

Vital rates, limiting factors and monitoring methods for moose in Montana



Federal Aid in Wildlife Restoration Grant W-157-R-4
Annual report, September 1, 2016

Nick DeCesare

Research Wildlife Biologist, MFWP
3201 Spurgin Rd. | Missoula, MT 59804
406-542-5558 | ndecesare@mt.gov

Jesse Newby

Research Technician, MFWP
490 N. Meridian | Kalispell, MT 59901
406-751-4588 | jnewby@mt.gov



State: Montana

Agency: Fish, Wildlife & Parks

Grant: Montana Shiras Moose Study

Grant number: W-157-R-4

Time period: 1 July, 2015 – 30 June, 2016

FUNDING PARTNERS:

Safari Club International Foundation:
Conservation Grant, FYs 2016–2017



Note: All results should be considered preliminary and subject to change; please contact the authors before citing or referencing these data.

Background and summary

Concern has arisen in recent years over widespread declines of North American moose (*Alces alces*) populations along the southern extent of their range. Populations in Montana appear to have declined since the 1990's, as evidenced by aerial survey trends and hunter harvest statistics. While declining populations have clear implications for hunting opportunity, moose hunting in Montana also suffers from a lack of rigorous data with which to monitor population trends and prescribe management actions.

In 2013, Montana Fish, Wildlife, & Parks (MFWP) began a 10-year study designed to improve our understanding of: 1) cost-effective means to monitor statewide moose populations, and 2) the current status and trends of moose populations and the relative importance of factors influencing moose vital rates and limiting population growth (including predators, parasites, habitat, and weather). We are using a mechanistic approach to hierarchically assess which factors are drivers of moose vital rates (e.g., adult survival, pregnancy, calf survival), and ultimately which factors are most important to annual growth of moose populations.

This document is the 4th annual report produced as part of this work. This report contains preliminary results from a subset of our work, including recent efforts to monitor moose with patch occupancy modeling of hunter sightings data, as well as results from the first 3 biological years of moose research and monitoring. All results should be considered preliminary as both data collection and analyses are works in progress.

Monitoring moose with hunter observations may offer a promising new approach to gathering statewide data. To date, we have collected >4,300 statewide moose sighting locations per year during 2012–2015 through the addition of questions about moose to big game hunters during annual hunter phone surveys. Initial occupancy modeling revealed an approximately 95% probability of detecting moose within a given 10 x 10 km grid cell across the statewide distribution of moose. No trend in statewide occupancy was evident across 2012–2015, though analyses are ongoing and results are subject to change pending more realistic models.

Moose vital rates measured with radio-collar studies currently indicate stable to increasing population trends in 2 study areas (Cabinet-Fisher and Rocky Mountain Front) and a declining population trend in the 3rd study area (Big Hole Valley). These estimated trends are largely driven by differences in adult female survival rates, which are relatively high in the first two areas and low in the third. To the contrary, calf survival rates appear lowest in the Cabinet-Fisher study area, though these rates have relatively less influence on the overall trajectory of the population. The average pregnancy rate of adults across these study areas (81%) is somewhat low relative to the North American average (84%), but not necessarily unlike that observed in other Shiras moose populations. During the past year we also began a remote camera-based study of multi-species predator occupancy among study areas and years. Monitoring of moose vital rates as well as potential limiting factors (predation, disease, and nutrition) will continue for the remainder of this 10-year study.

Web site: We refer readers to our project website for additional information, reports, publications, photos and videos. Go to fwp.mt.gov. Click on the “Fish & Wildlife” tab at the top... then near the bottom right click on “Wildlife Research”... and follow links for “Moose”.

Location

Moose vital rate research is focused primarily within Beaverhead, Lincoln, Pondera, and Teton counties, Montana. Other portions of monitoring (e.g., genetic and parasite sampling) involve sampling moose from across their statewide distribution.

Study Objectives (2015-2016)

For the 2015-2016 field season of this moose study, the primary objectives were;

- 1) Continue to evaluate moose monitoring data and techniques.
- 2) Monitor vital rates and limiting factors of moose in three study areas.

Objective #1: *Moose monitoring methods*

1.1. Calibrating existing moose monitoring data

A preliminary version of this research component was included in previous annual reports (2014, 2015). A peer-reviewed manuscript describing this work was accepted for publication within the Wildlife Society Bulletin during 2016, titled “*Calibrating minimum counts and catch per unit effort as indices of moose population trend.*” Below is the study Abstract, and .pdf copies of the final manuscript will be available on our website when published during fall, 2016:

Abstract: Monitoring wildlife population trends often involves indices assumed to correlate in proportion to abundance. We used aerial count data and harvest statistics for moose (*Alces alces*) populations in 16 hunting districts of Montana, USA, spanning 32 years (1983–2014) to assess population trends, drivers of uncertainty about those trends, and the relationship between aerial counts and hunter catch-per-unit-effort (CPUE). We found a great deal of statistical uncertainty surrounding population trends of moose measured with aerial minimum-count data, despite time series averaging >15 annual counts/district. State-space models of count-based trends suggested declining populations in 11 of 16 districts, yet 95% credible intervals overlapped 0 in all cases. The precision of count-based trends improved with increases in the number of years spanned by the time series ($\beta = -0.003$, $P < 0.001$) and average number of moose counted per survey ($\beta = -0.0006$, $P = 0.002$). Calibration of CPUE with count data showed positive correlations in only 5 of 16 (31%) districts and a catchability exponent (β) significantly <1. This indicated a generally poor level of agreement between these 2 indices, and evidence of ‘hyperstability,’ wherein declines measured by aerial counts were not reflected by proportionate declines in CPUE. Additionally, long-term trends measured with CPUE were not correlated to those in aerial counts ($P = 0.61$). We encourage explicit attention to the precision of trend estimates and local calibration of population indices to ensure both positive and proportionate relationships to underlying patterns of abundance.

1.2. Monitoring moose with sighting rates and patch occupancy modeling

Occupancy modeling allows biologists to estimate the spatial distributions of animals and trends of such over time, while controlling for variation in the probability of detection that can confound many sources of spatial data (MacKenzie et al. 2002, 2003). Because it does not require marked animals, occupancy modeling lends itself well to data collected by various means, including citizen science data collected by the general public (Hochachka et al. 2012, van Strien et al. 2013). For example, hunter sightings data have recently been used to monitor statewide populations of bobcats in New Hampshire (Mahard et al. 2016) and wolves in Montana (Rich et al. 2013). Rich et al. (2013) estimated wolf occupancy models by collecting hunter sightings of wolves and subdividing them into sampling sessions according to each week of the five-week hunting season. During 2012–2015 we have similarly collected hunter sightings data for moose, with the intention of evaluating the potential for using occupancy modeling to monitor statewide trends in moose presence and distribution.

Each year MFWP conducts phone surveys of a large sample of resident deer and elk hunters in Montana to facilitate estimation of various hunter harvest and effort statistics. Following the 2012–2015 hunting seasons, a subsample of these hunters were also asked to describe the location and group size of any moose sightings that occurred while hunting. These efforts resulted in an average of >4,300 statewide moose sighting locations per year, during 2012–2015, with approximately of 15% of sampled hunters reporting at least one moose sighting (Figure 1). We are currently building occupancy models to fit these data, but have conducted initial analyses to assess baseline levels of occupancy and the probability of detection by hunters.

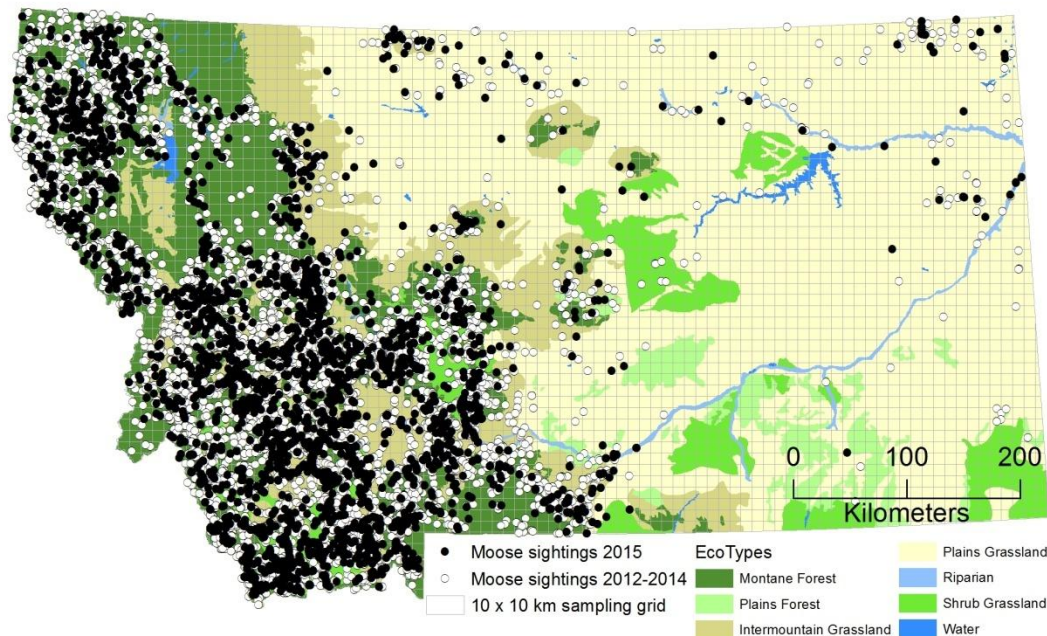


Figure 1. *Moose sightings collected using phone surveys of deer and elk hunters and a 10 x 10 km grid for sampling statewide occupancy during the fall, 2012–2015, Montana*

A first step towards translating sightings data into measures of occupancy is identifying a suitable resolution of grid cell size within which to compile sightings. Smaller grid cell sizes increase the spatial resolution of model predictions with regards to occupancy. However, given a finite amount of data, the probability of detecting moose also decreases within a given grid cell as cell size decreases. To optimize the balance between cost and model precision, MacKenzie and Royle (2005) recommended that methods should achieve a cumulative probability between 0.85 to 0.95 of detecting a given species across all sampling sessions, given that it is present. To select an optimal grid cell size, we estimated the cumulative probability of detection across grid cell sizes ranging from 16 km² (i.e., 4 x 4 km) up to 400 km² (i.e., 20 x 20 km) for the first two years of data, 2012–2013. This analysis revealed 3 possible grid cell sizes (8x8, 9x9 and 10x10) that would produce cumulative probabilities of detection within this range (Figure 2). We then selected 10 x 10, or 100 km², as a conservative grid cell size to achieve a mean cumulative probability of detection at or near $p=0.95$ across years of monitoring.

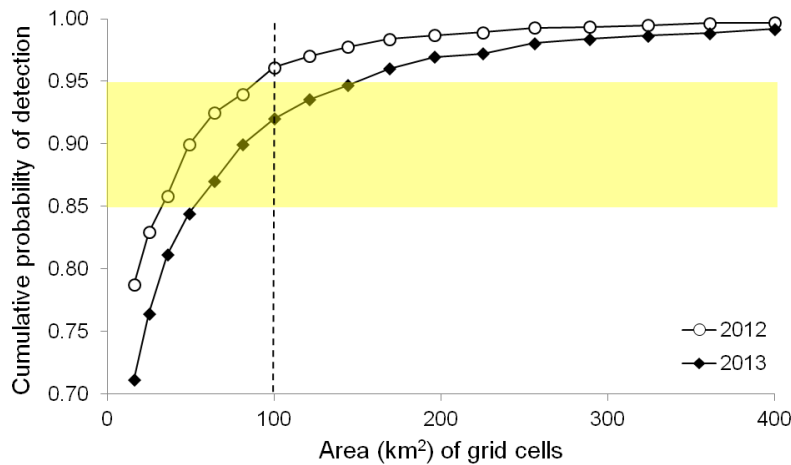


Figure 2. Variation in the cumulative probability of detecting moose with hunter sightings within grid cells of varying size across Montana, 2012–2013. The yellow shaded area represents the targeted level of 0.85–0.95, and the dotted line marks our selected size of 100km² for future monitoring.

We evaluated initial patterns of occupancy and probability of detection over the 4 years of study. Changes in the number of hunters contacted (and resulting cost) did appear to induce a change in the probability of detection, with 2012 being both the most expensive year and that with the highest probability of detection (Figure 3). However, despite varying sampling effort, underlying estimates of moose occupancy remained consistent across years, with overlapping confidence intervals of the mean occupancy per cell. Future analyses will assess spatial variation in occupancy across years as well as covariates predictive of rates of occupancy and detection.

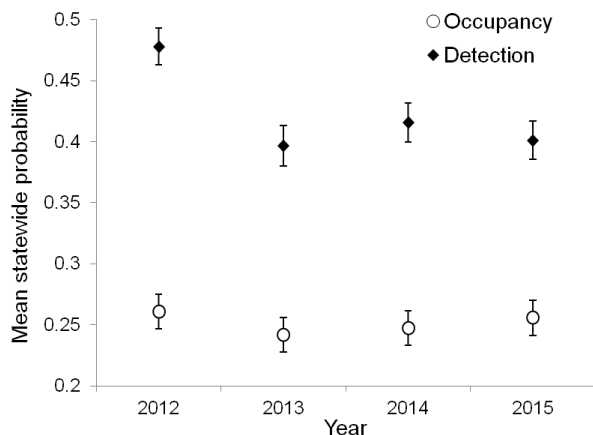


Figure 3. Annual estimates of the average rate of occupancy by moose per 100 km² grid cell as well as the weekly probability of detection within each week of the 5-week general hunting season, Montana, 2012–2015.

Objective #2: Monitor moose vital rates and potential limiting factors

2.1. Background

The study of vital rates allows important mechanistic insight into the factors driving population dynamics as well as estimation of population growth rates (DeCesare et al. 2012, Monteith et al. 2014b). In May, 2016 we reached the end of our third complete biological year of monitoring since beginning the study. Below we summarize the results of animal captures, monitoring of vital rates, and monitoring of limiting factors as components of our research into moose population dynamics over time. Specifically, we summarize vital rate estimates (adult female survival, calf survival, pregnancy) for the first two biological years. Researchers in other areas have found important effects of each of these vital rates upon moose dynamics (Berger et al. 1999, Keech et al. 2000, Lenarz et al. 2010, Sivertsen et al. 2012), thus baseline estimates of each will be important for understanding dynamics in Montana.

This research project is designed to provide inferences regarding moose population dynamics using a comparative study design. This involves replicating field methods at multiple study areas that contrast in the hypothesized ecological drivers of interest (Figures 4, 6). Monitoring moose vital rates, concurrently with potential limiting factors, will allow assessment of the importance of specific vital rates to population growth and the factors influencing those vital rates.

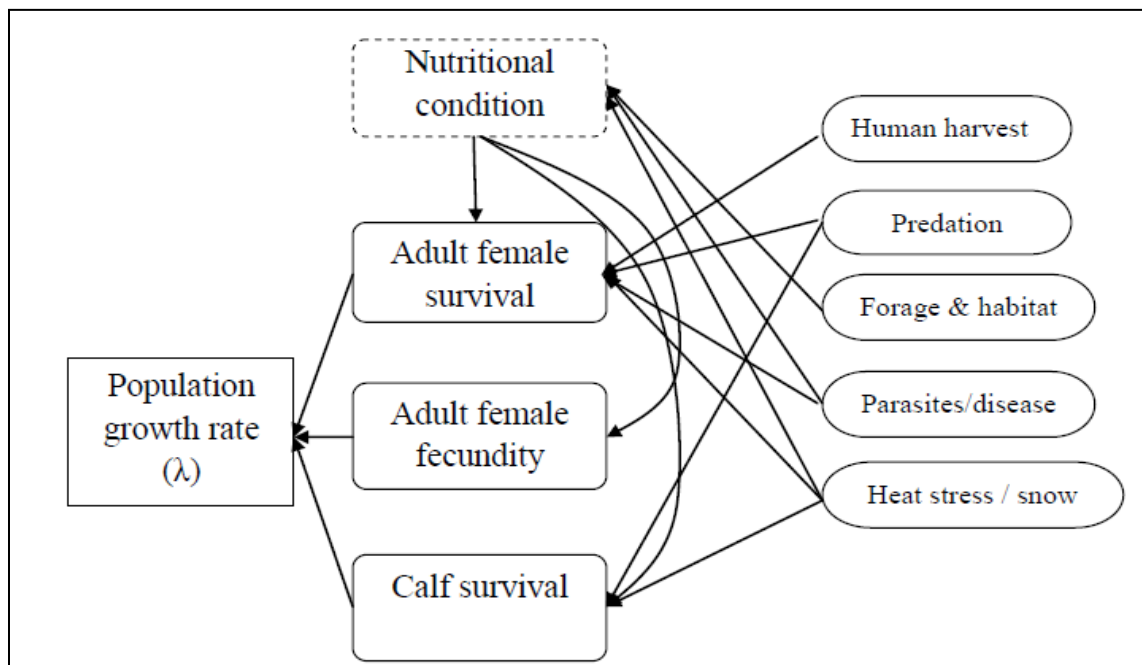


Figure 4. Ecological drivers hypothesized to influence specific moose population vital rates and ultimately population growth.

2.2. Animal capture and handling

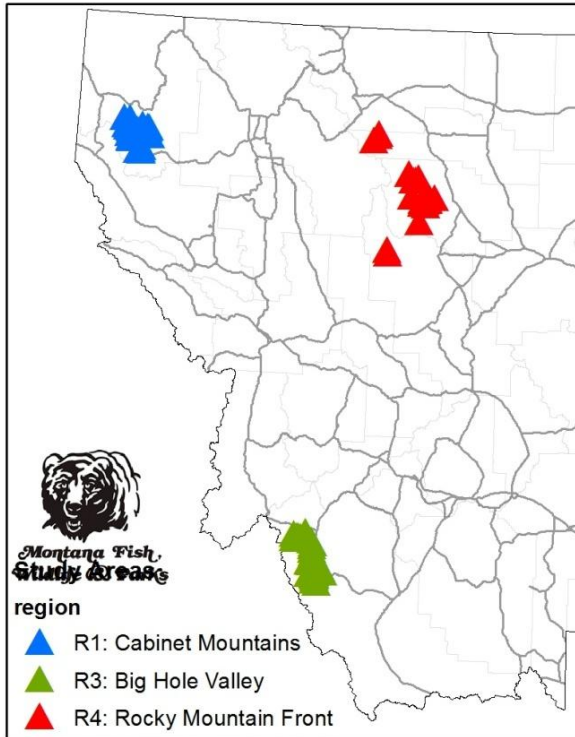
In February of 2016 we worked with a contracted helicopter capture company (Quicksilver Air) and local landowners to conduct captures and increase the sample of monitored moose. A total of 10 adult females were captured in 2 of the 3 study areas in 2016, with the goal of maintaining 30 collared animals in each area. Moose were fit with GPS radio-collars (Lotek LifeCycle and Vectronic Survey Globalstar). During 2013–2016 a total of 111 adult female moose have been captured and radio-marked, and as of August 1, 2016, 80 are currently being monitored (Table 1, Figures 5,6). A target sample size of 30 individuals/study area is sought achieve moderate precision in age-class specific annual survival estimates, while minimizing capture and monitoring costs.

Table 1. Sample sizes of radio-marked adult female moose by study area and year, excluding capture-related mortalities, and the number of adult females being monitored as of August, 2016.

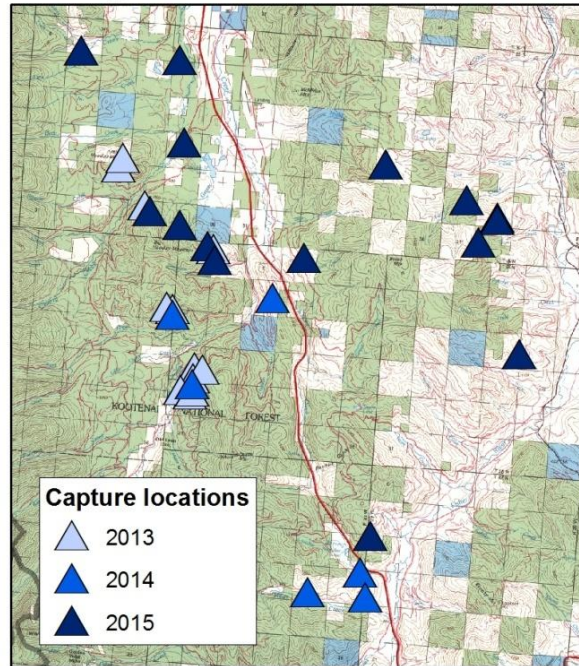
	Study Area			Total
	Cabinet-Fisher	Big Hole Valley	Rocky Mtn Front	
2013 captures	11	12	11	34
2014 captures	7	20	8	35
2015 captures	13	6	7	26
2016 captures	0	4	6	10
Total captures	31	42	32	105
Moose currently on-air (08/2016)	25	25	30	80



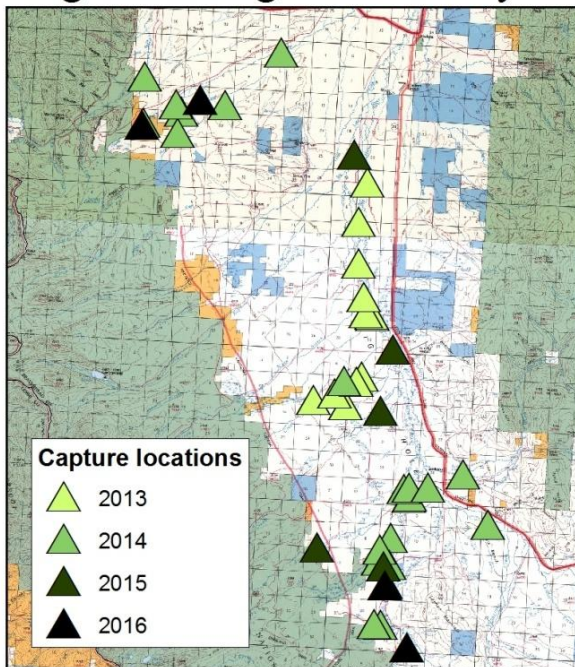
Figure 5. Helicopter darting (left) and handling (right) of moose F342 in the Big Hole Valley study area, February 2016.



Region 1: Cabinet-Fisher



Region 3: Big Hole Valley



Region 4: Rocky Mtn. Front

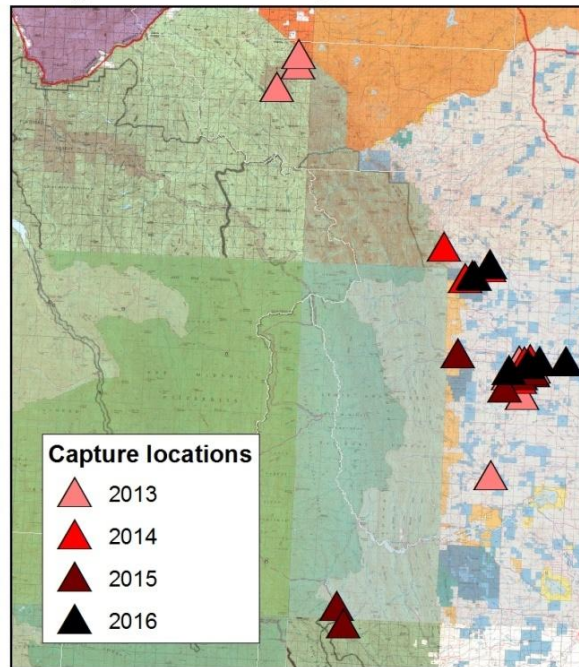


Figure 6. Moose winter capture locations during 2013–2015 across 3 study areas in Montana.

2.3. Monitoring vital rates

2.3.1. Adult female survival.— Our study of adult female survival to date includes 105 radio-collared adult female moose, with a staggered-entry design of individuals entering into the study across 4 winter capture seasons (see 2.2 Animal capture and handling). Animals have been deployed with both VHF ($N=67$) and GPS ($N=38$) collars, with mean survival monitoring intervals of 11.9 days and 1.4 days, respectively. For this analysis we estimated Kaplan-Meier annual survival rates for each study area during each biological year as well as across the 3 biological years pooled together.

Pooled annual survival estimates for each study area were 0.935 (SE=0.029, 95% CI=[0.88,0.99]) in the Cabinet-Fisher, 0.819 (SE=0.044, 95% CI=[0.74,0.91]) in the Big Hole Valley, and 0.970 (SE=0.021, 95% CI=[0.93,1.0]) on the Rocky Mountain Front (Figure 7). Non-overlapping confidence intervals suggest that annual adult survival in the Big Hole Valley is significantly lower than that on the Rocky Mountain Front.

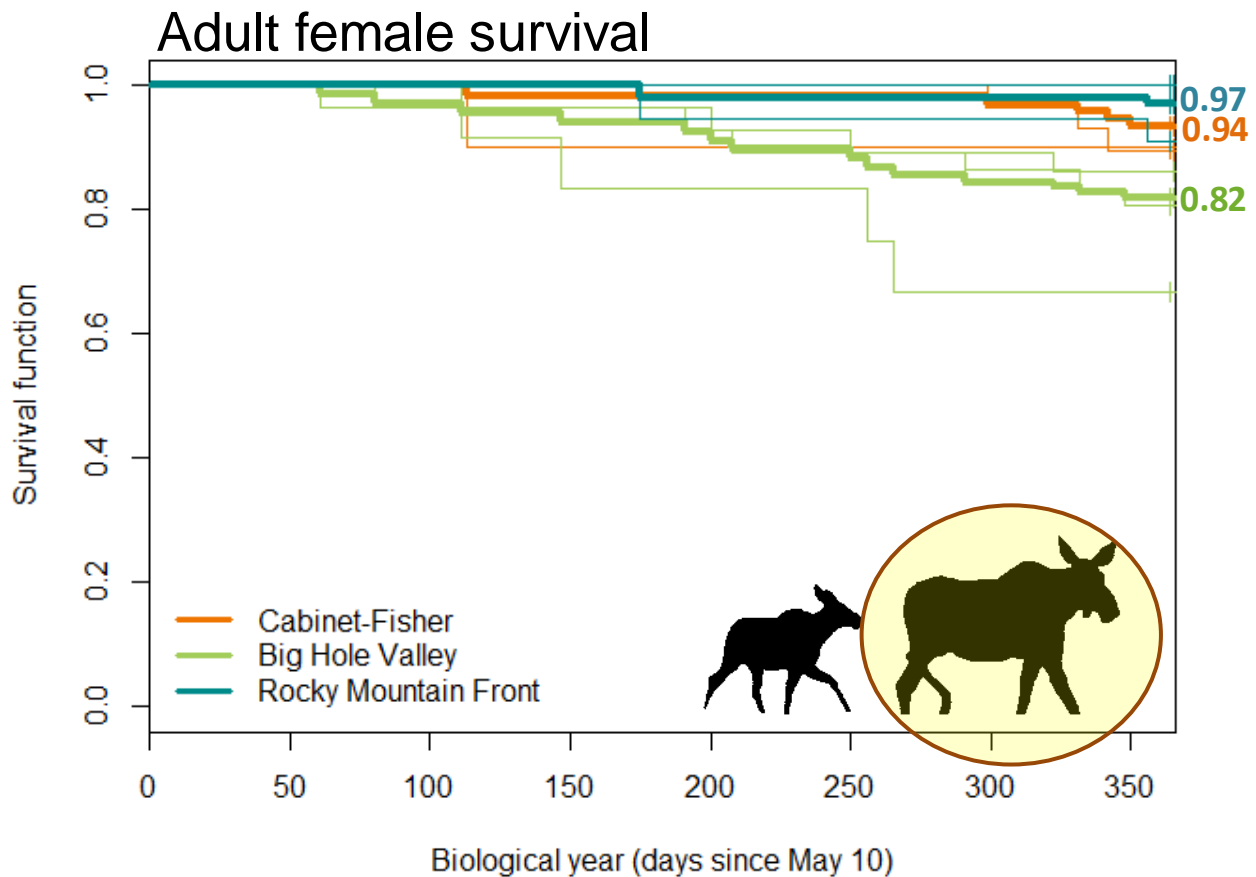


Figure 7. Kaplan-Meier estimates of annual adult female survival within each study, where bolded lines are pooled estimates across 3 biological years for each study area and thin lines are annual estimates for each study area and year, Montana, 2013–2015.

During the first 3 biological years of monitoring, we have documented 21 mortalities of collared adult moose across all study areas: 5 in the Cabinet-Fisher, 14 in the Big Hole Valley and 2 in the Rocky Mountain Front (Table 2). The Big Hole has experienced relatively high mortality due to disease or health-related causes (Figure 8). Ongoing research will attempt to better understand the causes and consequences of these mortalities.

Table 2. Numbers of mortalities by cause for radio-collared adult female moose documented during February 2013–June 2016, Montana.

Cause of Mortality	Study area		
	Cabinet-Fisher	Big Hole Valley	Rocky Mountain Front
Health-related (e.g., disease or malnutrition)	1	13	0
Hunter harvest	0	1	0
Poaching	0	0	1
Predation, wolf	3	0	1
Unknown	1	0	0



Figure 8. An example health-related mortality site of F334 in the Big Hole study area, 2015. Cause of death was not determined with certainty, but appeared acute given good nutritional condition. A high load of arterial worms (*Elaeophora schneideri*) was found which may have been a mortality factor.

2.3.2 Calf survival.— We used aerial telemetry to visually search for calves-at-heel with each collared adult female at approximately weekly intervals during 15 May – 15 July. In cases when animals were not well-observed from the air, we opportunistically followed-up with ground investigation to visually monitor calves. Flights were conducted with exclusively fixed-wing aircraft in the Big Hole Valley, rotary-wing in the Cabinet-Fisher, and a mix of both on the Rocky Mountain Front. We documented 20 total calves from 19 litters in 2013, 40 calves from 39 litters in 2014, and 59 calves from 56 litters in 2015. We then monitored the fates of these calves by visually locating them with their dams throughout their first year of life (Figure 9).

An unknown proportion of the true number of calves born is assumed to have died before we were able to visually confirm them. Thus, our sample is left truncated (Gilbert et al. 2014), and our Kaplan-Meier based estimates of calf survival should be considered as optimistic (potentially biased positive) estimates of survival of only those calves who survived long enough to be detected. Below we explore this assumption further by comparing pregnancy rate estimates with observed parturition rates (*see* Figure 12), and in the future we may consider applying nest success models developed to accommodate such unobserved mortality (Dinsmore et al. 2002).



Figure 9. We monitor calf survival with repeated visual observation of the presence or absence of calves-at-heel with collared adult females throughout each biological year (May – April).

Over the first 3 biological years (May 2013 – May 2016), pooled Kaplan-Meier survival estimates of calves-at-heel were 0.300 (SE=0.084, 95% CI=[0.17,0.52]) in the Cabinet-Fisher, 0.441 (SE=0.072, 95% CI=[0.32,0.61]) in the Big Hole Valley, and 0.597 (SE=0.078, 95% CI=[0.46, 0.77]) on the Rocky Mountain Front (Figure 10). Study area-specific survival curves suggest lowest calf survival in the Cabinet-Fisher relative to the other two study areas, though confidence intervals overlap.

We monitored calves-at-heel at approximately weekly intervals during mid-May to mid-June, monthly during summer, and every two to three months during fall and winter. Thus, the precision of estimates of the timing of mortalities is somewhat variable throughout the year, but basic seasonal comparisons of mortality rates will be possible. Thus far, an expected pulse of early mortality during the first month of life has been observed in one study area (*see* Cabinet-Fisher curve, Figure 10), but mortalities during fall and winter have also occurred.

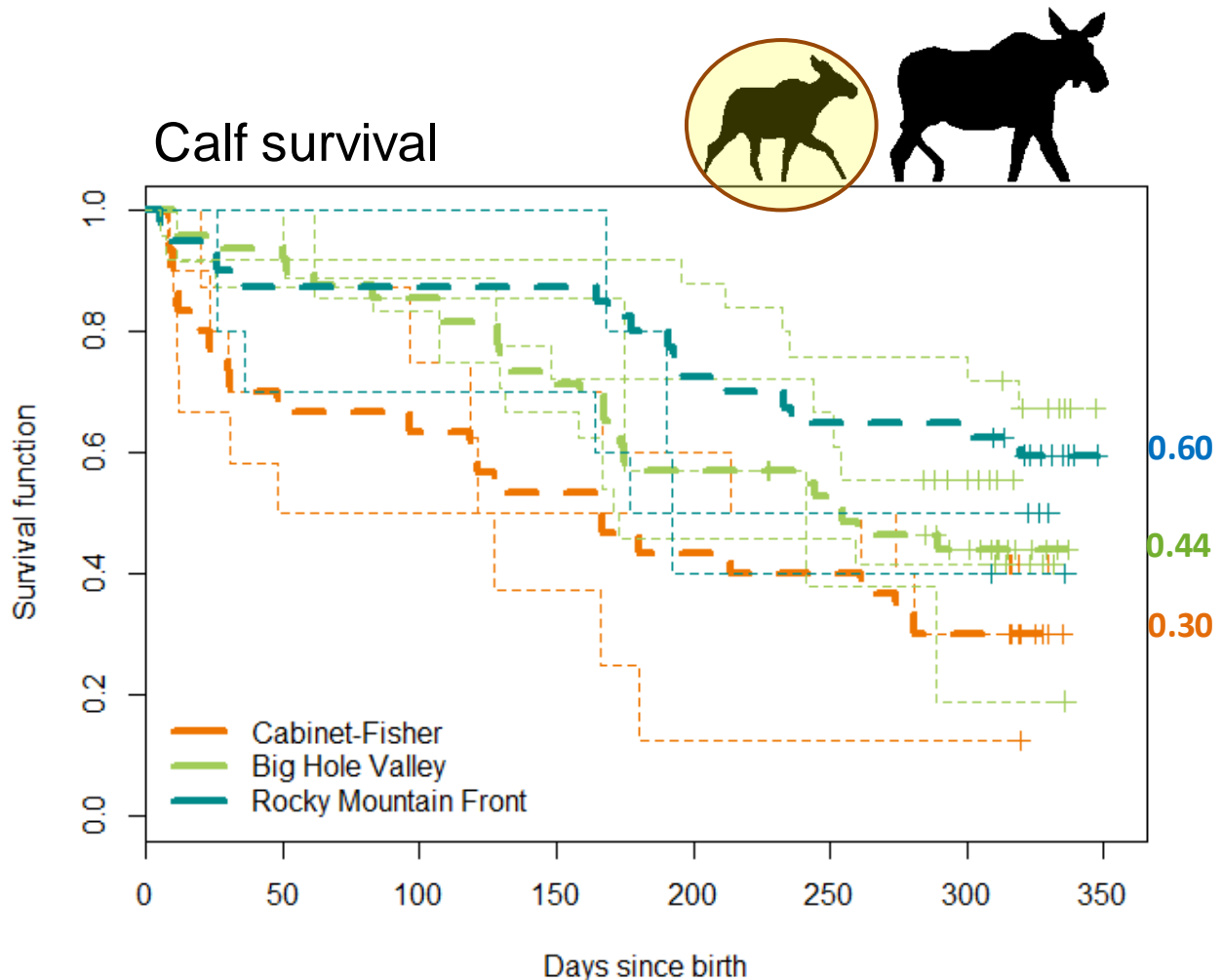


Figure 10. Kaplan-Meier estimates of annual calf survival for the first year of life within each study area, where bold lines are pooled estimates across 3 biological years and thin lines are annual estimates per year, Montana, 2013–2016.

2.3.3 Adult female fecundity.—Fecundity for moose is the product of pregnancy rate, survival rate of fetuses to parturition, and litter size. We monitor pregnancy of animals during winter with laboratory analyses of both blood and scat. Blood analyses are based on the presence of a pregnancy specific protein B (PSPB) within serum (Huang et al. 2000). The concentration of progesterone hormone metabolites in scat samples (i.e., fecal progestagens) can also be used to detect pregnancy in moose (Berger et al. 1999, Murray et al. 2012). We measured fecal progestagen (FP) concentrations with two sampling techniques: 1) capturing animals and collecting fecal samples concurrent with blood sampling, and 2) using ground-tracking of free-ranging radio-collared moose throughout the winter (January–April) to collect fecal samples from the snow.

Generally FP results were in agreement with PSPB results, and we used logistic regression to model the probability of PSPB-based pregnancy diagnosis as:

$$\Pr(PSPB_{pregnant}) = \frac{\exp(\beta_0 + (\beta_1 * FP))}{1 + \exp(\beta_0 + (\beta_1 * FP))},$$

using separate models for 2013, 2014, and 2015 and a single pooled model ($\beta_0 = -3.44$, $\beta_1 = 0.00405$). This pooled model estimates a predicted probability of being pregnant of 0.5 and 0.95 for fecal progesterone values of 850 and 1575 ng/g, respectively (Figure 11).

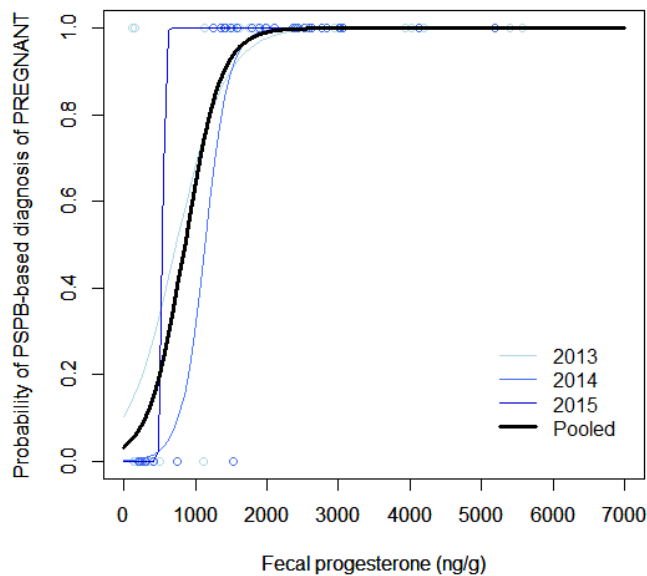


Figure 11. *Observed (points) and modeled (lines) relationship between fecal progesterone concentrations and pregnancy diagnoses (according to PSPB in serum) for moose captured in 2013–2015, Montana.*

Pregnancy rates: Pooled across 3 study areas and 3 years (2013–2015) of monitoring pregnancy with both PSPB and fecal progesterone, we have thus far estimated an average adult (ages ≥ 2.5) pregnancy rate of 81.4% and a yearling (age 1.5) pregnancy rate of 23.5%. Thus far, the adult pregnancy rate has not varied significantly among study areas (Figure 12). Adult pregnancy has been consistently below the 84.2% average of adult moose pregnancy rates across North American (Boer 1992). Low pregnancy rates from 48%–75% have been reported in other Shiras moose populations (Oates et al. 2012), and this may reflect generally lower productivity of this subspecies, or the habitat within which it resides, compared to northern populations.

Apparent parturition rates: Following winter pregnancy testing, we monitor radio-collared cows with aerial telemetry flights during the birthing season to document the presence and timing of birthed calves. We use visual observation of neonate calves to estimate an “apparent parturition” rate, representing the proportion of pregnant cows with which we detected calves each spring. An apparent parturition rate of 100% would indicate observation of calves with all pregnant cows, whereas values lower than 100% indicate calves that were lost either to abortion or reabsorption during pregnancy or to early mortality following birth. Apparent parturition rates have been higher in the Big Hole Valley (92%) and Rocky Mountain Front (88%), and lower in the Cabinet-Fisher (65%; Figure 12). These results are similar to those of other studies (e.g., Becker 2008) where parturition rates are lower than pregnancy rates due to presumed fetal losses throughout winter and/or death of neonatal calves prior to their detection during spring.

Twinning rates: Moose are capable of giving birth to 1–3 calves, though litters are most commonly composed of either 1 or 2 calves (Van Ballenberghe and Ballard 2007). Twinning rates in North American populations can vary from 0 to 90% of births (Gasaway et al. 1992), with variation linked to nutritional condition (Franzmann and Schwartz 1985) and animal age (Ericsson et al. 2001). Twinning rates for Shiras moose are typically low (e.g., <15%; Peek 1962, Schladweiler and Stevens 1973, Becker 2008). Thus far our observed twinning rates are 3.6% in the Cabinet-Fisher ($N=28$ litters), 0% in the Big Hole Valley ($N=49$ litters), and 12.9% in the Rocky Mountain Front study areas ($N=31$ litters), leading to average litter sizes of 1.04, 1.0, and 1.14, respectively (Figure 12).

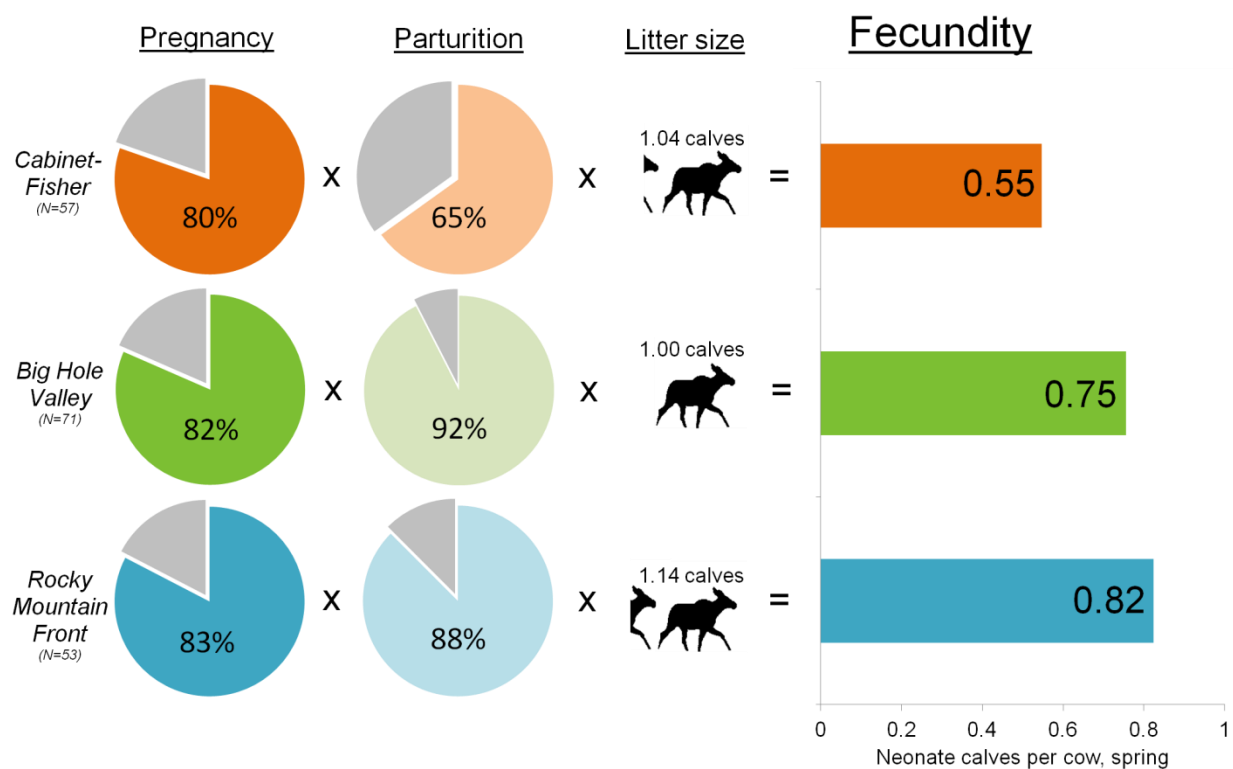


Figure 12. Estimated adult (aged ≥ 2.5) pregnancy rates, apparent parturition rates, average litter sizes, and net productivity of calves-at-heel during the spring May-June period for moose in 3 study areas of Montana during 3 biological years, 2013–2015.

2.3.4. Population growth rates. The overall status of a population may be best characterized by the annual growth rate. This parameter can be estimated by inserting key vital rates into mathematical models, most importantly the annual survival of adult females and the per capita number of calves born and surviving their first year. We estimated recruitment with calf/cow ratios specific to our collared sample of cow moose and measured in March/April of each year. We then estimated annual population growth rates, following DeCesare et al. (2012), for each study population across the first 3 biological years, 2013–2016 (Figure 13).

While moose on the Cabinet-Fisher study area have seen the lowest calf-survival rate of the 3 areas thus far, they have also shown relatively high adult survival. Given the high elasticity of adult female survival in long-lived, iteroparous species (Eberhardt 2002), adult female survival is the most important vital rate for determining population growth rates. High adult survival in the Cabinet-Fisher translated to a mean population growth rate of 1.02, or an 2% increase per year. The Rocky Mountain Front moose have seen very high survival rates of both adults and calves as well as high fecundity of adults, resulting in an estimated annual growth rate of 1.12. To the contrary, the Big Hole Valley population has shown relatively high calf survival, but the lowest adult survival rate, which resulted in an estimated population growth rate of 0.98, or an average of 2% decline per year.

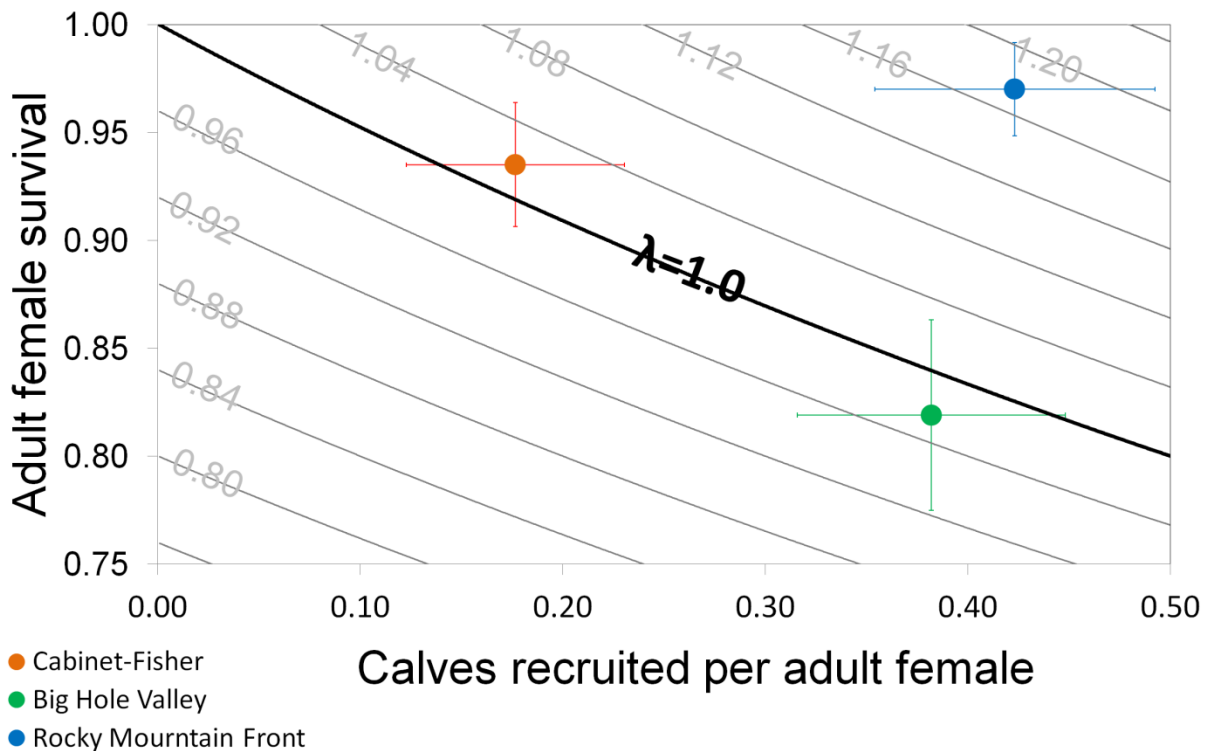


Figure 13. Contour plot showing the estimated mean annual population growth rates (λ , represented as contour lines) resulting from two-dimensional combinations of adult female survival and spring calf:cow ratios. Dots and error bars show the annual means and standard errors of these vital rates for 3 moose populations in Montana during 3 pooled biological years, 2013–2016. Growth rates above the bold line (where $\lambda = 1$) indicate a growing population, growth rates below $\lambda = 1$ indicate declining populations.

2.4. Nutrition

2.4.1. Hunter-based sampling of nutritional condition. Nutritional condition of ungulates can impact both survival (Roffe et al. 2001, Bender et al. 2008) and fecundity (Testa and Adams 1998, Keech et al. 2000, Testa 2004), and generally provides an indication of the extent to which habitat condition and density dependent effects drive ungulate dynamics (Franzmann and Schwartz 1985, Bertram and Vivion 2002). Rump fat thickness has a strong linear relationship with total body fat in moose (Stephenson et al. 1998). In addition to collecting measuring rump fat among all captured adult females, we have asked hunters to measure rump fat of harvested moose, beginning in 2013.

Moose hunters measured rump fat by marking a toothpick within provided sampling kits for 291 bull and 39 cow moose. Before comparing fat measurements across regions of Montana, we first assessed the relationship between the date each moose was harvested and its respective fat levels, as bull moose are known to lose fat with high energy expenditure during the rutting season (Cederlund et al. 1989). While there was much variation, we found a significant loss in rump fat depth among bull moose across all 3 years ($P < 0.001$), whereas fat among cows did not change with day of season ($P = 0.83$; Figure 14).

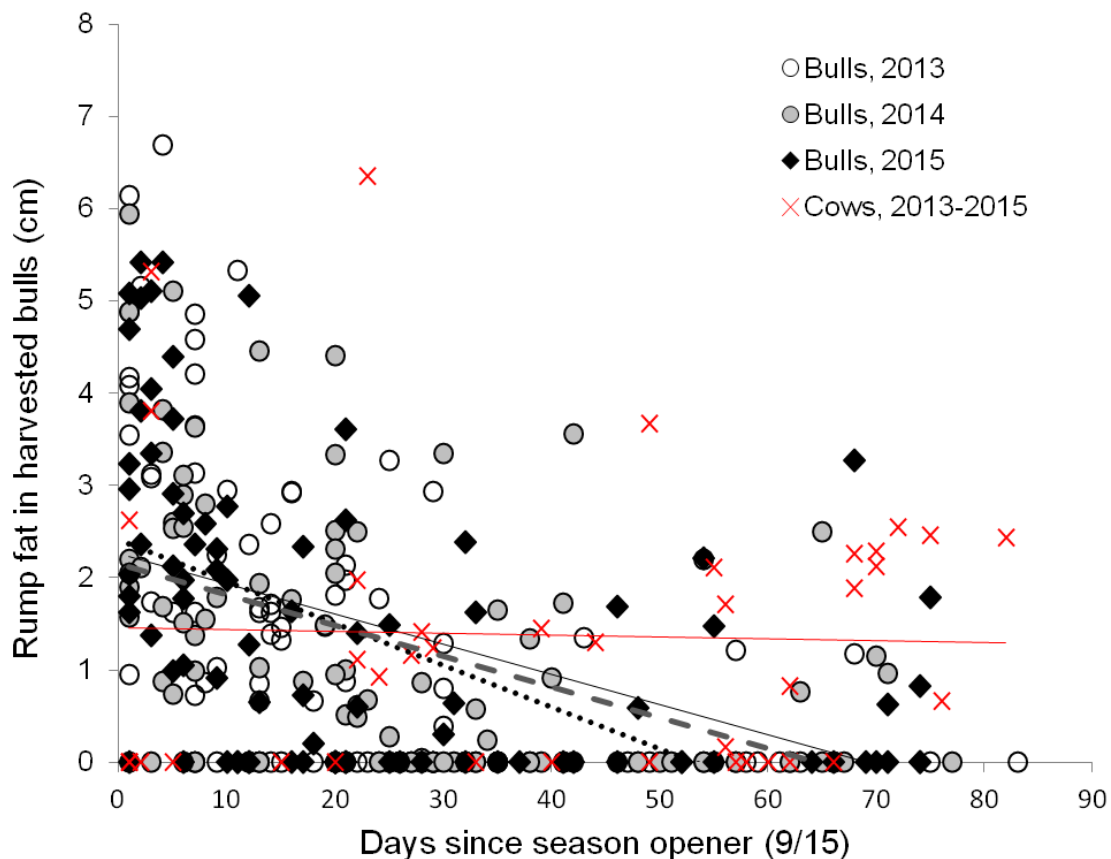


Figure 14. Depth of rump fat declined among harvested bull moose according to the date of harvest during the past 3 hunting seasons, whereas average fat depths among cow moose did not significantly change during the hunting season, Montana, 2013–2015.

After assessing how average fat levels changed during the season, we compared observed measurements of fat for each moose to the average expected amount of fat following the trend lines in Figure 22. We then estimated the residuals between observed and predicted values, where a positive value suggested an animal with more fat than expected given the date of harvest, and a negative value an animal with less fat than expected. We compared these residual values among all MFWP regions and found no evidence for statistical differences in the nutritional conditions of bull moose among regions (Figure 15).

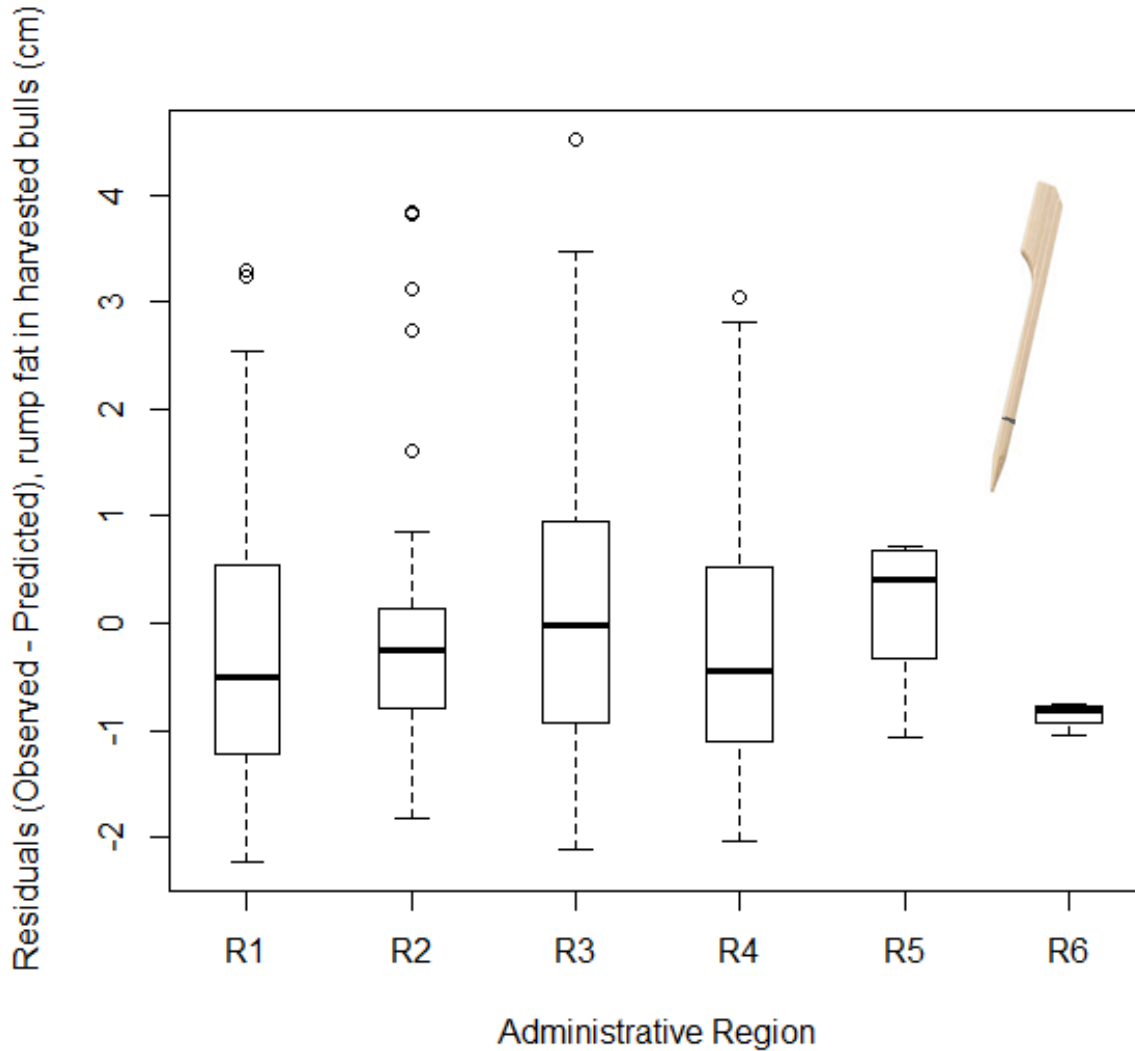


Figure 15. Average residual values comparing the thickness of rump fat in hunter-killed moose among regions while controlling for the date of harvest. These data were collected by hunters by marking a toothpick (inset photo) included in sampling kits mailed to all license-holders, Montana, 2013–2015.

2.4.2. Winter forage quality.

Previous research has suggested that nutritional indices measured from fecal samples can be used to monitor differences in the dietary quality of forage ingested by ungulates (Leslie et al. 2008). For example, Hodgman et al. (1996) showed that diet quality for mule deer, in the form of digestible energy, could be effectively monitored with measures of fecal neutral detergent fiber (FNDF; $r^2=0.93$), where increased FNDF corresponded to decreased digestible energy. Similarly, these authors and others have found significantly positive trends between fecal nitrogen (FN) and forage quality (Leslie and Starkey 1985, Osborn and Ginnett 2001, Leslie et al. 2008). Despite these encouraging results, a great deal of caution is needed when interpreting fecal indices due to the high potential for confounding effects of dietary components, such as tannins, differences due to lactation status, and others (Hobbs 1987, Robbins et al. 1987, Monteith et al. 2014a).

While comparisons of fecal indices across populations with different diet compositions may pose problems of confounding (Ueno et al. 2007), an alternate approach is to monitor differences in fecal indices within-population and over time (Blanchard et al. 2003, Ueno et al. 2007). Blanchard et al. (2003) found an inverse relationship between FN and the density of bighorn sheep, suggesting that FN may be used to monitor density-dependent negative effects on population-level forage quality.

Most studies of FN involve forage during the summer growing season when nitrogen is most abundant and variable. However, studies of moose forage to date have often focused on winter range quality, when densities and relative browsing pressure are typically highest (Seaton et al. 2011, Burkholder 2012). As a pilot assessment of FN and FNDF as metrics of forage for moose, we evaluated each during the first 3 winters of study across our study areas (Figure 16). While these data are yet unvalidated as metrics of forage quality, they do not show significant differences among study areas in either metric thus far. We will continue to explore these metrics as well as summer-season metrics as indices of moose forage quality.

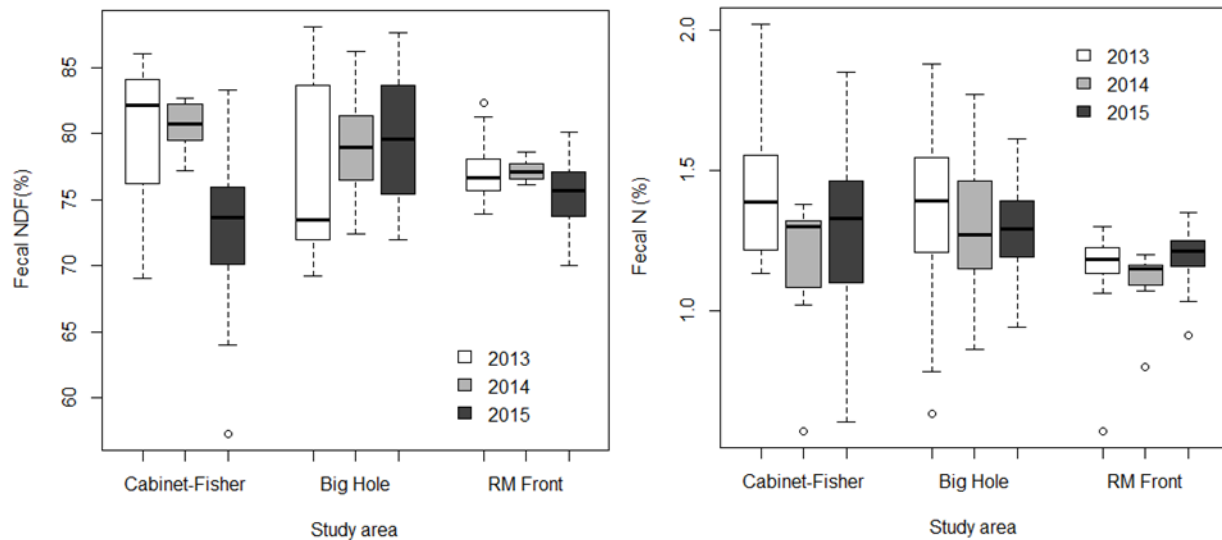


Figure 16. Winter fecal neutral detergent fiber (NDF) and nitrogen (N) measured from each radio-collared moose across three study areas and three years, Montana, 2013–2015.

2.5. Multi-species predator occupancy

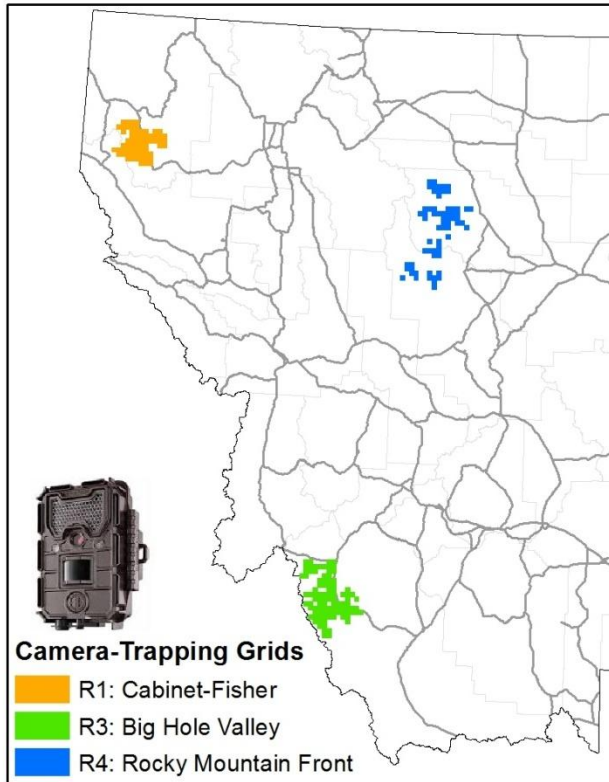
Assessing the extent predation limits moose populations is of basic concern to Montana Fish, Wildlife & Parks research on moose population ecology. Predator/prey relationships have been a major area of interest in moose ecology and management across their range. Primarily research has focused on the effects of brown bear (*Ursus arctos*), black bear (*Ursus americanus*) and wolf (*Canis lupus*) predation; though mountain lions (*Puma concolor*) are known to predate on moose to some extent and even coyotes (*Canis latrans*) may take calves (Ross and Jalkotzy 1996, Bartnick et al. 2013, Benson and Patterson 2013).

Past research indicates predation by brown bears can significantly impact calf survival rates (Ballard et al. 1981, Larsen et al. 1989, Swenson et al. 2007). Black bears, especially when occurring at high densities, can also be an important predator on moose calves (Stewart et al. 1985, Ballard et al. 1990). Predation by bears on moose calves predominantly occurs within the first 30-60 days after parturition and drops off after this period (Larsen et al. 1989, Testa et al. 2000, Swenson et al. 2007). However, grizzly bears are known to predate on yearling and adult moose with some regularity (Boertje et al. 1988).

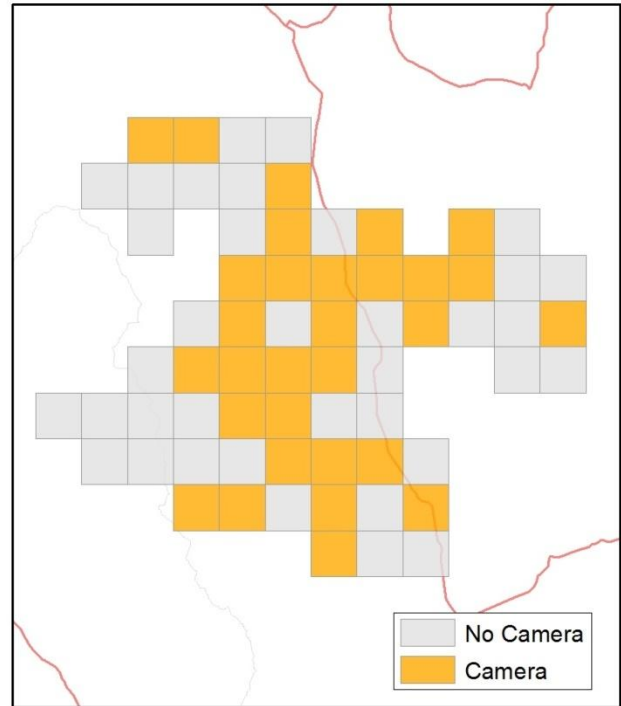
Previous research in areas where wolves overlap with moose and bears generally find bear predation on neonate moose to be more significant than wolf predation (Franzmann et al. 1980, Ballard et al. 1981, Boertje et al. 1988, Larsen et al. 1989). However, wolves are effective predators on moose calves year round and can significantly affect calf survival (Messier and Crête 1985, Ballard 1992). Wolves also predate upon adult moose and in some cases limit moose populations (Gasaway et al. 1983, Messier and Crête 1985, Wilmers et al. 2006).

Given the potential role of these carnivores in moose population dynamics, and perhaps more importantly the effects of the predator guild as a whole (Sih et al. 1998, Griffin et al. 2011, Keech et al. 2011), we are assessing the relationship between predator densities and moose vital rates in Montana. Remote camera trapping, combined with emerging statistical models, are being used to provide a non-invasive and cost-effective means of estimating occupancy and relative densities of multiple species simultaneously (Brodie et al. 2014, Burton et al. 2015).

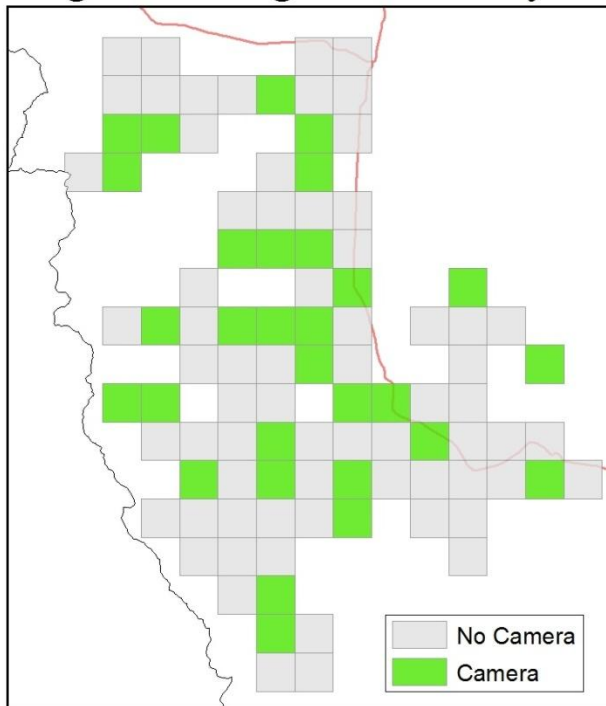
Beginning in September of 2015 we deployed remote camera traps across the 3 moose field study areas. Camera traps were distributed by establishing a sampling grid over the area with known summer and winter locations of marked moose and randomly selecting grid cells (Figure 17). We randomly selected 15 cells containing summer moose telemetry locations and 15 cells containing winter locations within each study area. This approach was taken to ensure cameras were distributed effectively across seasonal ranges, though there was much overlap among seasons. Within each selected cell, we established un-baited camera sets along trails, roads, and topographical features to maximize detections of multiple carnivore species. The successful establishment and continued maintenance of camera sets has been greatly helped by the participation of local landowners and managers.



Region 1: Cabinet-Fisher



Region 3: Big Hole Valley



Region 4: Rocky Mtn. Front

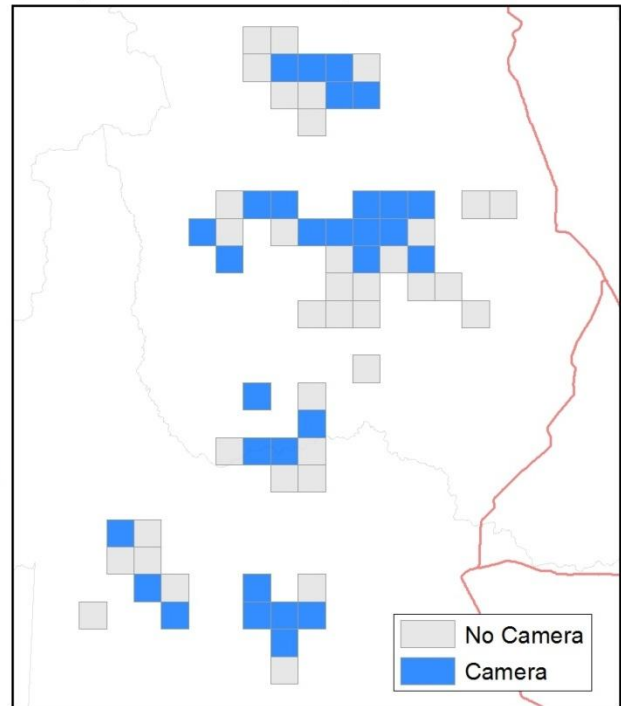


Figure 17. Sampling grids (2 x 2 miles) for deployment of remote cameras for monitoring multi-species predator occupancy across areas occupied by moose, Montana, 2016.

Analytical methods for estimating predator densities over space and time using detections of unmarked species is an active area of research (MacKenzie et al. 2002, Royle 2004, Chandler et al. 2013). Camera trapping efforts were implemented to take advantage of recent developments using hierarchical N-mixture models to estimate mean abundance of unmarked species at camera site while accounting for detectability (Royle 2004, Brodie et al. 2014). Through ongoing carnivore monitoring efforts conducted by state and federal agencies a number of wolves and grizzly bears have been marked in areas overlapping moose study field sites. Photos of these known individuals can be used to improve density estimates of these species (Royal 2004).

Since September 2015 we have deployed remote cameras at 113 sites, 88 of which are currently active. To date we have retrieved and stored 531,175 images spanning roughly 21,865 camera trap-days. Only a small portion of these images (9,832 photos) spanning approximately 660 trap-days have been formally classified. These classified images, along with photos incidentally observed during sorting, revealed a substantial number of detections for all target carnivore species, moose and ancillary species (Table 3, Figure 18).

Table 3. *Number of camera days in which select species were detected among 660 camera-days classified between September 2015 & June 2016. Note that camera days for which images have been classified represents a small subset (~3%) of camera days recorded to date.*

Species	# of days detected	% camera-days detected
Bear (total)	24	3.64%
Black bear	12	1.82%
Bobcat	15	2.27%
Coyote	29	4.39%
Elk	17	2.58%
Grizzly bear	10	1.52%
Moose	11	1.67%
Mountain lion	12	1.82%
Mule deer	32	4.85%
White-tailed deer	71	10.76%
Wolf	9	1.36%
Camera-days	660	660

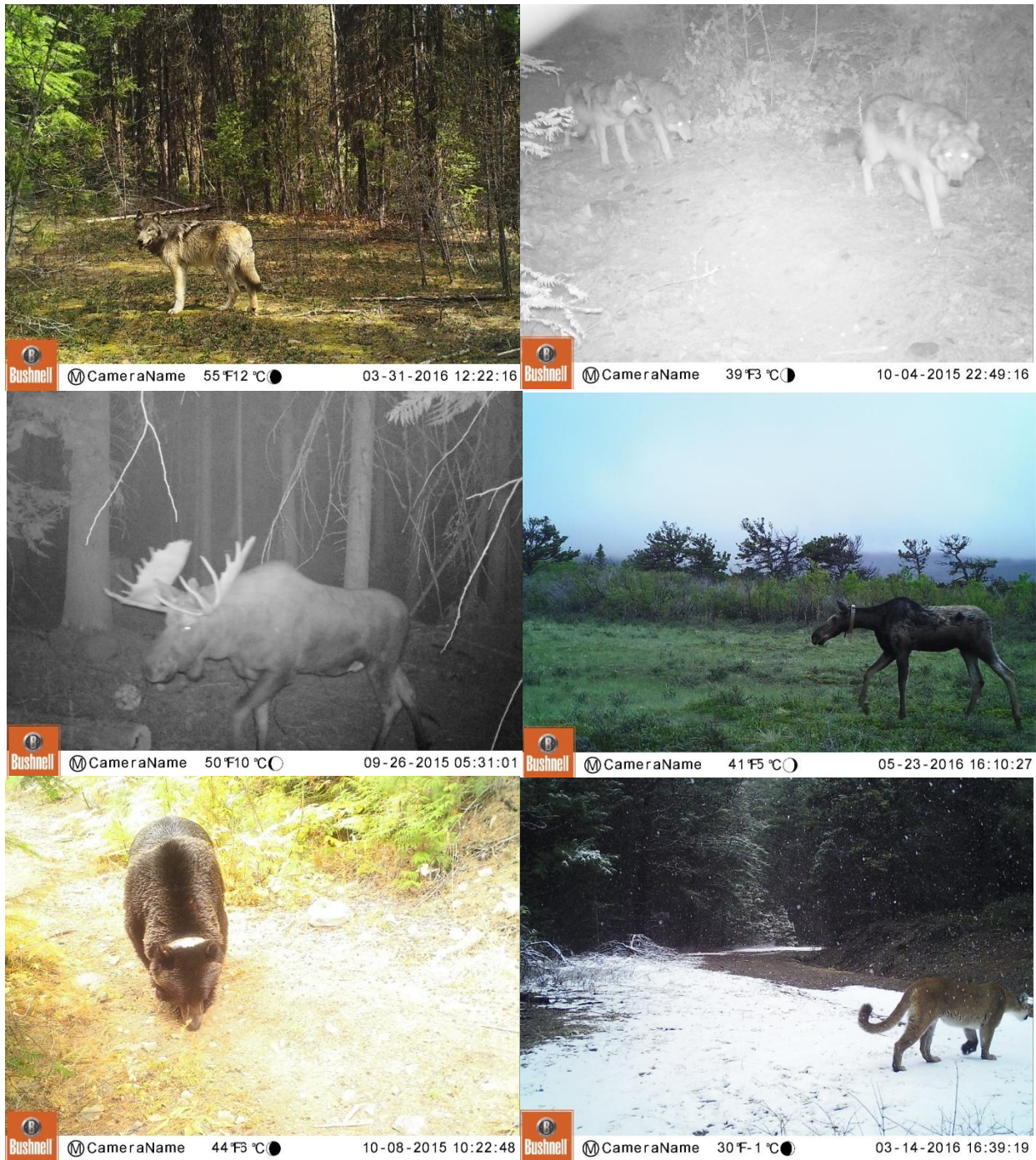


Figure 18. Example photos from remote camera-traps set within seasonal ranges of each moose study area to monitor multi-species occupancy of carnivores and other species, 2015–2016, Montana.

Deliverables

Below we list project deliverables (publications, reports, presentations, media communications, and value-added collaborations) stemming from this moose research project, during FYs 13–16 (July 2012–June 2016). In addition to those communications listed below, are frequent discussions with moose hunters statewide. Copies of reports and publications are available on the moose study’s website (note: the web address is case-sensitive):

<http://fwp.mt.gov/fishAndWildlife/diseasesAndResearch/research/moose/populationsMonitoring>

1. Annual Reports:

2013, 2014, 2015, 2016. DeCesare, N. J., and J. R. Newby. *Vital rates, limiting factors and monitoring methods for moose in Montana*. Annual reports, Federal Aid in Wildlife Restoration Grant W-157-R-1 through R-4.

2. Peer-reviewed Publications

DeCesare, N. J., T. D. Smucker, R. A. Garrott, and J. A. Gude. 2014. *Moose status and management in Montana*. *Alces* 50:31–51.

DeCesare, N. J., J. R. Newby, V. Boccadori, T. Chilton-Radandt, T. Thier, D. Waltee, K. Podruzny, and J. A. Gude. In press. *Calibrating minimum counts and catch per unit effort as indices of moose population trend*. *Wildlife Society Bulletin*.

Ruprecht, J. S., K. R. Hersey, K. Hafen, K. L. Monteith, N. J. DeCesare, M. J. Kauffman, and D. R. MacNulty. In press. *Reproduction in moose at their southern range limit*. *Journal of Mammalogy*.

3. Other Publications

DeCesare, N. J. 2013. *Research: Understanding the factors behind both growing and shrinking Shiras moose populations in the West*. *The Pope and Young Ethic* 41(2):58–59.

DeCesare, N. J. 2014. *Conservation Project Spotlight: What and where are Shiras moose?* *The Pope and Young Ethic* 42(4):26–27.

4. Professional Conference Presentations

DeCesare, N. J., J. Newby, V. Boccadori, T. Chilton-Radant, T. Their, D. Waltee, K. Podruzny, and J. Gude. 2015. *Calibrating indices of moose population trend in Montana*. North American Moose Conference and Workshop, Granby, Colorado.

Nadeau, S., E. Bergman, N. DeCesare, R. Harris, K. Hersey, P. Mathews, J. Smith, T. Thomas, and D. Brimeyer. 2015. *Status of moose in the northwest United States*. North American Moose Conference and Workshop, Granby, Colorado.

DeCesare, N. J., J. R. Newby, and J. M. Ramsey. 2015. *A review of parasites and diseases impacting moose in North America*. Montana Chapter of the Wildlife Society. Annual Meeting, Helena, Montana.

Newby, J. R., N. J. DeCesare, and J. A. Gude. 2016. *Assessing age structure, winter ticks, and nutritional condition as potential drivers of fecundity in Montana moose*. Montana Chapter of the Wildlife Society. Annual Meeting, Missoula, Montana.

5. Public and/or Workshop Presentations

FY	Organization (<i>Speaker</i>)	Location
2013	Helena Hunters and Anglers Association (<i>DeCesare</i>)	Helena, MT
	Marias River Livestock Association (<i>DeCesare</i>)	Whitlash, MT
	Plum Creek Timber Company, Staff meeting (<i>DeCesare</i>)	Libby, MT
	Sun River Working Group (<i>DeCesare</i>)	Augusta, MT
2014	Big Hole Watershed Committee (<i>DeCesare</i>)	Divide, MT
	Flathead Wildlife Incorporated (<i>DeCesare</i>)	Kalispell, MT
	MFWP R1, Regional Citizens Advisory Council (<i>Newby</i>)	Kalispell, MT
	MFWP R1, Biologists' Meeting (<i>Newby</i>)	Kalispell, MT
	MFWP R1, Bow Hunter Education Workshop	Kalispell, MT
	MFWP R2, Regional Meeting (<i>DeCesare</i>)	Missoula, MT
	MFWP, Wildlife Division Meeting (<i>DeCesare</i>)	Fairmont, MT
	Plum Creek Timber Annual Contractors Meeting (<i>DeCesare</i>)	Kalispell, MT
	Rocky Mountain Front Land Managers Forum (<i>DeCesare</i>)	Choteau, MT
	Swan Ecosystem Center Campfire Program (<i>Newby</i>)	Holland Lake, MT
	WCS Community Speaker Series (<i>Newby</i>)	Laurin, MT
2015	Big Hole Watershed Committee (<i>Boccardori</i>)	Divide, MT
	Flathead Chapter of Society of American Foresters (<i>Newby</i>)	Kalispell, MT
	Libby Chapter of Society of American Foresters (<i>Newby</i>)	Libby, MT
	MFWP R1, Regional Citizens Advisory Council (<i>Newby</i>)	Kalispell, MT
	MFWP R2, Bow Hunter Education Workshop (<i>DeCesare</i>)	Lolo, MT
	MFWP R2, Regional Citizens Advisory Council (<i>DeCesare</i>)	Missoula, MT
	Rocky Mountain Front Land Managers Forum (<i>Newby</i>)	Choteau, MT
	Sanders County Commission Meeting (<i>DeCesare</i>)	Thompson Falls, MT
2016	Sheridan Wildlife Speaker Series (<i>DeCesare</i>)	Sheridan, MT
	Ducks Unlimited State Convention (<i>Newby</i>)	Lewistown, MT
	Montana State University, Ecology Seminar Series (<i>DeCesare</i>)	Bozeman, MT
	Upper Sun River Wildlife Team Meeting (<i>DeCesare</i>)	August, MT
	Helena Hunters and Anglers Association (<i>DeCesare</i>)	Helena, MT
	Ravalli County Fish and Wildlife Association (<i>DeCesare</i>)	Hamilton, MT
	MFWP R1 Law Enforcement Annual Meeting (<i>Newby</i>)	Kalispell, MT
Confederated Salish & Kootenai Tribe, Nat Res Commission (<i>Newby</i>)	Marion, MT	

6. Media Communications

FY	Organization (Location)	Topic	Media
2013	Bozeman Chronicle (MT)	Moose research	Newspaper
	Liberty County Times (MT)	Moose research	Newspaper
	MFWP Outdoor Report (MT)	Moose research	Television
2014	Carbon County News (MT)	Moose research	Newspaper
	Flathead Beacon (MT)	Moose research	Newspaper
	Helena Independent Record (MT)	Moose research	Newspaper
	High Country News, blog	Moose research	Blog
	KPAX (MT)	Moose-human conflict	Television
	MFWP Outdoor Report	Moose research	Television
	Missoulian (MT)	Urban moose	Newspaper
	The Monocle Daily (London, UK)	Moose research	Radio
	Nature Conservancy Magazine (VA)	Moose research	Magazine
	New York Times (NY)	Moose research	Newspaper
	NWF Teleconference (MT)	Climate change	Newspaper
	Radio New Zealand (New Zealand)	Moose research	Radio
	Summit Daily (CO)	Moose research	Newspaper
	UM Science Source (MT)	Moose research	Newspaper
2015	KOFI (MT)	Moose research	Radio
	MFWP Outdoor Report (MT)	Moose research	Television
	Western News (MT)	Moose research	Newspaper
2016	Missoulian (MT)	Climate & moose	Newspaper
	Bozeman Daily Chronicle (MT)	Climate & moose	Newspaper
	Montana Standard (MT)	Climate & moose	Newspaper
	Billings Gazette (MT)	Climate & moose	Newspaper
	Daily Interlake (MT)	Moose research	Newspaper
	Ravalli Republic (MT)	Moose research	Newspaper
	Montana Public Radio (MT)	Moose research	Radio
	Montana Public Radio – Field Notes (MT)	Moose taxonomy	Radio
	KAJ18 (MT)	Moose research	Television

7. Other Project-related Collaborations

Partners	Title	Activities during FY16
Rick Gerhold & Caroline Grunenwald, University of Tennessee	Development of a serological assay for <i>Elaeophora schneideri</i> detection and surveillance in cervids	*Labwork is ongoing *Providing MT blood samples and worm samples for lab work
Biologists from western states and provinces (AB, BC, CO, ID, MT, OR, SK, UT, WA, WY)	Assessing range-wide genetic differentiation and spatial distribution of a moose subspecies, <i>Alces alces shirasi</i>	*Compiled sample collection of >1000 samples across 8 states and provinces *Final results are pending, report expected during FY17
Ky Koitzsch, K2 Consulting, LLC	Estimating population demographics of moose in northern Yellowstone National Park using non-invasive methods	*Providing MT scat samples for fecal pellet morphometry

Acknowledgements

We are particularly thankful to many private landowners and area residents who graciously allowed us to conduct captures and ground telemetry monitoring on their properties. They also have provided much logistical support and local knowledge about moose distributions and local flora. We are very grateful for the privilege to work on these properties and for all the help.

This project is a large collaboration among many FWP biologists. These include but are not limited to Justin Gude, Jennifer Ramsey, Neil Anderson, Keri Carson, Kevin Podruzny, Keri Wash, Jim Williams, Howard Burt, Graham Taylor, Tonya Chilton-Radant, Kent Laudon, John Vore, Vanna Boccadori, Brent Lonner, Gary Olson, and Ryan Rauscher. Undoubtedly this list should be larger to fully incorporate the many biologists and other personnel who have assisted with coordination of hunter sample collection, harvest statistics, opportunistic sampling of other moose throughout the state. We also acknowledge a great deal of help from other cooperating biologists and agency personnel including Nathan Birkeland, Dave Hanna, Dan Carney, Lorin Hicks, Allison Kolbe, and Jenna Roose.

Many thanks go to the pilots who have safely conducted capture and telemetry work, including Rick Geiger, Ken Justus, Blake Malo, Jim-Bob Pierce, Joe Rahn, Mark Stott, Rick Swisher, Guy Terrill, and Trever Throop.

Special thanks to field technicians Alissa Anderson and Kaitlyn Farrar for their initiative, adaptability and hard work implementing the multispecies predator monitoring effort.

Funding for this project during FYs 13–16 has been in part derived from FWP moose license auction sales, matched with USFWS Grants-in-Aid funds. We also thank the Safari Club International Foundation for a Conservation Grant to support this research during FY16–17. Thanks to Ducks Unlimited and the Rocky Mountain Elk Foundation for holding license auctions. Many thanks also go to Plum Creek Timber Company and Two Bear Aviation, which have supported the project with helicopter flights during capture and monitoring efforts.

Literature cited

- Ballard, W. B. 1992. Modelled impacts of wolf and bear predation on moose calf survival. *Alces* 28:79–88.
- Ballard, W. B., S. D. Miller, and J. S. Whitman. 1990. Brown and black bear predation on moose in southcentral Alaska. *Alces* 26:1–8.
- Ballard, W. B., T. H. Spraker, and K. P. Taylor. 1981. Causes of neonatal moose calf mortality in south central Alaska. *Journal of Wildlife Management*:335–342.
- Van Ballenberghe, V., and W. B. Ballard. 2007. Population dynamics. Pages 223–245 *Ecology and management of the North American moose*. 2nd edition. University Press of Colorado, Boulder, Colorado.
- Bartnick, T. D., T. R. Van Deelen, H. B. Quigley, and D. Craighead. 2013. Variation in cougar (*Puma concolor*) predation habits during wolf (*Canis lupus*) recovery in the southern Greater Yellowstone Ecosystem. *Canadian Journal of Zoology* 91:82–93.
- Becker, S. A. 2008. Habitat selection, condition, and survival of Shiras moose in northwest Wyoming. University of Wyoming.
- Bender, L. C., J. G. Cook, R. C. Cook, and P. B. Hall. 2008. Relations between nutritional condition and survival of North American elk *Cervus elaphus*. *Wildlife Biology* 14:70–80.
- Benson, J. F., and B. R. Patterson. 2013. Moose (*Alces alces*) predation by eastern coyotes (*Canis latrans*) and eastern coyote x eastern wolf (*Canis latrans x Canis lycaon*) hybrids. *Canadian Journal of Zoology* 91:837–841.
- Berger, J., J. W. Testa, T. Roffe, and S. L. Monfort. 1999. Conservation endocrinology: a noninvasive tool to understand relationships between carnivore colonization and ecological carrying capacity. *Conservation Biology* 13:980–989.
- Bertram, M. R., and M. T. Vivion. 2002. Moose mortality in eastern interior Alaska. *The Journal of wildlife management* 66:747–756.

- Blanchard, P., M. Festa-Bianchet, J.-M. Gaillard, and J. T. Jorgenson. 2003. A test of long-term fecal nitrogen monitoring to evaluate nutritional status in bighorn sheep. *The Journal of wildlife management*:477–484.
- Boer, A. H. 1992. Fecundity of North American moose. *Alces* (Supplement) 1:1–10.
- Boertje, R. D., W. C. Gasaway, D. V. Grangaard, and D. G. Kelleyhouse. 1988. Predation on moose and caribou by radio-collared grizzly bears in east central Alaska. *Canadian Journal of Zoology* 66:2492–2499.
- Brodie, J. F., A. J. Giordano, B. Dickson, M. Hebblewhite, H. Bernard, J. Mohd-Azlan, J. Anderson, and L. Ambu. 2014. Evaluating Multispecies Landscape Connectivity in a Threatened Tropical Mammal Community. *Conservation Biology*.
- Burkholder, B. O. 2012. Seasonal distribution, winter habitat selection and willow utilization patterns of the Shiras moose on the Mount Haggin Wildlife Management Area. Thesis, Montana State University, Bozeman, Montana.
- Burton, A. C., E. Neilson, D. Moreira, A. Ladle, R. Steenweg, J. T. Fisher, E. Bayne, and S. Boutin. 2015. REVIEW: Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. *Journal of Applied Ecology* 52:675–685.
- Cederlund, G. N., R. L. Bergström, and K. Danell. 1989. Seasonal variation in mandible marrow fat in moose. *The Journal of Wildlife Management*:587–592.
- Chandler, R. B., J. A. Royle, and others. 2013. Spatially explicit models for inference about density in unmarked or partially marked populations. *The Annals of Applied Statistics* 7:936–954.
- DeCesare, N. J., M. Hebblewhite, M. Bradley, K. G. Smith, D. Hervieux, and L. Neufeld. 2012. Estimating ungulate recruitment and growth rates using age ratios. *Journal of Wildlife Management* 76:144–153.
- Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modeling avian nest survival. *Ecology* 83:3476–3488.
- Eberhardt, L. L. 2002. A paradigm for population analysis of long-lived vertebrates. *Ecology* 83:2841–2854.
- Ericsson, G., K. Wallin, J. P. Ball, and M. Broberg. 2001. Age-related reproductive effort and senescence in free-ranging moose, *Alces alces*. *Ecology* 82:1613–1620.
- Franzmann, A. W., and C. C. Schwartz. 1985. Moose twinning rates: a possible population condition assessment. *The Journal of wildlife management* 49:394–396.
- Franzmann, A. W., C. C. Schwartz, and R. O. Peterson. 1980. Moose calf mortality in summer on the Kenai Peninsula, Alaska. *Journal of Wildlife Management* 44:764–768.
- Gasaway, W. C., R. D. Boertje, D. V. Grangaard, D. G. Kelleyhouse, R. O. Stephenson, and D. G. Larsen. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. *Wildlife Monographs*:3–59.
- Gasaway, W. C., R. O. Stephenson, J. L. Davis, P. E. K. Shepherd, and O. E. Burris. 1983. Interrelationships of wolves, prey, and man in interior Alaska. *Wildlife Monographs*:1–50.
- Gilbert, S. L., M. S. Lindberg, K. J. Hundertmark, and D. K. Person. 2014. Dead before detection: addressing the effects of left truncation on survival estimation and ecological inference for neonates. *Methods in Ecology and Evolution* 5:992–1001.
- Griffin, K. A., M. Hebblewhite, H. S. Robinson, P. Zager, S. M. Barber-Meyer, D. Christianson, S. Creel, N. C. Harris, M. A. Hurley, D. H. Jackson, B. K. Johnson, W. L. Myers, J. D. Raithe, M. Schlegel, B. L. Smith, C. White, and P. J. White. 2011. Neonatal mortality of elk driven by climate, predator phenology and predator community composition. *Journal of Animal Ecology* 80:1246–1257.
- Hobbs, N. T. 1987. Fecal indices to dietary quality: a critique. *The Journal of Wildlife Management*:317–320.
- Hochachka, W. M., D. Fink, R. A. Hutchinson, D. Sheldon, W.-K. Wong, and S. Kelling. 2012. Data-intensive science applied to broad-scale citizen science. *Trends in Ecology & Evolution* 27:130–137.
- Hodgman, T. P., B. B. Davitt, and J. R. Nelson. 1996. Monitoring mule deer diet quality and intake with fecal indices. *Journal of Range Management*:215–222.
- Huang, F., D. C. Cockrell, T. R. Stephenson, J. H. Noyes, and R. G. Sasser. 2000. A serum pregnancy test with a specific radioimmunoassay for moose and elk pregnancy-specific protein B. *Journal of Wildlife Management*:492–499.
- Keech, M. A., R. T. Bowyer, M. Jay, V. Hoef, R. D. Boertje, B. W. Dale, and T. R. Stephenson. 2000. Life-history consequences of maternal condition in Alaskan moose. *The Journal of Wildlife Management* 64:450–462.
- 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.
- 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*:548–557.
- Lenarz, M. S., J. Fieberg, M. W. Schrage, and A. J. Edwards. 2010. Living on the edge: viability of moose in northeastern Minnesota. *The Journal of Wildlife Management* 74:1013–1023.
- Leslie, D. M., R. T. Bowyer, and J. A. Jenks. 2008. Facts from feces: nitrogen still measures up as a nutritional index for mammalian herbivores. *The Journal of Wildlife Management* 72:1420–1433.
- Leslie, D. M., and E. E. Starkey. 1985. Fecal indices to dietary quality of cervids in old-growth forests. *The Journal of Wildlife Management* 49:142–146.
- MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology* 84:2200–2207.

- MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. Andrew Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83:2248–2255.
- MacKenzie, D. I., and J. A. Royle. 2005. Designing occupancy studies: general advice and allocating survey effort. *Journal of Applied Ecology* 42:1105–1114.
- Mahard, T. J., J. A. Litvaitis, P. Tate, G. C. Reed, and D. J. Broman. 2016. An evaluation of hunter surveys to monitor relative abundance of bobcats. *Wildlife Society Bulletin*.
- Messier, F., and M. Crête. 1985. Moose-wolf dynamics and the natural regulation of moose populations. *Oecologia* 65:503–512.
- Monteith, K. B., K. L. Monteith, R. T. Bowyer, D. M. Leslie, and J. A. Jenks. 2014a. Reproductive effects on fecal nitrogen as an index of diet quality: an experimental assessment. *Journal of Mammalogy* 95:301–310.
- Monteith, K. L., V. C. Bleich, T. R. Stephenson, B. M. Pierce, M. M. Conner, J. G. Kie, and R. T. Bowyer. 2014b. Life-history characteristics of mule deer: Effects of nutrition in a variable environment. *Wildlife Monographs* 186:1–62.
- Murray, D. L., K. F. Hussey, L. A. Finnegan, S. J. Lowe, G. N. Price, J. Benson, K. M. Loveless, K. R. Middel, K. Mills, D. Potter, A. Silver, M.-J. Fortin, B. R. Patterson, and P. J. Wilson. 2012. Assessment of the status and viability of a population of moose (*Alces alces*) at its southern range limit in Ontario.
- Oates, B., J. Goheen, M. J. Kauffman, K. Monteith, G. Fralick, and S. Smith. 2012. Assessing moose response to energy development in the Hoback Basin: 2012 annual report. University of Wyoming, Laramie, Wyoming.
- Osborn, R. G., and T. F. Ginnett. 2001. Fecal nitrogen and 2, 6-diaminopimelic acid as indices to dietary nitrogen in white-tailed deer. *Wildlife Society Bulletin*:1131–1139.
- Peek, J. M. 1962. Studies of moose in the Gravelly and Snowcrest Mountains, Montana. *The Journal of Wildlife Management* 26:360–365.
- Rich, L. N., E. M. Glenn, M. S. Mitchell, J. A. Gude, K. Podruzny, C. A. Sime, K. Laudon, D. E. Ausband, and J. D. Nichols. 2013. Estimating occupancy and predicting numbers of gray wolf packs in Montana using hunter surveys. *Journal of Wildlife Management* 77:1280–1289.
- Robbins, C. T., S. Mole, A. E. Hagerman, and T. A. Hanley. 1987. Role of tannins in defending plants against ruminants: reduction in dry matter digestion? *Ecology* 68:1606–1615.
- Roffe, T. J., K. Coffin, and J. Berger. 2001. Survival and immobilizing moose with carfentanil and xy lazine. *Wildlife Society Bulletin* 29:1140–1146.
- Ross, P. I., and M. G. Jalkotzy. 1996. Cougar predation on moose in southwestern Alberta. *Alces* 32:1–8.
- Royle, J. A. 2004. N-Mixture Models for Estimating Population Size from Spatially Replicated Counts. *Biometrics* 60:108–115.
- Schladweiler, P., and D. R. Stevens. 1973. Reproduction of Shiras moose in Montana. *The Journal of Wildlife Management*:535–544.
- Seaton, C. T., T. F. Paragi, R. D. Boertje, K. Kielland, S. DuBois, and C. L. Fleener. 2011. Browse biomass removal and nutritional condition of moose *Alces alces*. *Wildlife Biology* 17:55–66.
- Sih, A., G. Englund, and D. Wooster. 1998. Emergent impacts of multiple predators on prey. *Trends in ecology & evolution* 13:350–355.
- Sivertsen, T. R., A. Mysterud, and H. Gundersen. 2012. Moose (*Alces alces*) calf survival rates in the presence of wolves (*Canis lupus*) in southeast Norway. *European Journal of Wildlife Research*.
- Stephenson, T. R., K. J. Hundertmark, C. C. Schwartz, and V. Van Ballenberghe. 1998. Predicting body fat and body mass in moose with ultrasonography. *Canadian Journal of Zoology* 76:717–722.
- Stewart, R. R., E. H. Kowal, R. Beaulieu, and T. W. Rock. 1985. The impact of black bear removal on moose calf survival in east-central Saskatchewan. *Alces* 21:403–418.
- van Strien, A. J., C. A. M. van Swaay, and T. Termaat. 2013. Opportunistic citizen science data of animal species produce reliable estimates of distribution trends if analysed with occupancy models. *Journal of Applied Ecology* 50:1450–1458.
- Swenson, J. E., B. Dahle, H. Busk, O. Opseth, T. Johansen, A. Söderberg, K. Wallin, and G. O. R. Cederlund. 2007. Predation on moose calves by European brown bears. *Journal of Wildlife Management* 71:1993–1997.
- Testa, J. W. 2004. Population dynamics and life history trade-offs of moose (*Alces alces*) in south-central Alaska. *Ecology* 85:1439–1452.
- Testa, J. W., and G. P. Adams. 1998. Body condition and adjustments to reproductive effort in female moose (*Alces alces*). *Journal of Mammalogy* 79:1345–1354.
- Testa, J. W., E. F. Becker, and G. R. Lee. 2000. Temporal patterns in the survival of twin and single moose (*Alces alces*) calves in southcentral Alaska. *Journal of Mammalogy* 81:162–168.
- Ueno, M., C. Nishimura, H. Takahashi, K. Kaji, and T. Saitoh. 2007. Fecal nitrogen as an index of dietary nitrogen in two sika deer *Cervus nippon* populations. *Acta theriologica* 52:119–128.
- Wilmers, C. C., E. Post, R. O. Peterson, and J. A. Vucetich. 2006. Predator disease out-break modulates top-down, bottom-up and climatic effects on herbivore population dynamics. *Ecology Letters* 9:383–389.