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Kill rate of wolves on moose in a low density prey population: results from eastern interior Alaska

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Abstract

A study to estimate the kill rate of wolves on moose was initiated in eastern interior Alaska. This study is the first to examine kill rates in a system with such a low prey density (0.08 moose/km^2) and the presence of only a single prey species. Wolves were radio tracked daily during early February and March to locate kills. The estimated kill rate was 0.019 moose/wolf/day (95% CI: 0.011-0.028). This estimate was intermediary relative to previous work. The management implications of this result are discussed.

Introduction

In moose (*Alces alces*) and other long-lived species, the relative effect of adult female survival on population growth rate is greater than other demographic parameters such as reproductive effort or calf survival (Eberhardt et al. 1982, Nelson and Peek 1982, Stearns 1992, Testa 2004). Therefore, understanding patterns of mortality on adult females is valuable to managers. This is especially true in situations where numbers of a target species are below management goals and managers desire information on how best to stimulate an increase in population growth.

Moose in eastern interior Alaska on the Yukon Flats National Wildlife Refuge occur at some of the lowest densities in North America (0.08 moose/km^2) and are at levels below management goals (ADF&G 2002, Lake 2008). A study of mortality rates conducted during 1998-2000 demonstrated that 57% of adult female mortality was attributable to predation by wolves (*Canis lupis*) during winter (Bertram and Vivion 2002). This result generated interest in the role of wolf predation on moose in this system. Previous research has concluded that wolf predation can be a significant limiting factor on moose populations (Van Ballenberghe and Ballard 1994, Hayes et al. 2003) and especially in situations where moose occur at low densities (Gasaway et al. 1992). However, studies that have directly examined the rate at which wolves prey on moose have occurred in areas with greater moose densities and/or where multiple prey were present (reviewed in Messier 1994, Hayes et al. 2000, Hayes and Harestad 2000), questioning their applicability to a system with a single prey species that occurs at a low density. Understanding the kill rate of moose in this system will provide valuable information on the shape of the functional response curve at low prey densities (Hayes and Harestad 2000).

We marked wolves with radiocollars in order to study the rate at which they killed moose. Our objectives were to estimate kill rate of wolves on moose, estimate per capita consumption of moose by wolves, and determine the age and sex of killed moose. Our findings have implications for the management of moose in this system, in addition to providing a better understanding of the moose and wolf functional response at low prey densities.

Objectives

1. Estimate kill rate by wolves on moose.
2. Estimate per capita consumption of moose by wolves.
3. Determine age and sex of killed moose.

Methods

Capture

We captured fourteen wolves from seven packs during 8-11 November, 2008. Pilots in tandem seat aircraft searched for tracks in the snow and followed them until the pack was located (Stephenson 1978). We also captured wolves whose locations were recorded during a moose survey that occurred just prior to the wolf capture. During a second capture on 22 March, 2009, radio collars were added to four previously collared packs (n=5), and wolves from two new packs were collared (n=3). Wolves from the two new packs were captured southeast and northeast of Beaver, Alaska. All captured wolves were within 60km of Beaver, Alaska.

We chemically immobilized wolves by darting from a R-44 Robinson helicopter. Wolves were darted with a 3cc projectile syringe fitted with a 1.9cm barbed needle (Palmer Cap-chur™) loaded with 540 or 572 mg of tiletamine HCL and zolazepam HCL (Telazol®; Fort Dodge Animal Health, Ford Dodge, IA; Ballard et al. 1991). Each wolf was sexed, weighed, morphological measurements were recorded, and a VHF collar (Telonics model 500) was attached. From the 14 wolves in November 2008, we obtained samples of blood, fur, and tissue, and attached an ear tag. We aged wolves using a combination of tooth wear and staining, and body size. We examined each wolf to assess its overall condition and to note any obvious lesions.

Aerial Tracking

We visited each pack daily for a 13 day sampling interval in early February and an eight day sampling interval in early March, 2009 to locate kills made by wolves. These intervals were shorter than the planned 14 days due to weather constraints. On the first day of each sampling interval, we only located the pack. On the second and subsequent days, we first located the pack and then backtracked following tracks in the snow to the previous day's location. We employed the backtracking method in order to locate kills away from the pack, in addition to those kills that the pack was actively feeding on and were nearby. For each located kill, we recorded the species, age, sex, number of avian scavengers, number of mammalian scavengers, whether there were multiple kills (e.g., cow and calf moose), percent consumed following Carbyn (1983), and the probability that the kill was made by wolves (Mech et al. 2001). We used a helicopter to visit kills and collected a mandible and marrow sample. We also attempted to examine the skull or pelvis to assess the age and sex of kills on the ground if unable to do so previously from the air. During each daily visit, we also recorded the location of the pack, traveling pack size and colors, wolf activity (sleep, rest, walk, feed, run, social, other) and status (live, not heard, dead, disperse, not observed), snow conditions, and predominant habitat type.

Analysis

We used data from fresh kills made after day one to estimate kill rate. Kills located on the first day were excluded because inclusion would have positively biased the kill rate (Fuller and Keith 1980). We estimated kill rate using a ratio estimator (Hebblewhite et al. 2003), implemented with PROC SURVEYMEANS in SAS (SAS Institute 2007). Kill rate was kills/wolf/day and was calculated 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 for February and March and number of days the pack was under observation, excluding day one.

Home ranges of packs were calculated by generating minimum convex polygons around locations of daily visits during early February and March. This was accomplished using Hawth's Analysis Tools (Beyer 2007), implemented in ArcGIS 9.3.

Results

Aerial Tracking

Wolves were tracked during two sampling intervals in early February and March, 2009. Five packs were tracked daily for 13 days in February and six packs were tracked daily for eight days in March. Traveling pack sizes ranged from two to ten wolves and averaged 5.5 (Table 1).

Kill Rate

We observed a total of 18 fresh moose kills made by wolves during 21 days of monitoring (Table 1). Of those, 11 were made after day one and were included in estimation of kill rate. Kill rates for the six packs (moose/wolf/day) ranged from 0.012 to 0.048 (Table 1) and the mean kill rate was 0.019 (95% CI: 0.011-0.028). Relative to other studies, the estimated kill rate was intermediary (Figure 1).

During the 59 days of February and March, wolves in the study packs removed an estimated 38 moose (95% CI: 21-54). Assuming constancy in the kill rate, wolves in the study packs removed an estimated 118 moose (95% CI: 68-168) over the 184 days of winter (October 15-April 15).

Age and Sex Ratio

We were able to determine age and/or sex for seven kills. We identified one from the air and five from remains found on the ground at the kill site. Information on one was provided by a trapper. For the seven identified kills, two (29%) were calves of unknown sex and five (71%) were adult female moose. Specific ages (± 1 year) for the adult female moose based on counts of rings were 9, 10, 12, 13, and 14.

Per Capita Consumption

We were unable to estimate per capita consumption due to our inability to identify age and sex of all killed moose.

Snow Depth

Depth of snow was 27 inches at the Vunzik Lake marker on 9 February 2009. Depth of snow was 27 inches at the Beaver Creek marker on 9 February 2009 and 2 March 2009.

Home Range Size

Home ranges based on daily locations during the February and March sampling intervals ranged from 153.9 km^2 (Hodzana) to 556.1 km^2 (Bald Knob; Figure 2). Other home ranges were 188.7 km^2 (Hodzana Mouth), 264.8 km^2 (Lost Creek), 311.1 km^2 (Twin Lakes), and 364.4 km^2 (Marten Lake).

Discussion

Kill Rate

Our results indicated that 0.019 moose were killed per wolf per day or 1.9 moose per wolf per hundred days. Previous studies (Hebblewhite et al. 2003, McNay and Ver Hoef 2003) have expressed this value as a total number of ungulates, which is a more intuitive metric. During February and March (59 days), we estimated that wolves in our six study packs removed 38 moose and over the course of the winter (184 days) 118 moose. When considering these results and the work of McNay and Ver Hoef (2003), we suggest that removal of moose by wolves was higher than expected based on prey density. On the Tanana Flats of Alaska (GMU 20A), which has the highest density of moose (0.84 moose/km^2) in North America for an area of its size (Young 2004), McNay and Ver Hoef (2003) observed that 168 ungulates were removed by 8.2 wolf packs over 172 days in 1998 and 223 ungulates were removed by 7.8 packs over 172 days in 2000. Thus, wolves in our study removed 70% of that by wolves in 20A in 1998 and 53% in 2000, despite moose densities which were 89% lower in our study system. Some caution is advised when comparing these results as numbers from McNay and Ver Hoef (2003) were from a 12 day shorter time period, although estimates were from a greater number of packs (8.2 and 7.8 versus 6) and a system with caribou (*Rangifer tarandus*) present. Clearly, wolves in our study system are a significant predator of moose, despite low prey densities.

Wolf and Moose Functional Response at Low Densities

The kill rate in this study was lower than estimates in Hayes and Harestad (2000) who suggested a density dependent phase in the functional response at prey densities below 0.2 moose/km^2 (Figure 1). However, the kill rate was greater than predicted by Messier (1994), combined data from Messier (1994) and Hayes and Harestad (2000), and Eberhardt et al. (2003). Thus, the kill rate in this low density prey system does not fully resolve if and where the density dependent phase lies in the functional response curve. The importance of density independent factors, such as snow depth (Huggard 1993), have been suggested as confounding factors, and it is possible that kill rates may have been elevated in 2009 from snow depths slightly greater than average. That the kill rate was intermediary relative to previous studies has relevance to management. If densities of moose increase from current levels, wolves will likely respond by increasing the kill rate and taking more moose. Managers have advocated an increase in the harvest of predators (wolves and bears) in order to increase moose numbers (ADF&G 2002). It is known that bears are a significant predator of moose calves (Bertram and Vivion 2002) and efforts have been made by at least one tribal government to increase bear harvest by local residents. Increasing calf numbers through greater bear harvest alone, however, is likely to result in increased kill rates by wolves, thereby reducing the efficacy of bear harvest. To make bear harvest most effective, a similar type of wolf harvest is necessary.

Shortcomings and Future Improvements

We did not estimate the probability of detecting kills. We employed rigorous criteria in our study that included backtracking, but light conditions were not always optimal and some kills may have been missed, thereby negatively biasing the kill rate. We note, however, that the estimated kill rate was much greater than predicted by Messier (1994) and Eberhardt et al. (2003), suggesting that any bias may be minimal. There are several options for addressing detection of kills. First, a double observer method could be employed. Instead of a single airplane, two could be used and work independently to estimate the detection probability. However, this method may not be optimal with such a small sample size of kills. Another option is to use GPS collars to record locations of wolves every 2 hours, and infer kill sites based on clusters of locations (Webb et al. 2008). However, this method tends to result in a positive bias in kill rate because discerning clusters of a kill from clusters of a rest site is difficult. The GPS collar method is superior to daily tracking from the standpoint that data can be collected from across the winter instead of just a few months. In addition, weather constraints that limited sampling intervals are not a concern with the GPS collar method. GPS collars can also provide information on density (i.e., count of wolves in packs/sum of home ranges) of wolves (Burch et al. 2005). Of the two alternatives, the GPS collar method is preferred over the double observer. The Refuge already owns the needed GPS collars from a previous study and needs only to pay to have them refurbished. The total cost of refurbishment and data acquisition for 12 collars is about 24,060 dollars, and Telonics could have them ready in October if funds are available by August (C. Reindel, pers. comm.).

We were unable to accomplish the objective of estimating per capita consumption. It is unlikely that modifying the sampling protocol would allow for better identification of kills from the air and ground visits must be conducted soon after the wolves depart the kill otherwise snow covers up samples. A review of the literature may provide insight in how best to address this objective.

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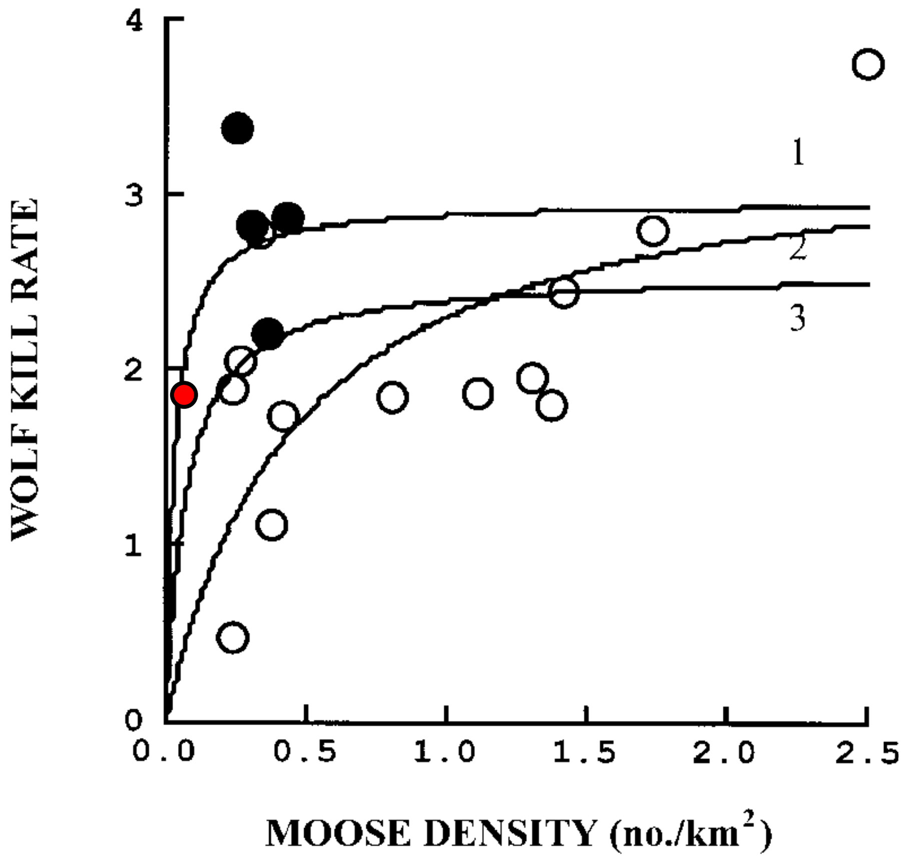

Figure 1. Wolf functional response to changes in moose density, based on kill rates from Hayes and Harestad 2000 and from Messier (1994). Curves are plotted on data from Hayes and Harestad 2000 (curve 1), cumulative data from Messier (1994; curve 2), and combined data (curve 3). The kill rate is the number of moose killed per wolf per 100 days. Adapted from Hayes and Harestad 2000. The red dot indicates the approximate location of the estimated kill rate from eastern interior Alaska in 2009.

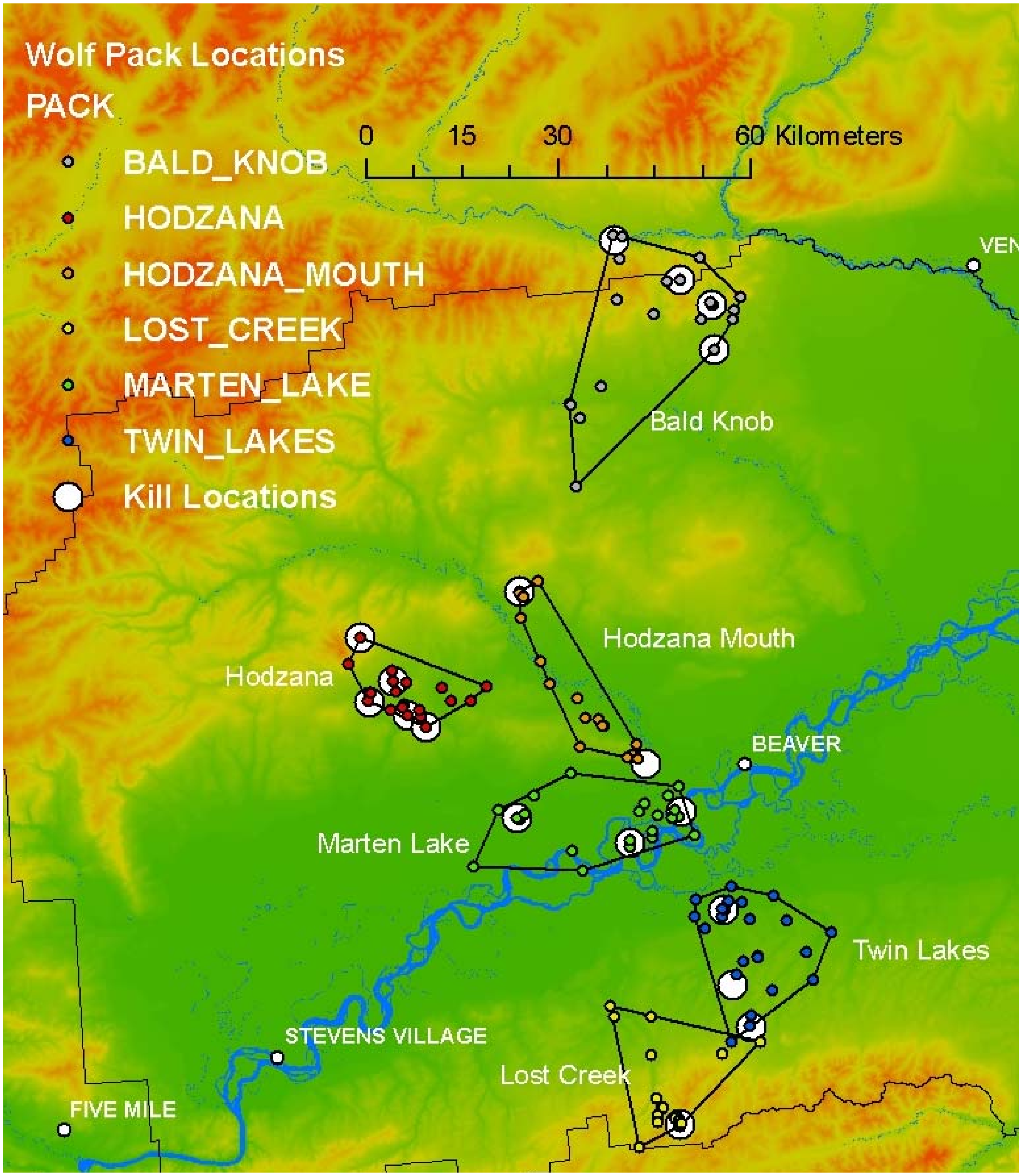

Figure 2. Daily locations of wolf packs during February and March, 2009 and locations of wolf kills made during those time periods. A minimum convex polygon is depicted for each wolf pack based on daily locations.

Table 1. Summary statistics for investigation of kill rate by wolves on moose in eastern interior Alaska. Wolves were tracked for 21 days; 13 during the first interval and eight during the second. Number of days in parentheses represents days included in estimation of kill rate, as the first day of each sampling interval was not used. Number of kills in parentheses represents those used to estimate kill rate, as kills located on the first day were not used. Pack size was the mean traveling pack size from the two sampling intervals. Wolf days was calculated as number of days tracked multiplied by pack size. Kill rate was calculated as number of kills divided by wolf days.

Pack	No. Days Tracked	No. Kills	Pack Size	Wolf Days	Kill Rate (moose/wolf/day)
Bald Knob	21 (19)	5 (4)	9	171	0.023
Hodzana	19 [a] (17)	5 (2)	10	170	0.012
Hodzana Mouth	21 (19)	2 (1)	2.25	47.5	0.023
Lost Creek	21 (19)	1 (1)	2	38	0.026
Marten Lake	20 [b] (18)	3 (2)	7	126	0.016
Twin Lakes	8 [c] (7)	2 (1)	3	21	0.048
$\overline{X}$	18.3 (16.5)	3 (1.8)	5.5	95.6	0.019

[a] The second sampling interval was truncated at six days when the collared wolf dispersed from the main pack.
[b] The second sampling interval was truncated at seven days when the alpha male was killed and the pack broke apart.
[c] The female of this two-wolf pack was killed at the beginning of the first interval. Daily tracking for estimation of kill rate was terminated until the male joined with another wolf, which occurred prior to the beginning of the second interval.

Appendix A. SAS code for estimating kill rate.

```
options linesize=80;
dm "clear output";
dm "clear log";

data WOLF_KILL_09;


proc print data=WOLF_KILL_09;
   title2 'raw data';

proc plot data=WOLF_KILL_09;
   plot KILLS * WOLFDAYS;

data kill_rate_pack;
set wolf_kill_09;

kill_rate_pack=kills/wolfdays;

proc print data=kill_rate_pack;

proc plot data=kill_rate_pack;
plot kill_rate_pack*packsize;

proc means;
var kills wolfdays packsize;

proc surveymeans data=WOLF_KILL_09   ratio clm   ;
   /* the ratio clm keywords request a ratio estimator and a confidence
interval. */
   title2 'Estimation using a ratio estimator';
   var KILLS WOLFDAYS;
   ratio KILLS / WOLFDAYS;
   ods output ratio=outratio;   /* extract information so that total
can be estimated */

   data outratio;
   /* compute estimates of the total for the months of february and
march (33.25wolves*59days) */
   set outratio;
   Est_total = ratio * 1961.75;
   Se_total  = stderr* 1961.75;
   UCL_total = uppercl*1961.75;
   LCL_total = lowercl*1961.75;
   format est_total se_total ucl_total lcl_total ;
   format ratio stderr lowercl uppercl;

   proc print data=outratio split='_';
   title2 'the computed estimates';
   var ratio stderr lowercl uppercl Est_total Se_total LCL_total
UCL_total;

   data outratio;
   /* compute estimates of the total for october 15-april 15
(33.25wolves*184 days)*/
```

```
   set outratio;
   Est_total = ratio * 6118;
   Se_total  = stderr* 6118;
   UCL_total = uppercl*6118;
   LCL_total = lowercl*6118;
   format est_total se_total ucl_total lcl_total ;
   format ratio stderr lowercl uppercl;

   proc print data=outratio split='_';
   title2 'the computed estimates';
   var ratio stderr lowercl uppercl Est_total Se_total LCL_total
UCL_total;

RUN;
QUIT;
```