



# Wolf Kill Rates Across Winter in a Low-Density Moose System in Alaska

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**ABSTRACT** Wolf (*Canis lupus*) kill rates are fundamental to understanding predation, but are not well known at low moose (*Alces alces*) densities. We investigated kill rates of 6 wolf packs (2–10 wolves/pack) during 2 winters on the Yukon Flats, a region of eastern Interior Alaska where moose were the sole ungulate prey of wolves occurring at densities  $<0.2$  moose/km<sup>2</sup>. Our objectives were to compare kill rates with those from areas of greater moose densities, and to determine potential trends in kill rates across the winter. We located moose killed by wolves in February–March 2009, and November 2009–March 2010 using aerial tracking techniques and global positioning system (GPS) location clusters. Wolves killed more moose in early than late winter ( $\beta_{\text{MONTH}} = -0.02$  moose/pack/day, 95% CI =  $-0.01$  to  $-0.04$ ), and kill rate estimates (mean, 95% CI) were greatest in November (0.033 moose/wolf/day, 0.011–0.055) and least in February (0.011, 0.002–0.02). Kill rates were similar between February and March 2009 (0.019 moose/wolf/day, 0.01–0.03) and 2010 (0.018, 0.01–0.03). Prey composition was primarily adult females (39%) and young-of-the-year (35%). We attribute an elevated kill rate in early winter to predation on more vulnerable young-of-the-year. Kill rates in our study were similar to those from other studies where moose occurred at greater densities. We suggest that very few, if any, wolf–moose systems in Alaska and the Yukon experience a density-dependent phase in the functional response, and instead wolves respond numerically to changes in moose density or availability in the absence of alternative prey. Through a numerical response, wolf predation rates may approximate the annual growth potential of the moose population, contributing to persistent low densities of moose and wolves on the Yukon Flats. Published 2013. This article is a U.S. Government work and is in the public domain in the USA.

**KEY WORDS** Alaska, *Alces alces*, *Canis lupus*, global positioning system telemetry, kill rate, monthly variation, moose, very high frequency telemetry, wolf.

Whether wolf (*Canis lupus*) kill rates are reduced at low moose (*Alces alces*) densities is of theoretical and applied interest to wildlife management (Messier 1994, Eberhardt 1997, Hayes and Harestad 2000). Support for the notion of a declining kill rate or functional response (Holling 1959) stems from the truism that no prey can be killed when the prey density is zero. For wolf–moose systems, reduced kill rates were observed in Quebec where densities of prey ranged from 0.17 to 0.23 moose/km<sup>2</sup> (Messier and Crete 1985, Messier 1994). However, after analyzing kill rates from these and other studies, Eberhardt (1997) found little evidence for reduced kill rates at low moose densities. Later, Hayes and Harestad (2000) observed that wolves in the Yukon maintained high kill rates at slightly greater moose densities (0.26–0.44 moose/km<sup>2</sup>) than in Quebec, questioning the moose densities at which kill rates may be reduced, and the impact of wolves on ungulate prey at low densities.

Predation rate, or the proportion of the prey population removed by predation, provides additional insights to understanding impacts of wolf predation on ungulate prey (Messier 1994, Hayes and Harestad 2000, Eberhardt et al. 2003, Vucetich et al. 2011). Predation rate can be calculated as the product of the number of wolves present and their per capita kill rate divided by the number of prey present (Vucetich et al. 2011). For moose at densities  $\leq 0.6$  moose/km<sup>2</sup>, the model of Messier (1994) suggested that the loss to wolves was density-dependent. Hayes and Harestad (2000) included additional estimates of kill rate that were not reduced at low moose densities, thus demonstrating that predation rates were previously underestimated at low prey densities. Vucetich et al. (2011) showed that in 3 systems, much of the variation in predation rate was related to the wolf to prey ratio.

Wolf densities down to 2–3 wolves/1,000 km<sup>2</sup> were observed in low-density moose systems (Gasaway et al. 1992, Messier 1994). The occurrence of wolves in these systems was likely tied to the availability of vulnerable ungulate prey (Peterson 1977, Mech and Peterson 2003),

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which often consisted of young-of-the-year and adult females (Peterson et al. 1984, Mech et al. 1995, Smith et al. 2004). Moreover, such patterns of predation may shift across the winter because of changing availability and vulnerability of the prey base (Carbyn 1983, Metz et al. 2012). For instance, Carbyn (1983) and Metz et al. (2012) observed that wolves preyed on elk (*Cervus elaphus*) young-of-the-year during early winter when they were most abundant, and on adult elk in late winter and spring. Although research in wolf–elk systems has demonstrated kill rates may vary across the winter (Carbyn 1983, Smith et al. 2004, Metz et al. 2012), this has not been investigated in wolf–moose systems in Alaska or the Yukon.

We had the unique opportunity to investigate wolf kill rates across the winter in a low-density ( $<0.2$  moose/km<sup>2</sup>), single ungulate system (Gasaway et al. 1992, Caikoski 2010, Lake 2010). We combined data from global positioning system (GPS) clusters (Sand et al. 2005, Webb et al. 2008, Ruth et al. 2010) and tracking with aerial telemetry (Peterson et al. 1984, Ballard et al. 1987, Hayes et al. 2000) in winters 2009 and 2010 to estimate kill rates. Our primary objectives were to compare kill rates on the Yukon Flats in eastern Interior Alaska to those in areas of greater moose densities, and to determine potential trends in kill rates across the winter.

## STUDY AREA

We marked wolves with radiocollars in the Yukon Flats of Alaska (Yukon Flats National Wildlife Refuge, Alaska Game Management Unit 25D), within 60 km of the village of Beaver, Alaska (Fig. 1; 66°21'N 147°23'W). No roads existed and all travel was by airplane or helicopter. This region was characterized by mixed forests of black spruce (*Picea mariana*), white spruce (*P. glauca*), balsam poplar (*Populus balsamifera*), quaking aspen (*P. tremuloides*), and paper birch (*Betula papyrifera*), as well as thickets of tall shrubs that included willow (*Salix* sp.) and alder (*Alnus* sp.). Many wetlands, meadows of graminoids (*Arctagrostis* spp., *Beckmannia erucaeformis*, *Bromus* spp., *Calamagrostis* spp., *Eriophorum* spp., *Glyceria* spp., *Hordeum jubatum*, *Poa glaucus*, *Triglochin* spp.), sedges (*Carex* spp.), and floating mats of bog vegetation (*Menyanthes trifoliata*, *Potentilla palustris*, *Caltha palustris*, *Equisetum* spp.) were distributed throughout. Uplands and mountains bounded our study area to the north and south with elevations ranging from 91 m to 912 m. Upland habitats were alder, willow, dwarf birch (*Betula nana*), Labrador tea (*Ledum decumbens*), crowberry (*Empetrum nigrum*), and blueberry (*Vaccinium uliginosum*).

The climate was subarctic, characterized by cold winters and dry summers, with a range of temperatures from  $-51^{\circ}\text{C}$  in January to  $37^{\circ}\text{C}$  in July. Snow depths were well below 90 cm, a critical value for moose movement and survival (Coady 1974, Gasaway et al. 1992). Depths measured at the Lower Beaver Creek and Vunzik Lake stations were moderate to low in March 2009 (69 cm) and March 2010 (48 cm), and averaged 52 cm and 64 cm, respectively, in March from 1999 to 2010 (National Resources Conservation Service 2010).

Primary prey for wolves was moose, and densities were low ( $<0.2$  moose/km<sup>2</sup>; Caikoski 2010, Lake 2010). Minor prey included beaver (*Castor canadensis*) and snowshoe hare (*Lepus americanus*). November 2009 and March 2010 wolf densities ranged from 3.5 to 3.7/1,000 km<sup>2</sup> (Lake et al. 2013). Black bear (*Ursus americanus*) densities were high at  $\geq 155$  independent bears/1,000 km<sup>2</sup> in 2010 (Caikoski 2011). Grizzly bear (*Ursus arctos*) were present and thought to be at low densities (Bertram and Vivion 2002). Reported harvest of moose averaged 130 annually during 2002–2009 (Lake 2010). Ratios of adult male to female moose were greater than a minimum management threshold of 30–100 (Young and Boertje 2008, Lake 2010), which reflected light to moderate harvest during 1992–2010.

## METHODS

### Moose Density

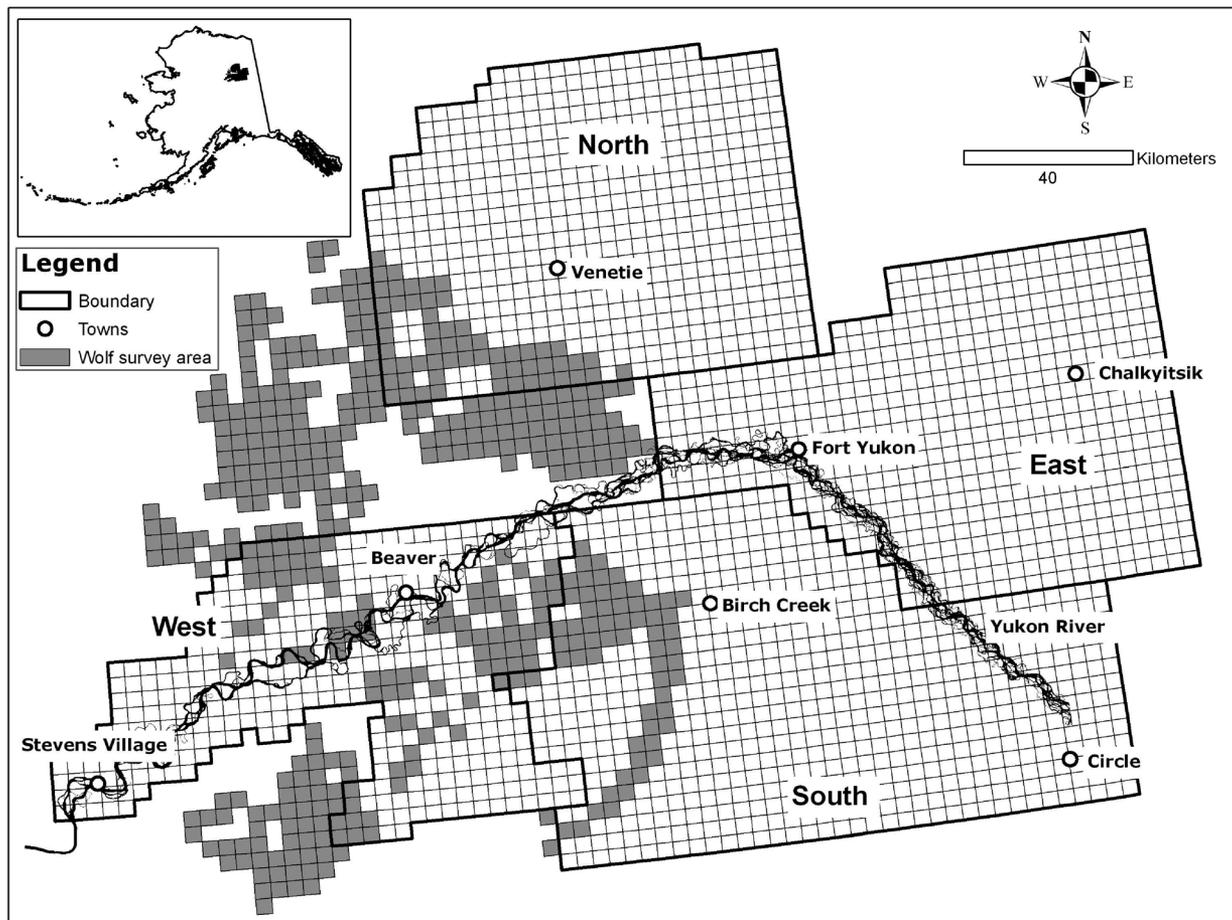
We conducted aerial moose surveys from fixed-wing aircraft, and used a geospatial population estimation (GSPE) method (Ver Hoef 2008) to estimate moose density. Kellie and DeLong (2006) provide description of the field methodology and data analysis for GSPE surveys and a software manual is available to assist with data entry and management (De Long 2006). Sample units encompassed 14 km<sup>2</sup>, and were defined using 2 minutes of latitude and 5 minutes of longitude (Fig. 1). Units were classified into high- and low-density strata by flying a single transect through the center and looking for moose or tracks. Moose density and variance were calculated by measuring spatial correlation among sample units, and modeling that relationship as a function of distance (Ver Hoef 2008).

We surveyed moose in 5 different areas across the Yukon Flats (Fig. 1) between 2001 and 2011. Not all survey areas were sampled in all years (Table 1) because of management needs, funding constraints, inadequate snow conditions, and poor flying weather. Four survey areas were established prior to this study. We established a fifth survey area, referred to as the wolf survey area, based on GPS locations obtained from 6 wolf packs with very high frequency (VHF) radiocollars in February and March 2009, and 6 wolf packs with GPS radiocollars during November 2009 to March 2010 (Fig. 1). We overlaid a grid of sample units on GPS locations to determine the extent of this survey area. The wolf survey area reflected those sample units that contained a GPS location. Observers conducted surveys in fall (Oct, Nov) or late winter (Mar), and sampled 60–174 units per survey (Table 1).

### Wolf Capture

We captured wolves during November 2008, March 2009, November 2009, and April 2010. Wolves were initially located by pilots experienced in aerial tracking who searched for tracks in the snow and followed them until the pack was located (Stephenson 1978). We conducted subsequent captures to radiocollar additional wolves in previously instrumented packs, and in March 2009 we radiocollared wolves in 2 newly located packs.

We chemically immobilized wolves by darting from a piston engine helicopter (U.S. Fish and Wildlife Service



**Figure 1.** Moose survey areas on the Yukon Flats, Alaska, USA, 2001–2011. Within each of the 5 areas, moose were counted in a sample of the 14-km<sup>2</sup> blocks. The wolf survey area (shaded blocks) corresponds to locations obtained from marked wolves in 8 packs during February and March 2009, and from November 2009 to March 2010. We also show the boundaries of 4 other moose surveys.

Region 7 Animal Care Protocol no. 2008022). We darted wolves with a 3-cm<sup>3</sup> projectile syringe fitted with a 1.9-cm barbed needle (Palmer Cap-chur<sup>TM</sup>; Powder Springs, GA) loaded with 540 mg or 572 mg of tiletamine HCL and

zolazepam HCL (Telazol<sup>®</sup>; Fort Dodge Animal Health, Fort Dodge, IA; Ballard et al. 1991). We used tooth wear and staining, body size, and swelling at the distal epiphysis of the radius to differentiate among young-of-the-year, year-

**Table 1.** Density of moose on the Yukon Flats, Alaska, USA in 5 survey areas, 2001–2011. Fall surveys were conducted in October and November.

Survey size (km <sup>2</sup> )	Month or season and year	No. units sampled	Density (moose/km <sup>2</sup> )	95% CI
Wolf study area-6332	Mar 2011	104	0.05	0.04–0.07
	West-5878	Fall 2001	100	0.11
West-5878	Mar 2003	85	0.09	0.06–0.12
	Mar 2004	91	0.11	0.08–0.13
	Fall 2004	93	0.09	0.06–0.11
	Fall 2006	97	0.07	0.05–0.09
	Mar 2008	91	0.05	0.04–0.06
	Fall 2008	174	0.08	0.07–0.10
	Fall 2010	104	0.08	0.05–0.10
	East-7516	Fall 2001	114	0.07
East-7516	Mar 2004	113	0.05	0.04–0.07
	Fall 2004	113	0.10	0.08–0.13
	Fall 2005	121	0.13	0.09–0.18
	Fall 2006	117	0.11	0.08–0.13
	Fall 2007	110	0.08	0.05–0.11
North-7316	Fall 2004	60	0.08	0.01–0.14
	Fall 2005	102	0.06	0.03–0.09
South-9293	Fall 2006	87	0.08	0.03–0.13

lings, and adults (Gipson et al. 2000, Adams et al. 2008). We attached Telonics (Mesa, AZ) model 500 VHF radiocollars to 21 wolves in 8 packs. In November 2009, we marked 9 wolves from 6 packs with Telonics model TGW-3580 GPS radiocollars, including 4 packs that previously contained wolves with VHF radiocollars. The GPS radiocollars included a VHF transmitter, were programmed to record 8 locations per day, and had an expected battery life through May 2010. These radiocollars were equipped with an Argos satellite uplink to obtain daily locations. We accessed location data stored on the radiocollar following recapture in April 2010.

### Kill Sites

We conducted telemetry flights to locate wolves with VHF radiocollars using a tandem airplane. Although we planned to aerially track wolves for 2 periods of 14 consecutive days each to locate kills, weather conditions truncated our sampling to a 13-day interval in February 2009 ( $n = 5$  packs) and an 8-day interval in March 2009 ( $n = 6$  packs). On each flight, we located the pack, recording the location, pack size, and presence of a kill. We then aerially backtracked following tracks in the snow to the location the previous day to locate all moose kills made by each pack during the sampling interval (Ballard et al. 1987, Dale et al. 1995). We attempted to determine the age (young-of-the-year and adult) and sex of fresh kills. However, assessment from the air was often not possible because frequently the kill was consumed and the skeleton was disarticulated.

We programmed GPS radiocollars to record a location every 3 hours, although we received only 6 of 8 daily locations because of data transfer limitations with the satellite uplink. Webb et al. (2008) reported that detection of large prey kills, such as moose, was 100% when locations were acquired at intervals up to 4 hours. After GPS locations were uplinked, they were collected and processed by CLS America, Inc. (Largo, MD) before being made available for download through their website. We decoded the raw data to an interpretable format with the ADC-T03 Argos data converter for Gen3 GPS. We then filtered the data with a program (SAS version 9.1.3; SAS Institute, Cary, NC) to eliminate redundant locations, converted times from Coordinated Universal Time to Alaska Standard Time, and adjusted dates accordingly. From 9 November 2009 to 31 March 2010, we obtained 5,734 locations from 9 GPS radiocollars in 6 packs.

We used wolf locations received via satellite uplink and the algorithm developed by Knopff et al. (2009) to identify GPS location clusters. To specify the distance at which locations were considered a cluster, we inspected the spatial distribution of wolf GPS locations at 9 kills aerially located during 25 November to 21 December 2009. Consistent with Webb et al. (2008),  $\geq 75\%$  of wolf locations were within 300 m of kills and we used that distance to identify clusters. For each cluster, the algorithm identified the geometric center and produced a table of descriptive statistics.

We began identification of GPS clusters on 11 November 2009 to allow wolves at least 7 days to recover following

capture. We monitored 4 packs (Lost Creek, Hodzana, Beaver Creek, and Crazy Slough) until 31 March 2010, producing 521 clusters. We lost contact with the Hodzana Mouth pack in January 2010 when all 3 radiocollared individuals were killed by other wolves; we identified 37 clusters in the 3 months of monitoring. We monitored the Bald Knob pack from December 2009 until 31 March 2010 and 86 clusters formed. All GPS radiocollars exhibited a high fix success ( $\bar{x} = 98\%$ , range = 96–99%), likely because of the flat terrain and lack of forest canopy cover during winter.

We aerially located the geometric center of each cluster within 14 days of its establishment using a GPS in a tandem airplane that flew 100–120 km/hour and 50–100 m above ground level. From each cluster center, we searched for kills by flying in concentric circles, about 150–200 m apart, and moving progressively outwards. We noted sign in the snow (tracks, beds) and terminated the search of a cluster when we stopped encountering sign other than the travel path of the wolf pack. The pilot and observer both searched for any sign of a kill (evidence of a chase, blood in the snow) or presence of a moose carcass or remains (rumen contents, hair, rib cage, legs, and pelvis). If we encountered a kill, we recorded kill data similar to aerial tracking. We recorded the condition of tracks in the snow at each cluster as fresh, old, or none given that we were not confident that we would observe a kill if present where old or no tracks were encountered. We later used these observations when identifying kill sites with a predictive model and eliminated clusters that had old or no tracks. Fresh tracks had no snow in them and shined in the sun, old tracks had drifted or new snow in them but were still discernible in the snow, and in some instances following a recent snowfall or wind storm, tracks were completely covered by snow and classified as none. We planned to aerially locate all clusters weekly following our specification of a clustering algorithm distance (Knopff et al. 2009); however, this was not possible because of adverse weather. Furthermore, although the radiocollars began recording locations in early November 2009, we did not begin aerially locating clusters until 22 December 2009, with the oldest GPS cluster initiated on 9 December 2009. Prior to 22 December 2009, we focused field efforts on aerial telemetry to establish distance parameters that identified a cluster in algorithms, as described above. To identify the presence of kills made prior to 22 December 2009, we approached clusters with a helicopter on 25 April 2010 following snowmelt, which facilitated observation of kills. Use of a helicopter allowed us to search for evidence of kills from the ground or by hovering just above trees and brush when landing was not possible. We note that we terminated collection of GPS locations on 31 March 2010, but the flight was timed with snowmelt, which was not completed until late April.

We did not receive all locations per day because of satellite uplink limitations described earlier; therefore, some clusters that began 3 hours prior to or terminated 3 hours following missing locations were not identified, and thus not aerially located. Locations not received were analogous to location fix failure. With a similar fix interval of 3 hours, Knopff et al.

(2009) concluded that estimation of kill rate for species with long prey handling times, such as wolves in our study ( $\bar{x} = 82$  hr at a kill from GPS data), was not biased by location fix failure until it dropped below 45%.

To evaluate our approach for identifying and aerially locating kills with GPS clusters, we conducted 2 additional 11- and 12-day aerial tracking periods in late winter 2010. We located kills using methods identical to data collection with VHF radiocollars on wolves. Following the aerial tracking periods, we identified and then aerially located all clusters. We compared whether we identified a GPS cluster at kills located by aerial tracking, and whether we then aerially located a kill at those clusters. Furthermore, by aerially locating all GPS clusters, we compared whether we missed any kills by aerial tracking but then identified and located them with clusters. Our method for evaluation of the GPS clusters was identical to that of Franke et al. (2006) and analogous to that of Smith et al. (2004) who used a double count method, and compared ground and aerial locations of kills to estimate the number of kills not found by either method.

Prey composition at kill sites was primarily determined from flying to kills ( $n = 57/89$  kills) with a helicopter ( $n = 52$ ), or an airplane ( $n = 5$ ), and locating prey remains on the ground. We flew to 12 of 18 kills aerially located during February and March 2009 with a helicopter on 3 March and 21 April 2009, and previously landed at 1 with an airplane. For kills aerially located during November 2009 to March 2010, we randomly selected 30 (approx. 5/pack) and flew to them with a helicopter on 25 April 2010. On that date, we also opportunistically sampled 10 kills with a helicopter that were associated with clusters made during November and early December 2009. We previously landed at 4 kills with an airplane. Because of a lack of open terrain, we were not able to land at some kill sites ( $n = 22/52$ ) with a helicopter. We located prey remains (skull, pelvis) at some sites where we landed, which enabled us to determine the sex and age composition for a sample of killed moose ( $n = 19/57$ ; Edwards et al. 1982). Additionally, we also determined prey composition for 4 kills based on observations from the air. We observed a freshly killed young-of-the-year, an adult female and young-of-the-year that were alive the day before a cluster formed, and 1 fully articulated adult skeleton of unknown sex. We collected a mandible from adult moose whenever possible ( $n = 10$ ). All incisor tooth samples were aged by sectioning and counting cementum annuli (Matson's Laboratory, Milltown, MT).

### Kill-Site Model

We developed a logistic regression (SAS version 9.1.3) model to predict whether a kill was present (1) or absent (0) at clusters that we were not able to aerially locate or where wolf tracks were old or absent. Model development included only clusters where we detected fresh wolf tracks and/or a kill. We originally identified clusters for field visits with GPS locations immediately available for uplink (6 locations/day); however, cluster attribute data used in model development included all GPS locations that became available upon radiocollar retrieval (8 locations/day). Thus, we formulated the model

with a dataset that represented kill presence or absence at clusters aerially located using a dataset of 6 locations/day, and applied this information to attributes associated with each cluster that represented 8 locations/day. Attributes included the number of locations at a cluster, number of days at a cluster, and average distance of each location to the cluster center (Anderson and Lindzey 2003, Webb et al. 2008, Knopff et al. 2009). We also developed a binary variable that reflected whether a wolf left and then returned to a cluster (1), or left a cluster and did not return (0), over the duration of the cluster (approx. 2–14 days). During our sampling, variation among packs in time spent at kills was evident, and we included pack as a categorical fixed effect. The specific pack of wolves represented variation in handling time due to pack size, and other factors that we were unable to quantify but suspected were influential, including age and sex structure of the pack and social structure of the pack (e.g., breeding adults with only young-of-the-year and breeding adults with multiple generations of young).

We developed a set of 20 models that included all combinations of the 5 predictors, and all models with more than 2 parameters included only additive effects. We evaluated the goodness-of-fit of the most parameterized (global) model in our set with the Hosmer–Lemeshow test (Hosmer and Lemeshow 1989). We selected among competing models using Akaike's Information Criterion corrected for small sample size (AIC<sub>c</sub>; Burnham and Anderson 2002). We assessed the importance of individual variables using 95% confidence limits of regression coefficients ( $\beta$ s; Johnson 1999). We used the area under the receiver operating characteristic (ROC) curve to assess the overall discrimination ability of the best approximating model. We also used the ROC curve to determine the optimal probability cutoff for characterization of kill or no-kill based on maximizing sensitivity and specificity simultaneously (Fielding and Bell 1997, Guisan and Zimmermann 2000). We classified all clusters with a probability value  $\geq$  the optimal value as a kill, whereas we classified all others as a non-kill.

### Winter Kill Rates and Predation Rate

We estimated kill rates during February and March 2009 with data acquired from aerial tracking of wolves with VHF radiocollars, and during November 2009 to March 2010 with GPS radiocollars on wolves, and aerial investigation of clusters of GPS locations. We used only fresh kills made after the first day of the sampling interval to estimate kill rates. We excluded kills located on the first day because inclusion would have positively biased the kill rate (Fuller and Keith 1980). For clusters where we observed fresh tracks or a kill, we used information on the presence or absence of a kill from aerial location of clusters. For clusters where we did not observe fresh tracks or a kill, we applied the predictive model to assign whether a kill was present or absent at a cluster (Webb et al. 2008; Knopff et al. 2009, 2010).

We estimated kill rates using a ratio estimator (Hebblewhite et al. 2003) implemented with PROC SURVEYMEANS (SAS version 9.1.3). We calculated

kill rate (moose/wolf/day) by dividing the number of kills by the estimated wolf days for a given pack (Becker et al. 2009). Wolf days was the product of the mean traveling pack size (Messier 1985) and number of days the pack was under observation. Traveling pack size reflected an average number of wolves (2–10; Table 2) that traveled and fed together during a month based on 2–15 aerial observations. Increases or decreases in pack size resulted in traveling pack sizes that were not whole numbers. We estimated winter kill rates monthly during November 2009 to March 2010 and for February to March in 2009 and 2010. Although we used different approaches in 2009 (VHF aerial tracking) and 2010 (GPS cluster data), this comparison between years was reasonable because we aurally located 81% of all clusters during late winter 2010 to verify kills, and of the clusters not located, all were classified as no-kill by the kill-site model.

We investigated variation in monthly kill rates by pack (moose/pack/day) using the general linear models procedure (SAS version 9.1.3) and a model selection approach based on AIC<sub>c</sub> (Burnham and Anderson 2002). We included pack size in all models because prior research demonstrated the influence of pack size when examining variation in kill rates (Thurber and Peterson 1993, Hayes et al. 2000, Becker et al. 2009). We examined 3 competing models: a null model of no change (intercept only), change between months (intercept and month as a categorical variable), and a linear trend (intercept and month as a continuous, trending variable) to

examine the hypothesis that kill rates increased or decreased across the winter (Smith et al. 2004).

We estimated the winter predation rate ([wolf density × kill rate]/moose density; Messier 1994, Hayes and Harestad 2000, Vucetich et al. 2011) during 151 days (Nov 2009–Mar 2010) of winter wolf kill rate study. Other researchers extrapolated winter wolf kill rates to annual rates with a correction factor to account for lower predation during other times of the year (Messier 1994, Hayes and Harestad 2000, Vucetich et al. 2011), but we lacked data on non-winter kill rates necessary to estimate an annual rate.

## RESULTS

Moose density in the wolf study area in March 2011 was 0.05 moose/km<sup>2</sup> (95% CI = 0.04–0.07; Table 1). Across the Yukon Flats, densities of moose from fall and spring surveys have all been uniformly low since at least 2001 (Table 1). Moose densities in the west survey area that overlapped with 20% of the wolf study area ranged between 0.05 moose/km<sup>2</sup> (95% CI = 0.04–0.06; 2008) and 0.11 (0.08–0.13; 2004) in the spring, and 0.07 (0.05–0.09; 2006) and 0.11 (0.08–0.15; 2001) in the fall.

We used data from 280 clusters where we detected fresh wolf tracks or a kill to predict the probability that a cluster represented a kill or non-kill. Most of the clusters (*n* = 221) were non-kills and 59 were kills. A goodness-of-fit test indicated that the global model fit the logistic model

**Table 2.** Summary statistics for an investigation of wolf kill rates on moose on the Yukon Flats, Alaska, USA, 2009–2010. For each pack-month combination during November 2009–March 2010, we present traveling pack size, wolf days (traveling pack size × observation days), number of kills, and kill rate. We also present means for values in each column. Late winter estimates are from 21 days of aerial tracking during early February and March 2009, and cluster data from the same period in 2010.

Wolf pack-month	Traveling pack size	Wolf days	No. kills	Kill rate (moose/wolf/day)
Bald knob-Dec	4	124	2	0.016
Bald knob-Jan	4	124	4	0.032
Bald knob-Feb	4	112	2	0.018
Bald knob-Mar	4	124	2	0.016
Beaver creek-Nov	10	200	6	0.030
Beaver creek-Dec	8	248	9	0.036
Beaver creek-Jan	8	248	5	0.020
Beaver creek-Feb	8	224	1	0.004
Beaver creek-Mar	8	248	5	0.020
Crazy slough-Nov	4	80	2	0.025
Crazy slough-Dec	4	124	4	0.032
Crazy slough-Jan	4	124	4	0.032
Crazy slough-Feb	4	112	1	0.009
Crazy slough-Mar	4.71	146	3	0.021
Hodzana-Nov	5	100	4	0.040
Hodzana-Dec	5	155	4	0.026
Hodzana-Jan	5	155	4	0.026
Hodzana-Feb	5	140	2	0.014
Hodzana-Mar	5	155	1	0.006
Hodzana mouth-Nov	5	100	1	0.010
Hodzana mouth-Dec	5	155	3	0.019
Hodzana mouth-Jan	5	95	1	0.010
Lost creek-Nov	2	40	4	0.100
Lost creek-Dec	2	62	3	0.048
Lost creek-Jan	2	62	5	0.081
Lost creek-Feb	2	56	1	0.018
Lost creek-Mar	2	62	3	0.048
$\bar{X}$	4.8	132	3.2	0.024
Late winter 2009	5.5	569	11	0.019
Late winter 2010	4.6	437	8	0.018

**Table 3.** Model selection results for discriminating wolf kills from non-kills and wolf kill rate on moose from data collected on the Yukon Flats, Alaska, USA, 2009–2010. Models are ranked by relative differences in corrected Akaike’s Information Criterion values ( $\Delta AIC_c$ ). We present the number of parameters ( $K$ ) and weight of evidence for being the best approximating model ( $\omega_i$ ). We show all models with  $\Delta AIC_c \leq 4.0$ .

Response variable	Model	$K$	$-2 \log(L)$	$\Delta AIC_c$	$\omega_i$
Kill, non-kill	Number of locations, pack	8	97.5	0.0	0.54
	Number of locations, pack, days at cluster	9	97.3	2.0	0.20
	Number of locations	3	110.4	2.4	0.16
Kill rate (moose/pack/day)	Linear trend in month, pack size	4	-136.5	0.0	0.85
	Null, pack size	3	-129.7	4.0	0.12

moderately well ( $\chi^2_8 = 12.70$ ,  $P = 0.12$ ). The model best supported by the data included individual pack and number of locations at a cluster (Table 3). The probability of a cluster being a kill increased with number of locations at a cluster ( $\beta_{\text{number of locations}} = 0.43$ , 95% CI = 0.31–0.55). Among the 6 packs, clusters with 16–27 locations had a >90% probability of being a kill site. A model that included the number of days at a cluster also received some support ( $\Delta AIC_c = 2.0$ ), but the coefficient for number of days at a cluster was not different from zero ( $\beta_{\text{days}} = -0.17$ , 95% CI = -0.98 to 0.65). The sum of model weights ( $\omega_i$ ) for models incorporating the number of locations at a cluster and pack was 1.0 (Table 3). The best model provided excellent discrimination between kills and non-kills with a ROC area under the curve of 0.97. Using the optimal cutoff of 0.18, the best model was 96.9% concordant and 2.8% discordant with the classification of the observed data. When we applied the best-supported model to 334 clusters that were not aerially located or where fresh wolf tracks were not observed, the model predicted 15 clusters were kills.

We identified a cluster of GPS locations at every kill ( $n = 10$ ) located during the 2 aerial tracking periods in late winter 2010. We verified the presence of a kill by flying to 9 of those clusters following the aerial tracking period. High winds in mountainous terrain prevented us from flying to 1 cluster where a kill had previously been located by aerial tracking. Furthermore, we flew to every cluster identified during the aerial tracking periods, and we verified that no kills were missed when radio tracking wolves daily. Thus, errors of omission (not identifying a kill and classifying it as a non-kill site) were zero for both aerial tracking and cluster methods. Also, when radio tracking wolves during November 2009–March 2010, we aerially located 22 kills and we identified clusters at 100% of these kills, further demonstrating the utility of the GPS cluster method for our system.

Kill rates during February and March 2009 (0.019 moose/wolf/day, 95% CI = 0.01–0.03; Table 2) and 2010 (0.018, 0.01–0.03) were similar. Monthly estimates of kill rate from November 2009 to March 2010 averaged 0.024 moose/wolf/day (95% CI = 0.019–0.029; Table 2) and varied from 0.011 in February (95% CI = 0.002–0.02) to 0.033 in November (0.011–0.055; Fig. 2). We found more support for a negative trend across the winter ( $\beta_{\text{MONTH}} = -0.02$  moose/pack/day, 95% CI = -0.01 to -0.04) than for a constant kill rate (null model; Table 3). From the trend model, kill rate (moose/pack/day) increased with pack size ( $\beta_{\text{pack size}} = 0.01$ , 95% CI = 0.002–0.025). Minimum estimates of kill rate from the 71 observed kills ranged from 58% of the total in

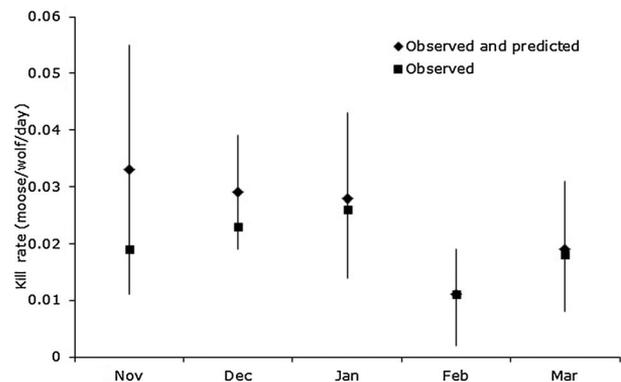
November to 100% in February (Fig. 2), indicating that we located more than half or all of the kills in some months. Kill rates were within the range of those reported by other studies, greater than predicted by the Type II functional response curve of Messier (1994), and 6 of 7 were greater than predicted by Hayes and Harestad (2000; Fig. 3).

We aerially observed 89 moose kills during flights and determined the age and sex of 23 moose (Table 4), of which 19 were from ground inspection of prey remains and 4 were based on observation from the air. Eighteen kills were from February and March 2009 and 71 kills from November 2009 to March 2010. Adult females (39%) and young-of-the-year (35%) comprised the majority of prey. Few (25%) young-of-the-year were from February or March (Table 4). Ages of 7 female moose ranged from 6 to 15.

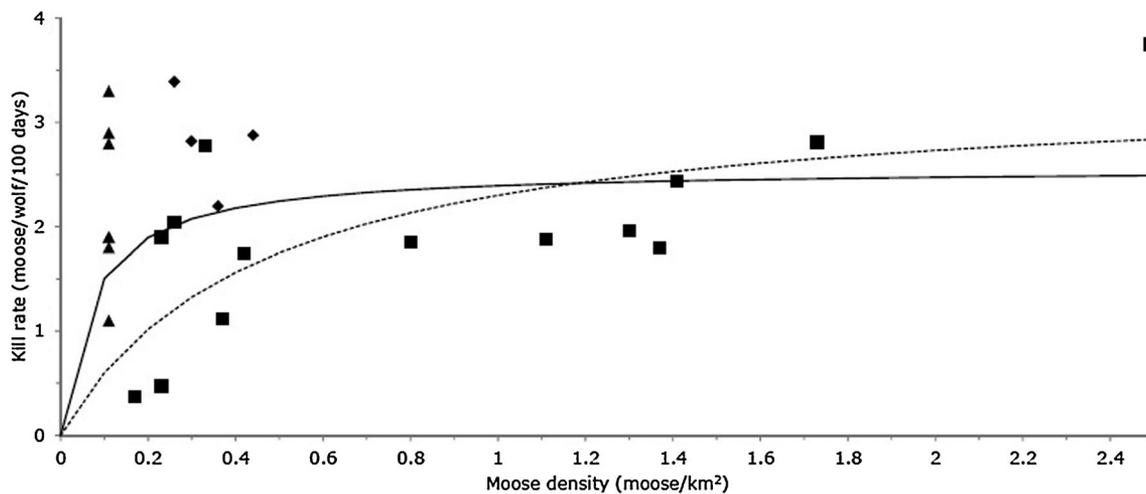
Predation rate was 12% during the 151-day period between November 2009 and March 2010. This ratio reflected a November wolf density of 3.7 wolves/1,000 km<sup>2</sup> (Lake et al. 2013), wolf winter kill rate of 0.024 moose/wolf/day, and November moose density of 0.11 moose/km<sup>2</sup>. Moose density was 0.08 moose/km<sup>2</sup> in the 2010 fall survey (Table 1), adjusted by 30% moose missed in Interior Alaska (Keech et al. 2011).

## DISCUSSION

The idea that wolf kill rates were reduced at low moose densities was promoted by Messier and Crete (1985) and Messier (1994). Eberhardt (1997) disagreed and Eberhardt



**Figure 2.** Monthly estimates of wolf kill rate on moose from the Yukon Flats, Alaska, USA, 2009–2010. Estimates for observed and predicted (mean and 95% CI) represent the 71 observed kills and 15 predicted. Estimates (mean only) for observed are a minimum and represent the 71 observed kills.



**Figure 3.** Estimates of wolf kill rate on moose from Messier (1994; squares), Hayes and Harestad (2000; diamonds), and this study (triangles). Data from this study were from the Yukon Flats, Alaska, USA during 2009–2010, and kill rate estimates were from February and March 2009 and 2010, and monthly from November 2009 to March 2010. We show Type II functional relationships of wolf kill rate and moose density from Messier (1994; dashed line) and Hayes and Harestad (2002; solid line).

(2000) advocated for additional kill rates to further resolve the wolf and moose functional response. In our study, where moose occurred at densities  $<0.2$  moose/km<sup>2</sup>, wolf kill rates were not consistent with the hypothesis of reductions at low moose densities (Messier 1994, Hayes and Harestad 2000; Fig. 3), and instead wolves exhibited kill rates that were similar to other North American studies where densities of moose were 2–10 times greater (Peterson et al. 1984, Messier 1994, Hayes et al. 2000; Fig. 3). Support for this finding was enhanced by our use of GPS clusters to locate kills, which was an improvement over past studies (Peterson et al. 1984, Ballard et al. 1987, Hayes et al. 2000) because we examined kill rates across the winter, and monthly kill rates represented all kills made by packs rather than a sample of kills. Moreover, we documented that we did not miss any kills, and observed that wolves were cohesive during the winter, as evidenced by both GPS radiocollared wolves in a pack being present at 100% of kills ( $n = 26$ ). Based on our study, which occurred at some of the lowest moose densities in North America (Gasaway et al. 1992, Caikoski 2010, Lake 2010), we suggest that very few, if any, wolf–moose systems in Alaska and the Yukon experience a density-dependent phase in the functional response.

Messier (1985) speculated that 0.2 moose/km<sup>2</sup> was a threshold below which wolves could not persist without

alternate ungulate prey. Wolves in Alaska and the Yukon occurred at lower moose densities (Gasaway et al. 1992), and we observed that wolves could maintain kill rates where alternate prey were not present. In our system, we conclude that wolf persistence was due to maintenance of kill rates with a large-bodied prey, as moose provided 1.8–24.8 kg of biomass/day, greater than a minimum daily requirement of 1.4 kg (Mech and Peterson 2003). We further suggest that wolves in our study consumed a relatively constant biomass of prey across the winter, despite our observation that kill rates declined. In early winter, we attributed an elevated kill rate to predation on more vulnerable young-of-the-year that had less biomass and required shorter handling time (Messier and Crete 1985, Ballard et al. 1987, Webb et al. 2008). This was supported by most young-of-the-year being killed in November to January, although we note our sample size was limited. In late winter, as availability of young-of-the-year declined, we suspect lower kill rates reflected a shift to adults with greater biomass (Carbyn 1983, Metz et al. 2012). Therefore, the observed decline in kill rates likely reflected differences in prey composition and biomass. This was consistent with the argument that variation in wolf kill rates was better explained by factors other than prey density, such as relative frequency of young-of-the-year in the diet (Sand et al. 2012).

**Table 4.** Frequency of wolf kills on moose on the Yukon Flats, Alaska, USA, 2009–2010. Numbers in parentheses indicate ages of moose from counts of cementum annuli.

	2009		2009–2010					
	Feb	Mar	Nov	Dec	Jan	Feb	Mar	Total
Adult male	0	0	1	0	2 (2, 14)	0	0	3
Adult female	3 (10, 13, 15)	2 (10, 15)	0	1	1 (6)	2 (11)	0	9
Adult sex unknown	0	0	2 (14)	0	1	0	0	3
Young-of-the-year	0	2	1	3	2	0	0	8
Total	3	4	4	4	6	2	0	23

The most plausible explanation for the absence of reduced kill rates at low moose densities was that wolves responded numerically (Eberhardt 1997, Adams et al. 2008). Wolf densities were positively correlated with ungulate biomass across North America (Fuller 1989, Fuller et al. 2003), and wolf populations were likely limited by ungulate availability at low to moderate ungulate biomass (<8; Cariappa et al. 2011). On the Yukon Flats, moose and wolf densities have been consistently low (Bentley 1961, Gasaway et al. 1992, Messier 1994, Bertram and Vivion 2002), a situation that was described by Gasaway et al. (1992) as a low-density dynamic equilibrium. We observed numeric adjustments in our study, which included wolf mortality and dispersal of subadult wolves from their natal pack (Adams et al. 2008). Mortality of wolves was likely due to aggression between neighboring packs as territories expanded. Dispersal was common in the life history of wolves and we suggest that if available, vulnerable prey became scarce, subadult wolves may have dispersed. As smaller packs had greater per capita kill rates (Thurber and Peterson 1993, Hayes et al. 2000, Becker et al. 2009), dispersal may have resulted in an increased biomass of prey/wolf.

We speculate at least 3 mechanisms contribute to the ability of wolves to maintain kill rates at low moose densities. First, wolves are highly mobile and may have large territories (Ballard et al. 1998, Mech et al. 1998, Fuller et al. 2003, Lake et al. 2013). Such large territories are a response to low prey densities (Peterson 1977, Fuller et al. 2003), and are maintained to ensure an adequate supply of vulnerable prey (Peterson 1977). Second, wolves were often observed traveling on riparian corridors during our study. We suspect this was to capitalize on the smooth surface afforded by frozen streams and rivers, which can increase ease of travel and speed (Peterson 1995). Moose also tend to occur along riparian corridors during winter while foraging for willow (MacCracken et al. 1997, Renecker and Schwartz 1997, Baigas et al. 2010). If moose abundance tends to be greater in these corridors, then wolves may benefit functionally by selecting travel paths of greater prey densities than the landscape as a whole (McPhee et al. 2012). Finally, kill rates of wolves in low-density moose systems of Alaska and the Yukon may benefit from a relatively greater proportion of vulnerable moose characteristic of an older age structure owing to persistent low recruitment. These systems commonly exhibit low annual survival of moose in their first year (Larsen et al. 1989, Gasaway et al. 1992, Bertram and Vivion 2002, Keech et al. 2011); thus, such low recruitment may skew the age structure toward older individuals (Page 1989, Mackie et al. 1998, Festa-Bianchet et al. 2003). On Isle Royale, moose in older age classes were more vulnerable to predation, and wolf numbers were linked to old, vulnerable moose (Peterson 1977, 1995).

Low-density wolf and moose populations on the Yukon Flats coupled with the wolf kill rate resulted in a winter predation rate that was comparable to annual estimates from other systems (Boutin 1992, Messier 1994, Eberhardt 1997, Hayes and Harestad 2000, Vucetich et al. 2011). Annual wolf predation rate was likely higher, as predation by wolves

was known to occur outside of winter, but at very low rates (Bertram and Vivion 2002). Consequently, our winter predation rate was probably not much lower than an annual rate. Annual population dynamics of moose on the Yukon Flats was characterized by high pregnancy (89%) and twinning rates (63%) but low survival of young in the first year (20%), resulting in recruitment to age 1 (14 yearling females/100 adult females) that barely replaced losses of adult females (12%; Bertram and Vivion 2002). Accordingly, moose densities have not noticeably changed on the Yukon Flats since at least the 1960s (Bentley 1961, Gasaway et al. 1992, Caikoski 2010, Lake 2010). We suggest that numerical adjustment by wolves resulted in a winter predation rate that was maintained within a range that approximated the annual growth potential of the moose population after losses from black and grizzly bears primarily on young in spring, and human harvest in fall (Bertram and Vivion 2002). If moose in low-density systems at equilibrium (Gasaway et al. 1992) became more vulnerable, for instance because of adverse winter conditions (Mech et al. 2001, Smith et al. 2004), wolf kill rates and their resulting predation rates may increase, but such conditions tend to be short-lived (i.e., lasting for 1 winter). Conversely, if moose became less vulnerable and wolves could not maintain adequate kill rates, social factors such as emigration and increased inter-pack strife may result in numerical adjustments to wolf density, and a reduction in predation rates. A numerical response by wolves is further supported by observations in 3 systems where much of the variation in predation rate was attributed to the predator to prey ratio, and not the wolf kill rate (Vucetich et al. 2011).

## MANAGEMENT IMPLICATIONS

Previously, Gasaway et al. (1992) observed that wolves persisted throughout Alaska and the Yukon where moose occurred at densities from 0.04 to 0.42 moose/km<sup>2</sup>. Our results indicated that wolves can persist in low-density moose systems by maintaining kill rates comparable to those in systems of high moose densities. The expected reduction in wolf kill rates at moose densities <0.2 moose/km<sup>2</sup> may not occur because of a numerical response by wolves. Such a numerical response may contribute to an equilibrium (Gasaway et al. 1992) between wolf and moose densities where predation rate approximates the annual growth potential of the moose population. This equilibrium may help explain why yield of moose is lower and harvest conservative in low-density systems of Alaska and the Yukon (Gasaway et al. 1992, Hayes et al. 2003, Boertje et al. 2009). Moreover, on the Yukon Flats, the wolf numerical adjustment coupled with other losses to the moose population (Bertram and Vivion 2002) has resulted in consistently low densities of wolves and moose over recent decades. Managers of systems with smaller-bodied prey like white-tailed deer (*Odocoileus virginianus*) should carefully consider the applicability of our results, as wolf kill rates on deer were lower than where wolves preyed on larger-bodied ungulates such as caribou (*Rangifer tarandus*), elk, or moose (Mech and Peterson 2003). If kill rates decline across the

winter, as our data indicated, extrapolation to unsampled periods should be done cautiously when modeling predation impacts.

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## LITERATURE CITED

- Adams, L. G., R. O. Stephenson, B. W. Dale, R. T. Ahgook, and D. J. Demma. 2008. Population dynamics and harvest characteristics of wolves in the Central Brooks Range, Alaska. *Wildlife Monographs* 170:1–25.
- Anderson, C. R., and F. G. Lindzey. 2003. Estimating cougar predation rates from GPS location clusters. *Journal of Wildlife Management* 67:307–316.
- Baigas, P. E., R. A. Olson, R. M. Nielson, S. N. Miller, and F. G. Lindzey. 2010. Modeling seasonal distribution and spatial range capacity of moose in southeastern Wyoming. *Alces* 46:89–112.
- Ballard, W. B., L. A. Ayres, K. E. Roney, and T. H. Spraker. 1991. Immobilization of gray wolves with a combination of tiletamine hydrochloride and zolazepam hydrochloride. *Journal of Wildlife Management* 55:71–74.
- Ballard, W. B., M. Edwards, S. G. Fancy, S. Boe, and P. R. Krausman. 1998. Comparison of VHF and satellite telemetry for estimating sizes of wolf territories in northwest Alaska. *Wildlife Society Bulletin* 26:823–829.
- Ballard, W. B., J. S. Whitman, and C. L. Gardner. 1987. Ecology of an exploited wolf population in south-central Alaska. *Wildlife Monographs* 98:1–54.
- Becker, M. S., R. A. Garrott, P. J. White, R. Jaffe, J. J. Borkowski, C. N. Gower, and E. J. Bergman. 2009. Wolf kill rates: predictably variable? Pages 339–369 in R. A. Garrott P. J. White, and F. G. Watson, editors. *The ecology of large mammals in central Yellowstone*. Academic Press Terrestrial Ecology Series, Elsevier, London, United Kingdom.
- Bentley, W. W. 1961. Moose population inventories—interior and Arctic Alaska. Pages 161–171 in D. Klein, coordinator. *Annual report of progress, 1960–1961*. Alaska Department of Fish and Game, Juneau, Alaska, USA.
- Bertram, M. R., and M. T. Vivion. 2002. Moose mortality in eastern Interior Alaska. *Journal of Wildlife Management* 66:747–756.
- Boertje, R. D., M. A. Keech, D. D. Young, K. A. Kellie, and C. T. Seaton. 2009. Managing for elevated yield of moose in Interior Alaska. *Journal of Wildlife Management* 73:314–327.
- Boutin, S. 1992. Predation and moose population dynamics: a critique. *Journal of Wildlife Management* 56:116–127.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. Springer-Verlag, New York, New York, USA.
- Caikoski, J. R. 2010. Units 25A, 25B, and 25D moose. Pages 611–642 in P. Harper, editor. *Moose management report of survey and inventory activities 1 July 2007–30 June 2009*. Alaska Department of Fish and Game, Project 1.0, Juneau, Alaska, USA. <[http://www.adfg.alaska.gov/static/home/library/pdfs/wildlife/mgt\\_rpts/10\\_moose.pdf](http://www.adfg.alaska.gov/static/home/library/pdfs/wildlife/mgt_rpts/10_moose.pdf)> Accessed 29 Mar 2013.
- Caikoski, J. R. 2011. Unit 25D black bear. Pages 257–261 in P. Harper, editor. *Black bear management report of survey and inventory activities 1 July 2007–30 June 2010*. Alaska Department of Fish and Game, Project 17, Juneau, Alaska, USA. <[http://www.adfg.alaska.gov/static/home/library/pdfs/wildlife/mgt\\_rpts/11\\_blb.pdf](http://www.adfg.alaska.gov/static/home/library/pdfs/wildlife/mgt_rpts/11_blb.pdf)>. Accessed 29 Mar 2013.
- Carbyn, L. N. 1983. Wolf predation on elk in Riding National Park, Manitoba. *Journal of Wildlife Management* 47:963–976.
- Cariappa, C. A., J. K. Oakleaf, W. B. Ballard, and S. W. Breck. 2011. A reappraisal of the evidence for regulation of wolf populations. *Journal of Wildlife Management* 75:726–730.
- Coady, J. W. 1974. Influence of snow on behavior of moose. *Le Naturaliste Canadien* 101:417–436.
- Dale, B. W., L. G. Adams, and R. T. Bowyer. 1995. Winter wolf predation in a multiple ungulate prey system, Gates of the Arctic National Park, Alaska. Pages 223–230 in L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. *Ecology and conservation of wolves in a changing world*. Canadian Circumpolar Institute, Edmonton, Alberta, Canada.
- De Long, R. A. 2006. *Geospatial population estimator software user's guide*. Alaska Department of Fish and Game, Fairbanks, AK, USA. <<http://winfonet.alaska.gov/sandi/moose/surveys/documents/GSPESoftwareUsers-Guide.pdf>>. Accessed 29 Mar 2013.
- Eberhardt, L. L. 1997. Is wolf predation ratio-dependent? *Canadian Journal of Zoology* 75:1940–1944.
- Eberhardt, L. L. 2000. Reply: predator–prey ratio dependence and regulation of moose populations. *Canadian Journal of Zoology* 78:511–513.
- Eberhardt, L. L., R. A. Garrott, W. D. Smith, P. J. White, and R. O. Peterson. 2003. Assessing the impact of wolves on ungulate prey. *Ecological Applications* 13:776–783.
- Edwards, J. K., R. L. Marchinton, and G. F. Smith. 1982. Pelvic girdle criteria for sex determination of white-tailed deer. *Journal of Wildlife Management* 46:544–547.
- Festa-Bianchet, M., J.-M. Gaillard, and S. D. Cote. 2003. Variable age structure and apparent density dependence in survival of adult ungulates. *Journal of Animal Ecology* 72:640–649.
- Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* 24:38–49.
- Franke, A., T. Caelli, G. Kuzyk, and R. J. Hudson. 2006. Prediction of wolf (*Canis lupus*) kill-sites using hidden Markov models. *Ecological Modelling* 197:237–246.
- Fuller, T. K. 1989. Population dynamics of wolves in north-central Minnesota. *Wildlife Monographs* 105:1–41.
- Fuller, T. K., and L. B. Keith. 1980. Wolf population dynamics and prey relationships in northeastern Alberta. *Journal of Wildlife Management* 44:583–602.
- Fuller, T. K., L. D. Mech, and J. F. Cochrane. 2003. Wolf population dynamics. Pages 161–191 in L. D. Mech, and L. Boitani, editors. *Wolves: behavior, ecology, and conservation*. University of Chicago Press, Chicago, IL, USA.
- Gasaway, W. C., R. D. Boertje, D. V. Grangaard, and D. G. Kelleyhouse. 1992. The role of predation in limiting moose at low densities in Alaska

- and Yukon and implications for conservation. *Wildlife Monographs* 120:1–59.
- Gipson, P. S., W. B. Ballard, R. M. Nowak, and L. D. Mech. 2000. Accuracy and precision of estimating age of gray wolves by tooth wear. *Journal of Wildlife Management* 64:752–758.
- Guisan, A., and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* 135:147–186.
- Hayes, R. D., A. M. Baer, U. Wotschikowsky, and A. S. Harestad. 2000. Kill rate by wolves on moose in the Yukon. *Canadian Journal of Zoology* 78:49–59.
- Hayes, R. D., R. Farnell, R. M. Ward, J. Carey, M. Dehn, G. W. Kuzyk, A. M. Baer, C. L. Gardner, and M. O'Donoghue. 2003. Experimental reduction of wolves in the Yukon: ungulate responses and management implications. *Wildlife Monographs* 152:1–35.
- Hayes, R. D., and A. S. Harestad. 2000. Wolf functional response and regulation of moose in the Yukon. *Canadian Journal of Zoology* 78:60–66.
- Hebblewhite, M., P. C. Paquet, D. H. Pletscher, R. B. Lessard, and C. J. Callaghan. 2003. Development and application of a ratio estimator to estimate wolf kill rates and variance in a multiple-prey system. *Wildlife Society Bulletin* 31:933–946.
- Holling, C. S. 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *Canadian Entomologist* 91:293–320.
- Hosmer, D. W., and S. Lemeshow. 1989. *Applied logistic regression*. John Wiley and Sons, New York, New York, USA.
- Johnson, D. H. 1999. The insignificance of statistical significance testing. *Journal of Wildlife Management* 63:763–772.
- Keech, M. A., M. S. Lindberg, R. D. Boertje, P. Valkenburg, B. D. Taras, T. A. Boudreau, and K. B. Beckmen. 2011. Effects of predator treatments, individual traits, and environment on moose survival in Alaska. *Journal of Wildlife Management* 75:1361–1380.
- Kellie, K. A., and R. A. DeLong. 2006. *Geospatial survey operations manual*. Alaska Department of Fish and Game, Fairbanks, AK, USA. <<http://winfonet.alaska.gov/sandi/moose/surveys/documents/GSPEO-perationsManual.pdf>>. Accessed 29 Mar 2013.
- Knopff, K. H., A. A. Knopff, A. Kortello, and M. S. Boyce. 2010. Cougar kill rate and prey composition in a multiprey system. *Journal of Wildlife Management* 74:1435–1447.
- Knopff, K. H., A. A. Knopff, M. B. Warren, and M. S. Boyce. 2009. Evaluating global positioning system telemetry techniques for estimating cougar predation parameters. *Journal of Wildlife Management* 73:586–597.
- Lake, B. C. 2010. Moose population survey of the western Yukon Flats—November 2010. <[http://alaska.fws.gov/nwr/yukonflats/pdf/lake\\_moose\\_report\\_nov\\_2010.pdf](http://alaska.fws.gov/nwr/yukonflats/pdf/lake_moose_report_nov_2010.pdf)>. Accessed 29 Mar 2013.
- Lake, B. C., J. R. Caikoski, and M. R. Bertram. 2013. Wolf density and territory size in a low biomass ungulate prey system estimated with global positioning system (GPS) technology. <[http://alaska.fws.gov/nwr/yukonflats/pdf/wolf\\_report\\_2013.pdf](http://alaska.fws.gov/nwr/yukonflats/pdf/wolf_report_2013.pdf)> Accessed 29 Mar 2013.
- Larsen, D. G., D. A. Gauthier, and R. L. Markel. 1989. Causes and rate of moose mortality in the southwest Yukon. *Journal of Wildlife Management* 53:548–557.
- MacCracken, J. G., V. V. VanBallenberghe, and J. M. Peek. 1997. Habitat relationships of moose on the Copper River Delta in South-Central Alaska. *Wildlife Monographs* 136:1–52.
- Mackie, R. J., D. F. Pac, K. L. Hamlin, and G. L. Dusek. 1998. Ecology and management of mule deer and white-tailed deer in Montana. *Montana Fish, Wildlife and Parks*, Helena, USA. <<http://fwp.mt.gov/fwpDoc.jsp?id=50732>>. Accessed 29 Mar 2013.
- McPhee, H. M., N. F. Webb, and E. H. Merrill. 2012. Hierarchical predation: wolf (*Canis lupus*) selection along hunt paths and at kill sites. *Canadian Journal of Zoology* 90:555–563.
- Mech, L. D., L. G. Adams, T. J. Meier, J. W. Burch, and B. W. Dale. 1998. *The wolves of Denali*. University of Minnesota Press, Minneapolis, USA.
- Mech, L. D., T. J. Meier, J. W. Burch, and L. G. Adams. 1995. Patterns of prey selection by wolves in Denali National Park, Alaska. Pages 231–243 in L. N. Carbyn, S. H. Fritts, and D. R., Seip, editors. *Ecology and conservation of wolves in a changing world*. Canadian Circumpolar Institute, Edmonton, Alberta, Canada.
- Mech, L. D., and R. O. Peterson. 2003. Wolf-prey relations. Pages 131–160 in L. D. Mech, and L. Boitani, editors. *Wolves: behavior, ecology, and conservation*. University of Chicago Press, Chicago, Illinois, USA.
- Mech, L. D., D. W. Smith, K. M. Murphy, and D. R. MacNulty. 2001. Winter severity and wolf predation on a formerly wolf-free elk herd. *Journal of Wildlife Management* 65:998–1003.
- Messier, F. 1985. Social organization, spatial distribution, and population density of wolves in relation to moose density. *Canadian Journal of Zoology* 63:1068–1077.
- Messier, F. 1994. Ungulate population models with predation: a case study with the North American moose. *Ecology* 75:478–488.
- Messier, F., and M. Crete. 1985. Moose-wolf dynamics and the natural regulation of moose populations. *Oecologia* 65:503–512.
- Metz, M. C., D. W. Smith, J. A. Vucetich, D. R. Stahler, and R. O. Peterson. 2012. Seasonal patterns of predation for gray wolves in the multi-prey system of Yellowstone National Park. *Journal of Animal Ecology* 81:555–563.
- National Resources Conservation Service. 2010. Snow course and monthly SNOTEL data tables for Lower Beaver Creek and Vunzi Lake. <<http://www.wcc.nrcs.usda.gov/cgibin/state-site.pl?state=AK&report=snowcourse>>. Accessed 29 Mar 2013.
- Page, R. E. 1989. *The inverted pyramid: ecosystem dynamics of wolves and moose on Isle Royale*. Dissertation. Michigan Technological University, Houghton, USA.
- Peterson, R. O. 1977. *Wolf ecology and prey relationships*. U.S. National Park Service scientific monograph series No. 11. U.S. Government Printing Office, Washington, D.C., USA. <[http://www.nps.gov/history/history/online\\_books/science/11/index.htm](http://www.nps.gov/history/history/online_books/science/11/index.htm)>. Accessed 29 Mar 2013.
- Peterson, R. O. 1995. *The wolves of Isle Royale: a broken balance*. Willow Creek Press, Minocqua, Wisconsin, USA.
- Peterson, R. O., J. D. Woolington, and T. N. Bailey. 1984. *Wolves of the Kenai Peninsula, Alaska*. *Wildlife Monographs* 88:1–52.
- Renecker, J. A., and C. C. Schwartz. 1997. Food habits and feeding behavior. Pages 403–440 in A. W. Franzmann and C. C. Schwartz, editors. *Ecology and management of the North American moose*. Smithsonian Institution Press, London, United Kingdom.
- Ruth, T. K., P. C. Buotte, and H. B. Quigley. 2010. Comparing ground telemetry and global positioning system methods to determine cougar kill rates. *Journal of Wildlife Management* 74:1122–1133.
- Sand, H., J. A. Vucetich, B. Zimmermann, P. Wabakken, C. Wikenros, H. C. Pedersen, R. O. Peterson, and O. Liberg. 2012. Assessing the influence of prey-predator ratio, prey age structure, and packs size on wolf kill rates. *Oikos* 121:1454–1463.
- Sand, H., B. Zimmermann, P. Wabakken, H. Andren, and H. C. Pedersen. 2005. Using GPS technology and GIS cluster analyses to estimate kill rates in wolf-ungulate ecosystems. *Wildlife Society Bulletin* 33:914–925.
- Smith, D. W., T. D. Drummer, K. M. Murphy, D. S. Guernsey, and S. B. Evans. 2004. Winter prey selection and estimation of wolf kill rates in Yellowstone National Park, 1995–2000. *Journal of Wildlife Management* 68:153–166.
- Stephenson, R. O. 1978. Characteristics of exploited wolf populations. *Alaska Department of Fish and Game, Juneau Alaska, USA*.
- Thurber, J. M., and R. O. Peterson. 1993. Effects of population density and pack size on the foraging ecology of gray wolves. *Journal of Mammalogy* 74:879–889.
- Ver Hoef, J. M. 2008. Spatial methods for plot-based sampling of wildlife populations. *Environmental Ecological Statistics* 15:3–13.
- Vucetich, J. A., M. Hebblewhite, D. W. Smith, and R. O. Peterson. 2011. Predicting prey population dynamics from kill rate, predation rate and predator-prey ratios in three wolf-ungulate systems. *Journal of Animal Ecology* 80:1236–1245.
- Webb, N. F., M. Hebblewhite, and E. H. Merrill. 2008. Statistical methods for identifying wolf kill sites using global positioning system locations. *Journal of Wildlife Management* 72:798–807.
- Young, D. D., and R. D. Boertje. 2008. Recovery of low bull: cow ratios of moose in Interior Alaska. *Alces* 44:65–71.

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