations on the periphery of the survey area. We recommend that managers consider the limitations of each method and the finding of low density common to both methods when interpreting wolf density information for the Yukon Flats.

An example of the utility of wolf density is its use to manage the harvest. Recently, much research has been devoted to understanding how human-induced mortality affects wolf population density. Several thresholds of human-caused annual mortality that did not affect wolf population growth have been reported: 29% (Adams et al., 2008), 24% for non-northern Rocky Mountain populations (Creel and Rotella, 2010), 34% (Webb et al., 2011), and 48% (Gude et al., 2012). Therefore, from a November density of wolves on the Yukon Flats (3.6 wolves/1000 km^2), 0.86 wolves/1000 km^2 could be harvested at the minimum mortality rates (24%; Creel and Rotella, 2010) and 1.7 wolves/1000 km^2 at the maximum rate (48%; Gude et al., 2012). Annual harvest in this region from 1996 to 2012 (Alaska Game Management Unit 25D; Caikoski, 2009, unpubl. data) averaged 0.46 wolves/1000 km^2 (21 wolves/45 731 km^2) and ranged from 0.09 to 0.92 wolves/1000 km^2 (4 – 42 wolves/45 731 km^2). We conclude that in most years wolves were lightly harvested, and a moderate harvest was rare.

Adams et al. (2010) documented use of salmon by wolves in an ungulate prey system in Alaska and concluded that this alternative prey explained why wolf densities in a portion of their study area were only 17% lower (4.4 – 5.8 vs. 5.8 – 7.2 wolves/1000 km^2) even though ungulate densities were 78% lower. These differences in ungulate and wolf densities resulted in a threefold difference in predation rates, which has important implications for wolf-ungulate relations (Adams et al., 2010; Vucetich et al., 2011). On the Yukon Flats, moose are the sole ungulate prey of wolves, but each summer more than a million chum (*O. keta*) and Chinook (*O. tshawytscha*) salmon are counted traveling up the Yukon River (U.S. – Canada Yukon River JTC, 2011). These salmon are potentially available to wolves in the numerous tributaries that branch from the Yukon River, and in September 2010, collared wolves were observed adjacent to a stream that contained salmon and were presumed to be foraging (N. Guldager, pers. comm. 2010). Understanding whether wolves on the Yukon Flats benefit numerically from use of a seasonal, non-ungulate food would be valuable, as use of alternative prey may inflate wolf densities and the impact of predation on ungulates (Adams et al., 2010).

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