

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



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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 and elsewhere also suffers from a lack of rigorous data from which to monitor population trends and prescribe management directions.

In 2013, Montana Fish, Wildlife, & Parks (MFWP) began a 10-year study designed to improve our understanding of: 1) the most cost-effective means to monitor statewide moose populations and maximize hunter opportunity, 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 3rd annual report produced as part of this work. This report contains preliminary results from a sample of our recent efforts to calibrate statewide monitoring data, as well as results from the first two full biological years of moose research and monitoring. All of these results should be considered preliminary as both data collection and statistical analyses are works in progress.

Analysis of population trends monitored with aerial surveys are suggestive of population declines in 12 of 16 hunting districts analyzed, yet there is quite a bit of statistical uncertainty surrounding these trend estimates. Calibration of trends monitored with aerial survey data to those within hunter harvest statistics (moose killed per hunter day) generally show little agreement between these two metrics, though these analyses are still in progress. On the other hand, monitoring moose with hunter observations (moose seen per hunter day) may offer a promising new approach to gathering statewide data, whether via phone surveys or check station surveys.

Moose vital rates measured with radio-collar studies currently indicate stable to increasing population trends in two study areas (Cabinet Mountains and Rocky Mountain Front) and a declining population trend in the third 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 in the Big Hole Valley study area may be the highest of the three areas, though these rates have relatively less influence on the overall trajectory of the population relative to adult female survival. The average pregnancy rate of adults across these study areas (78%) is somewhat low relative to the North American average (84%), but not necessarily unlike that observed in other Shiras moose populations. Lastly, hunter-collected measurements of rump fat among harvested bulls showed no regional differences across the state thus far. Monitoring of these vital rates as well as potential limiting factors (predation, disease, nutrition) will continue for the remainder of this 10-year study.

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 (Year 3 of 10-year study)

For the 2014-2015 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

Preface: A preliminary version of this research component was included in a previous annual report (1 Sept 2014). Since then, we have updated the statistical analyses to better represent both the population trend data and the calibration of trends monitored with aerial surveys and hunter statistics. A complete description of this work will be submitted for peer-review during FY16.

1.1.1. Background

Monitoring of moose and other ungulate populations by Montana Fish, Wildlife & Parks (MFWP) biologists is conducted through a combination of annual aerial survey counts and hunter harvest statistics from phone surveys. Time series of aerial count data allow unbiased estimates of population trend as long as the mean sightability remains constant over time (Harris 1986, Eberhardt and Simmons 1992, Humbert et al. 2009). While aerial surveys often represent the ‘gold standard’ for monitoring moose populations, such methods can be costly, and in some scenarios, hunter statistics, such as catch per unit effort (CPUE; i.e., kills per hunter day) may provide a cost-effective means of monitoring population trends (Ericsson and Wallin 1999, Bontaities et al. 2000, Ueno et al. 2014). Here we use aerial count data and harvest statistics for moose populations in 16 hunting districts of Montana to assess: 1) count-based population trends and the relationship between trends monitored with both CPUE and aerial counts.

1.1.2. Population trends from aerial counts

We compiled monitoring data spanning 1985–2013 for 16 hunting districts (Figure 1).

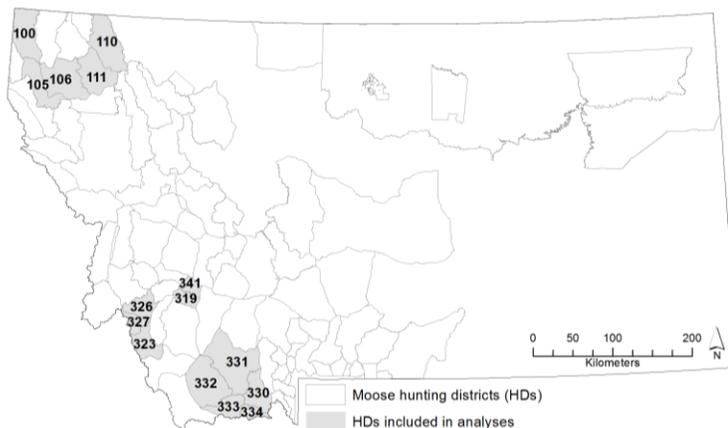


Figure 1. Moose hunting districts in Montana and the subset of HDs for which both aerial survey and harvest data were collected during 1985–2013.

We used state-space models (Kéry and Schaub 2012) to estimate population trends with associated 95% confident intervals for 16 hunting districts (HDs) and a total of 235 annual aerial surveys, averaging 14.7 surveys per HD (Range=6–24; Figure 2). Point estimates of mean annual growth rates (\hat{r}) were negative for 12 of the 16 hunting districts (Figure 2). However, 95% credible intervals surrounding mean growth rates overlapped 0 in all districts.

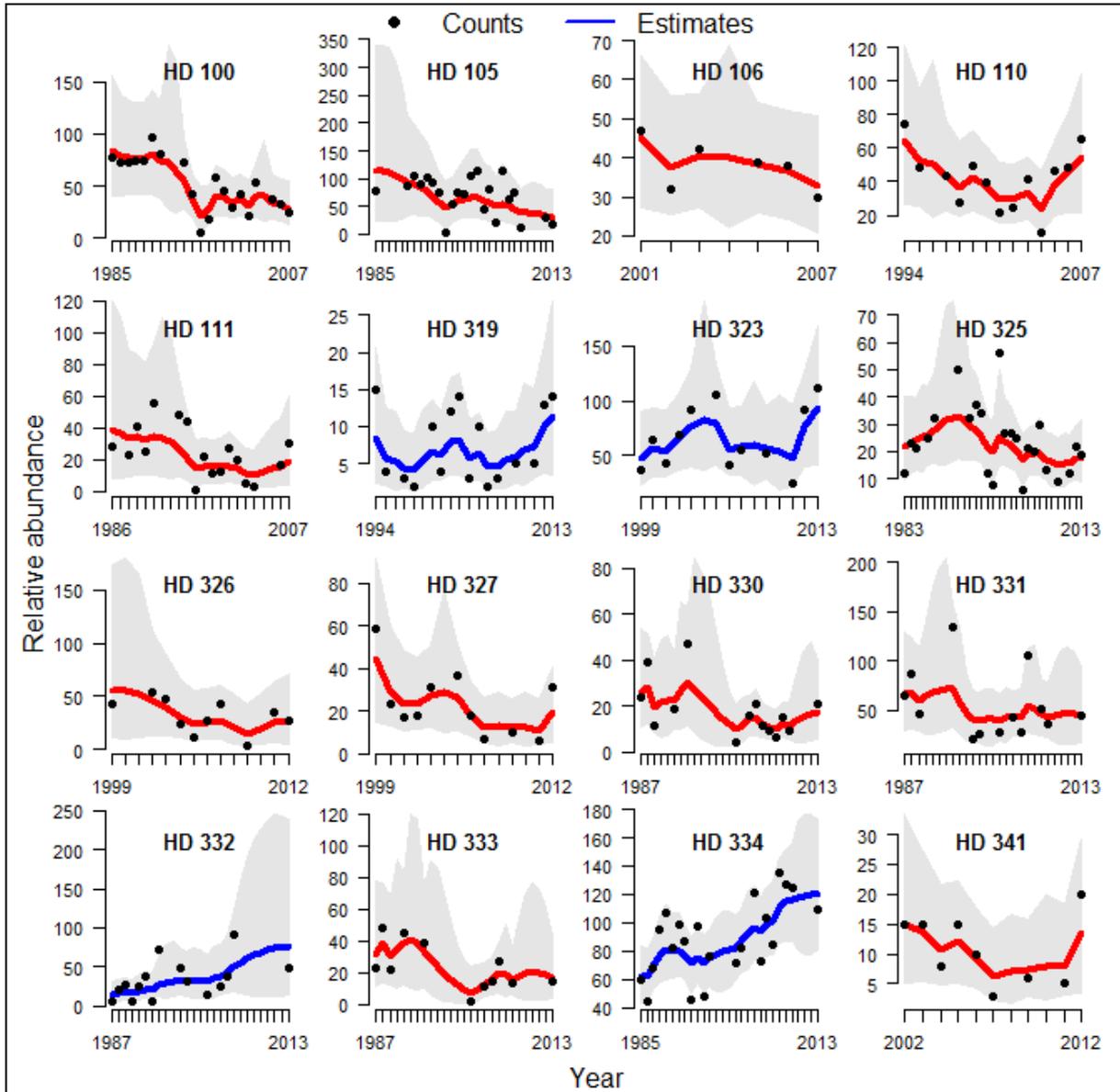


Figure 2. Aerial counts indicated 4 increasing (blue) and 12 decreasing populations (red) across 16 HDs in Montana, 1983–2013.



1.1.3. Evaluating CPUE as an index of count-based trends

We also paired aerial survey data with harvest data collected during 1985–2013 across 16 HDs to assess the relationship between population trends estimated using aerial counts and those estimated using hunter catch per unit effort (CPUE). A complete description of this analysis will be available during FY16 after peer-review. For this report, we focus on a simple comparison of long-term trends documented with time series of both count and CPUE indices of abundance. We applied the same state-space modeling approaches used above for count data to estimate mean rates of change per HD as measured with CPUE, and then used reduced major axis regression to compare paired trend estimates measured with each approach for each HD (Erisman et al. 2011). We conducted all analyses using R, 3.1.1 (R Core Team 2014), and conducted RMA regressions using the lmodel2 package (Legendre 2013).

Regression analysis of these paired data revealed no significant relationship, as evidenced by the correlation coefficient ($r=-0.219$), its test of significance ($P=0.414$), and the coefficient of determination ($R^2=0.048$; Figure 3).

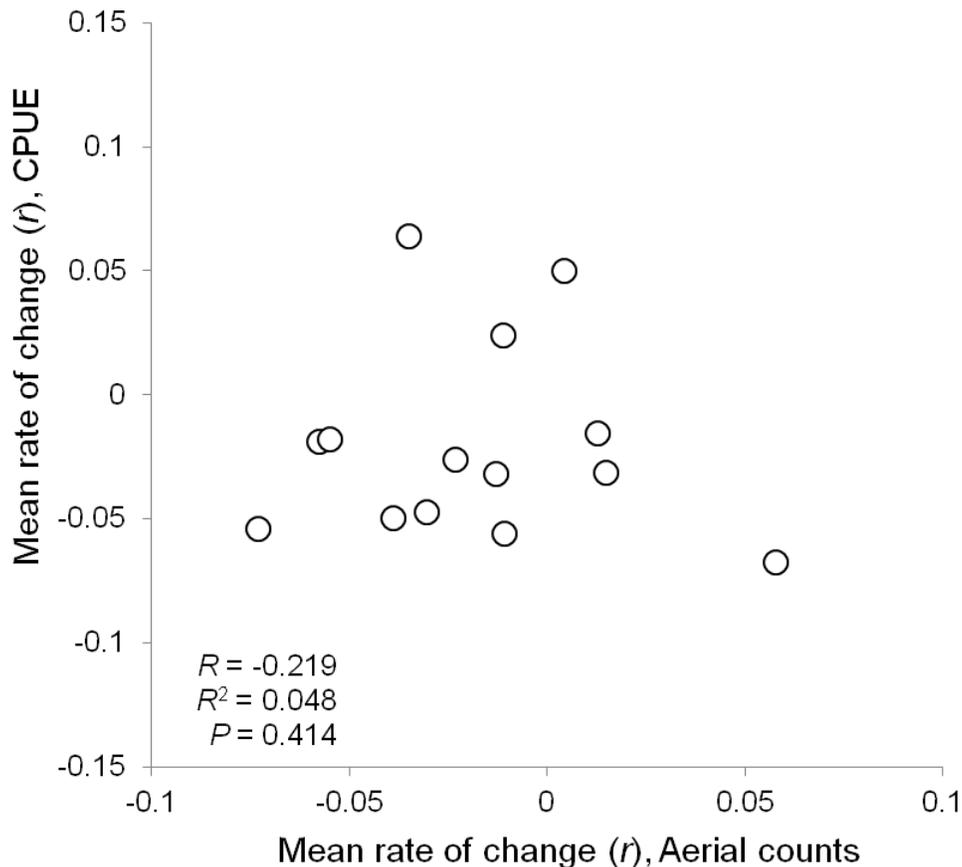


Figure 3. The relationship between long-term growth rates for moose populations in 16 hunting districts estimated using both aerial count data and hunter catch per unit effort (CPUE) in Montana, 1983–2013.

1.1.4. Discussion of count- and CPUE-based monitoring

Our results reveal some statistical uncertainty surrounding population trends of moose in Montana when using aerial-based minimum count data, despite time series including an average of ~15 annual counts, per district. A recent review of the status of moose in Montana indicated concerns among management biologists over potential population declines since the 1990's (DeCesare et al. 2014). While our point estimates of r do corroborate concerns over widespread declines to some degree, these data are generally insufficient to conclude with confidence that populations have in fact declined. Because these data are minimum count data rather than statistical estimates of population size, estimates of trend also hinge upon an assumption of a constant mean sightability over time. While there are no data to suggest a change in sightability over the time period considered, it is conceivable that reduced timber harvest (Spoelma et al. 2004), changes to riparian willow habitats (whether degradation or restoration), or changes in rancher practices that alter the availability of alternative food sources (such as winter hay stacks) over this same time period may also be responsible for changes in counts by inducing gradual changes in mean sightability during surveys.

Comparing these count-based trends to those measured with another commonly used index of abundance, CPUE, revealed a general lack of agreement between data sets. We have conducted additional analyses comparing annual variation in these two indices that are not presented here. These results will be available following peer-review during FY16. In general, we encourage managers to pay explicit attention to the precision of trend estimates when monitoring small or poorly visible populations with count data. It may be that repeated surveys within years (potentially at the allowable expense of conducting surveys every year; Humbert et al. 2009) are needed to provide sufficiently precise estimates of trend. For populations like moose in Montana, with small, harvested populations, multiple lines of evidence about population dynamics may help managers interpret results when making harvest recommendations.

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, Rich et al. (2013) recently estimated occupancy models for wolves in Montana by collecting hunter sightings of wolves and subdividing them into sampling sessions according to each week of the five-week hunting season. During 2012–2014 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 2012–2014 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 5,782; 4,046; and 4,039 statewide moose sighting locations in 2012, 2013, and 2014,

respectively, with an average of 15% of hunters asked reporting at least one moose sighting (Figure 4).

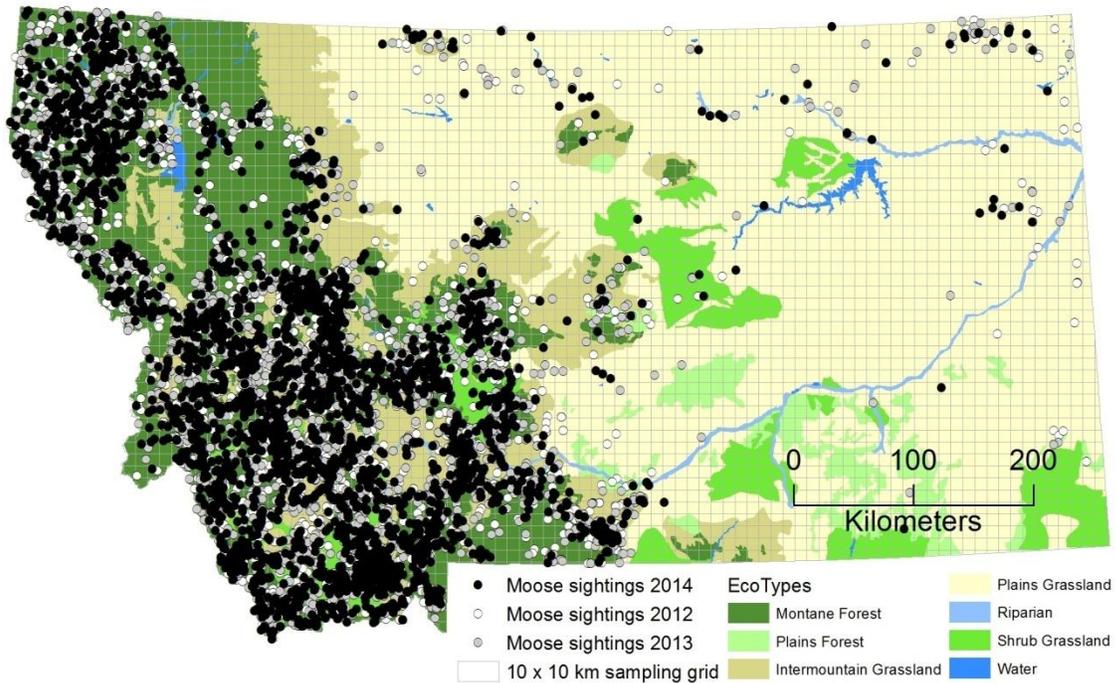


Figure 4. *Moose sightings collected using phone surveys of deer and elk hunters and an example 10 x 10 km grid for sampling statewide occupancy during the fall, 2012–2014, Montana.*

We are still in the preliminary stages of applying occupancy models to these data, but have done some initial analyses to assess spatial variation in the numbers of moose sightings with respect to amounts of hunter effort. Here we map these patterns with respect to deer-elk hunting districts (Figure 5). We show consistently higher numbers of moose seen per hunter day in southwest Montana, which may reflect differences in moose abundance and/or habitat-mediated visibility of moose to hunters.

We also compared sighting rates measured with phone call surveys to those measured from data collected by asking hunters for moose sightings at check stations in Region 1. The primary intent of collecting moose observations at check stations is to supply distributional information to area wildlife biologists. However, these data also can be used to estimate sighting rates after estimating the number of hunter-days sampled in each district by check stations. The analysis is very preliminary but shows encouraging signals of agreement in measuring moose sighting rates across deer-elk hunting districts using each of these two methods of data collection (Figure 6).

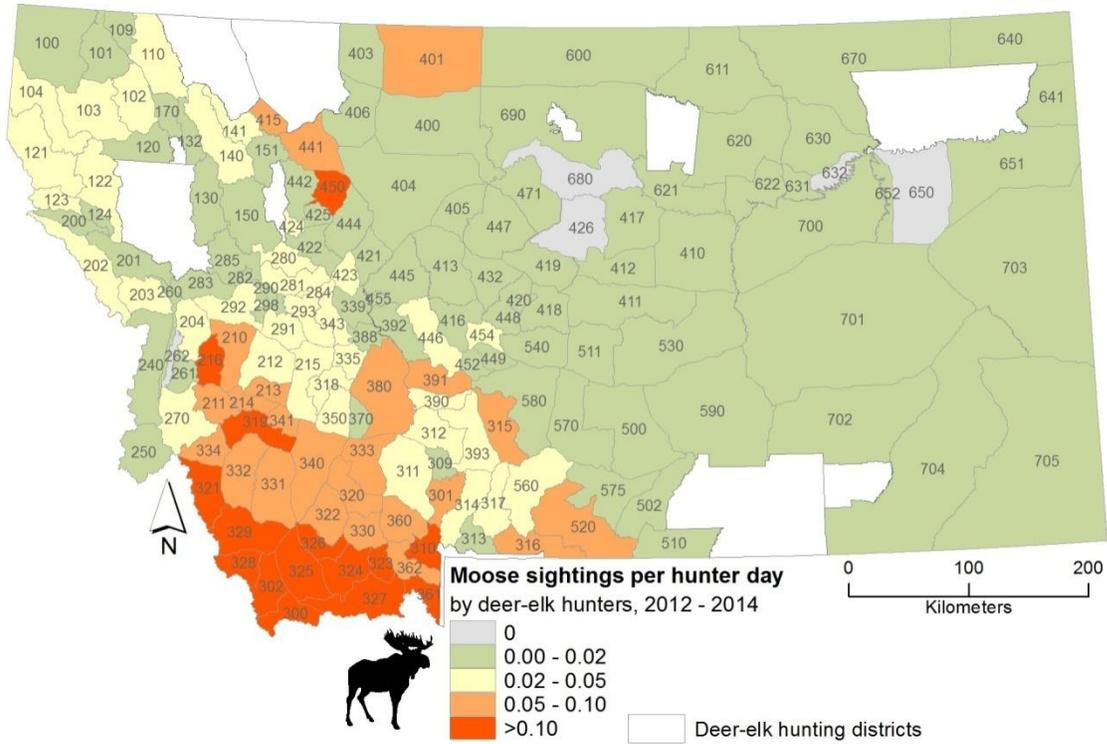


Figure 5. Number of moose sightings per hunter-day, observed by deer-elk hunters during fall 2012–2014, and mapped with respect to total deer and elk hunting days within each deer-elk hunting district, Montana.

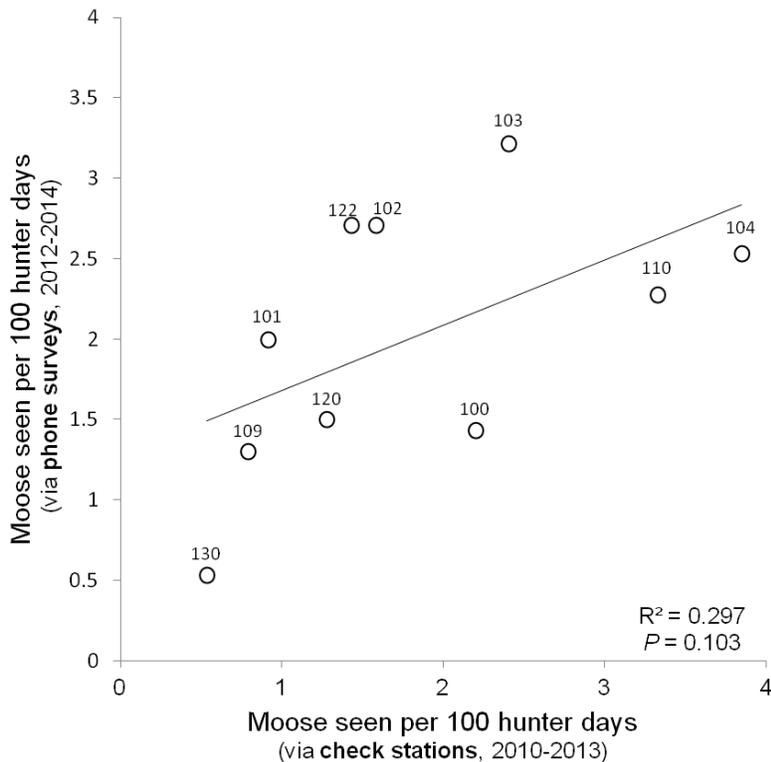


Figure 6. A preliminary comparison of two forms of data collection (phone surveys and check station surveys) regarding the number of moose seen per 100 hunter-days suggests a general pattern of agreement. Each point represents a deer-elk hunting district, and labels are the specific deer-elk district names. Years of data collection between the two methods were different, but overlapping.

1.3. Sampling statewide moose genetic population structure.

An assessment of moose population genetic structure in Montana could provide information on population connectivity and have implications for designating biologically relevant population units for future management and monitoring. Interest in this aspect of study has led to an added side project involving collaboration with neighboring states and provinces to study moose genetic structure across the entire range of Shiras moose. This work is currently underway and the results will have implications for our own study of genetic structure within Montana. Here we present preliminary analyses of genetic structure of a subset of animals captured in our 3 research study areas. We analyzed nuclear DNA from animals captured during 2013–2014 to assess if the genotypes of moose in each area were distinctive enough to reliably assign them to their respective groups. We analyzed 72 samples from the Cabinet-Fisher ($N=18$), Big Hole Valley ($N=33$), and Rocky Mountain Front ($N=21$) study areas.

The Conservation Genetics Lab at USFS-RMRS determined genotypes for each moose at 13 microsatellite loci. Using program Structure (Pritchard et al. 2000), we ran a Bayesian clustering routine to estimate the number of genetically defined groups across these 72 moose. We would expect *a priori* that animals would be most likely to lump into 3 distinct groups if study areas were in fact genetically distinct, this was the result, with $K=3$ groups most supported (Figure 7).

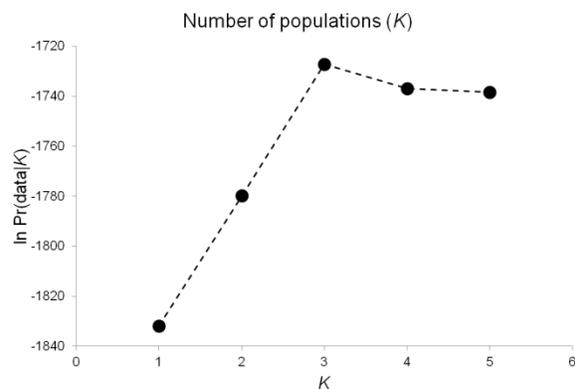


Figure 7. Genetic analysis of moose from 3 research study areas showed clustering into $K=3$ genetically-based populations, indicating genetic differentiation among areas.

We then assigned moose to each of 3 genetic populations for comparison with study area membership (Figure 8). Moose from each study area were generally assigned to distinct genetic groups, though there were some exceptions where moose were more genetically related to individuals from a different study area than to those in the same area where they were captured. These results suggest some level of genetic structuring, but additional analyses of more samples and across a greater range will add much needed perspective of relative degrees of differentiation across broader spatial scales.

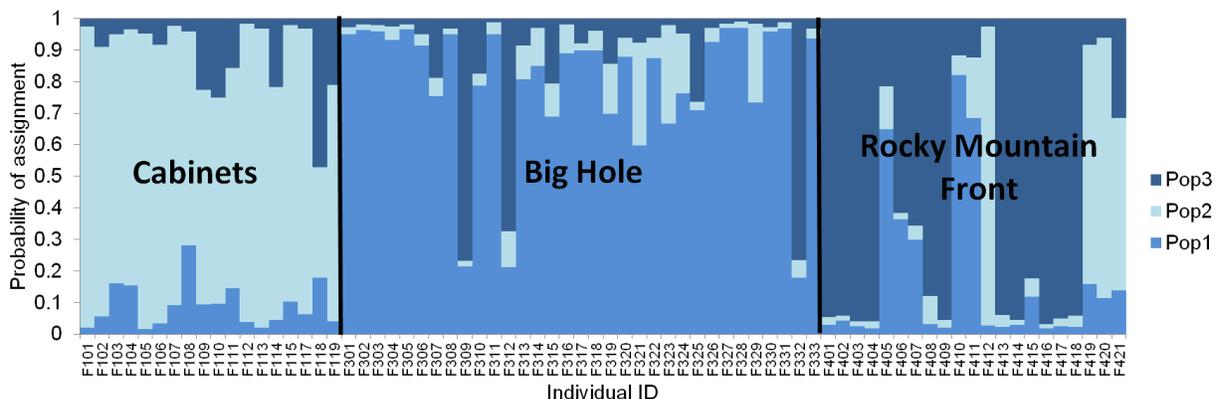


Figure 8. Preliminary assignment of captured moose to 3 genetically-derived populations largely aligned with study areas within which they were captured, though with some exceptions.

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. 2014). In May, 2015 we reached the end of our second 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 9, 11). 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.

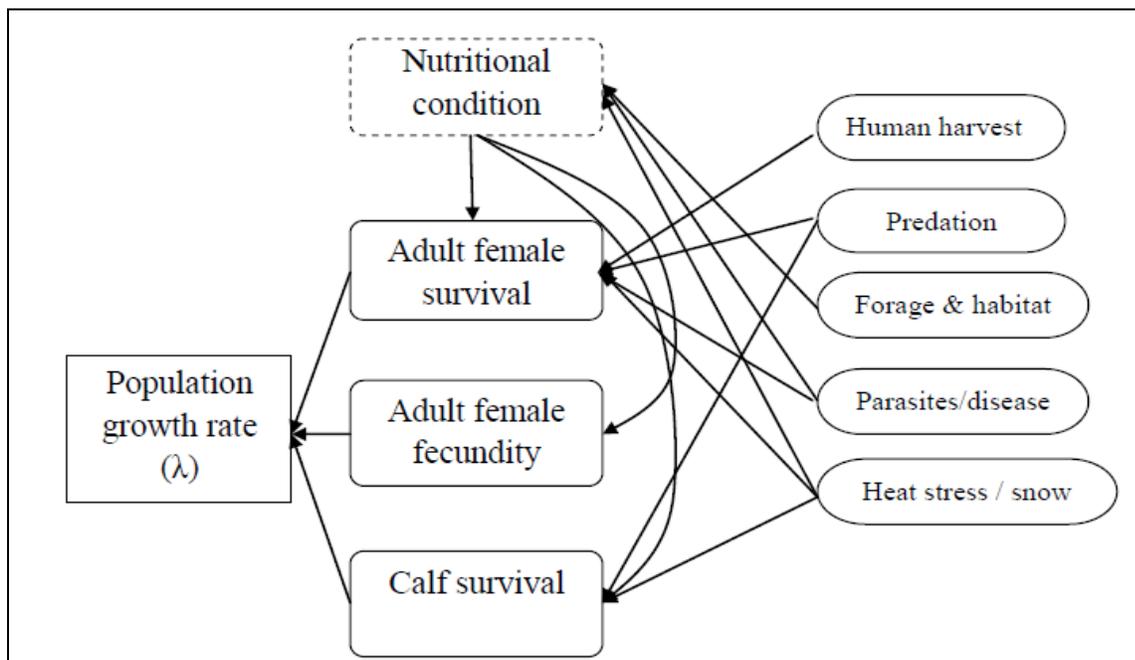


Figure 9. Ecological drivers hypothesized to influence specific moose population vital rates and ultimately population growth.

2.2. Animal capture and handling

In January of 2015 we worked with a contracted helicopter capture company (Quicksilver Air) and also with Two Bear Aviation (in R1) and local landowners to conduct captures and increase the sample of monitored moose. A total of 28 adult females were captured in the 3 study areas in 2015. Moose were fit with either VHF (LMRT-4 model) or GPS (LifeCycle model) radio-collars from Lotek Wireless, Newmarket, Ontario. During 2013–2015 a total of 101 adult female moose have been captured and radio-marked, and as of August 1, 2015, 80 are currently being monitored (Table 1, Figures 10,11). This third year of captures allowed us to reach or approach our ultimate goal of maintaining a sample of 30 marked adult females in each study area. 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, 2015.*

	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
Total captures	31	38	26	95
Moose currently on–air (08/2015)	29	27	24	80

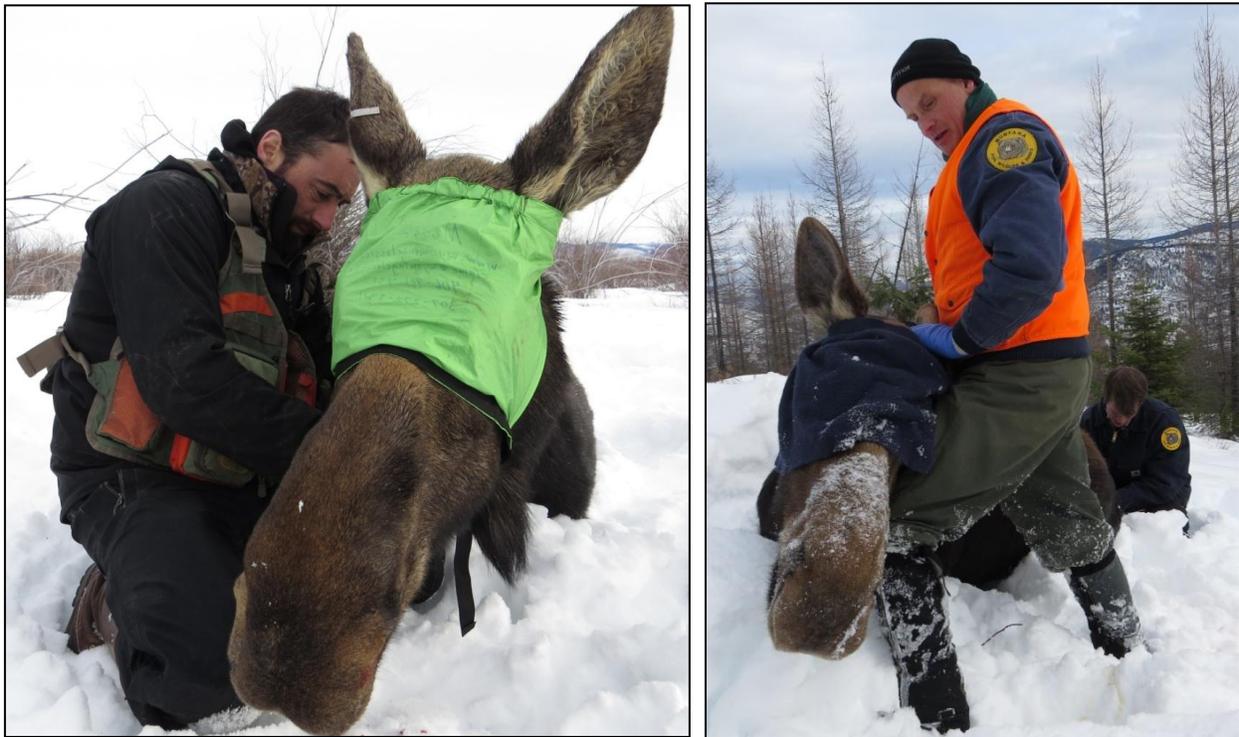
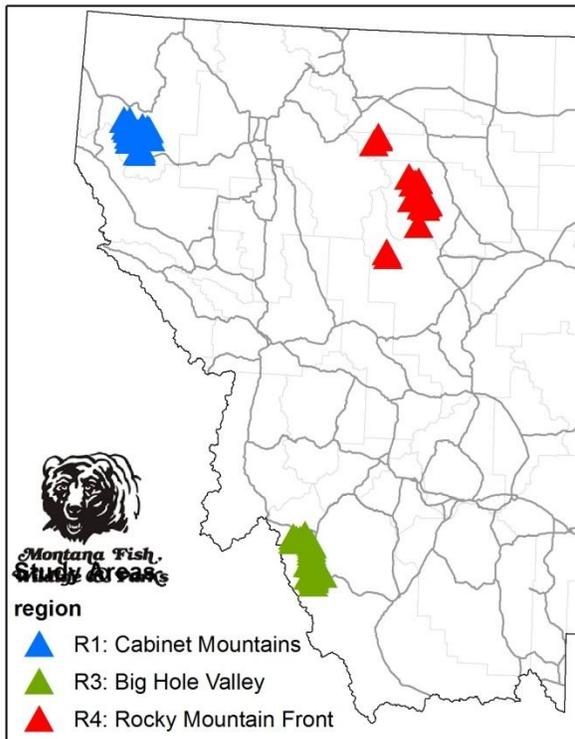
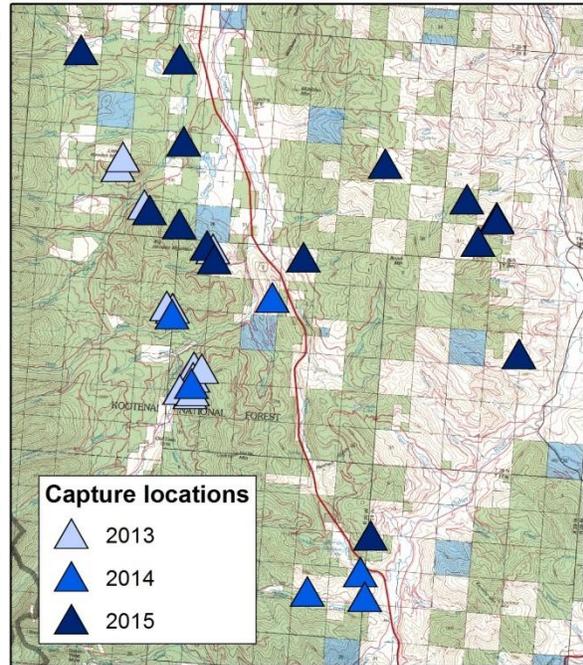


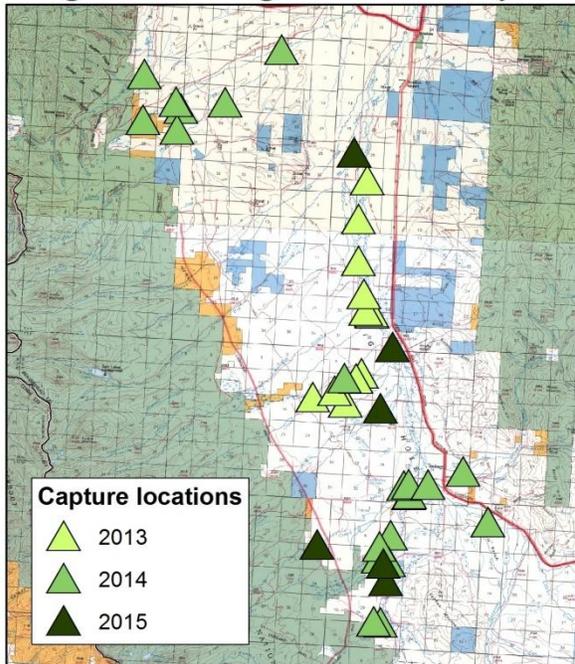
Figure 10. *Jesse Newby (left) administering drug reversal to moose F334 in the Big Hole Valley and Neil Anderson (right) with captured moose F133 in the Cabinet-Fisher study area, 2015.*



Region 1: Cabinet-Fisher



Region 3: Big Hole Valley



Region 4: Rocky Mtn. Front

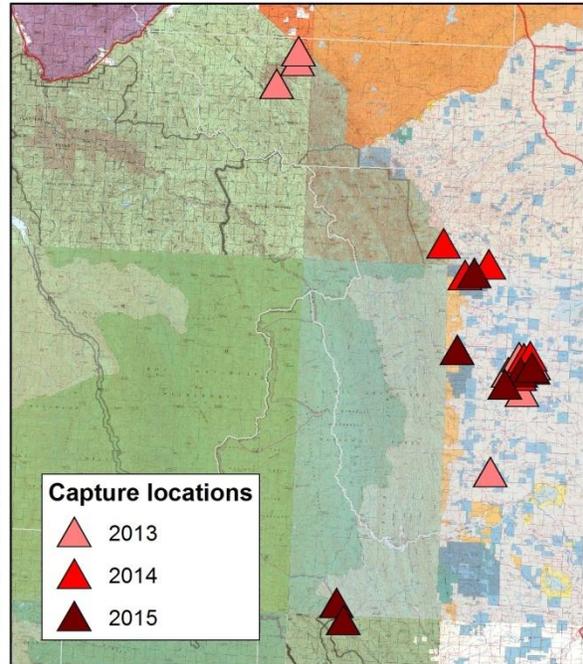


Figure 11. Moose winter capture locations during 2013–2015 across 3 study areas in Montana.

2.3. Monitoring vital rates

2.3.1. Adult female survival.— Our study of adult female survival to date includes 95 radio-collared adult female moose, with a staggered-entry design of individuals entering into the study across 3 winter capture seasons (*see* 2.2 Animal capture and handling). Animals have been deployed with both VHF ($N=67$) and GPS ($N=28$) collars, with mean survival monitoring intervals of 11.9 days and 1.4 days, respectively. For this analysis, we pooled data across the 2013-14 and 2014-15 biological years, and estimated Kaplan-Meier survival rates for each study area and for the entire pooled sample across all study areas.

During the past 2 biological years, the pooled Kaplan-Meier annual survival estimate was 0.882 (SE=0.031), with a 95% confidence interval of (0.824, 0.945). Though study area-level confidence intervals overlap, some study area differences in adult survival are suggested (Figure 12). Specifically, estimates of annual adult survival in the Big Hole Valley are relatively low. Precision of estimates will be improved during the 2015–16 biological year with improved sample sizes of 25–30 individuals in each area.

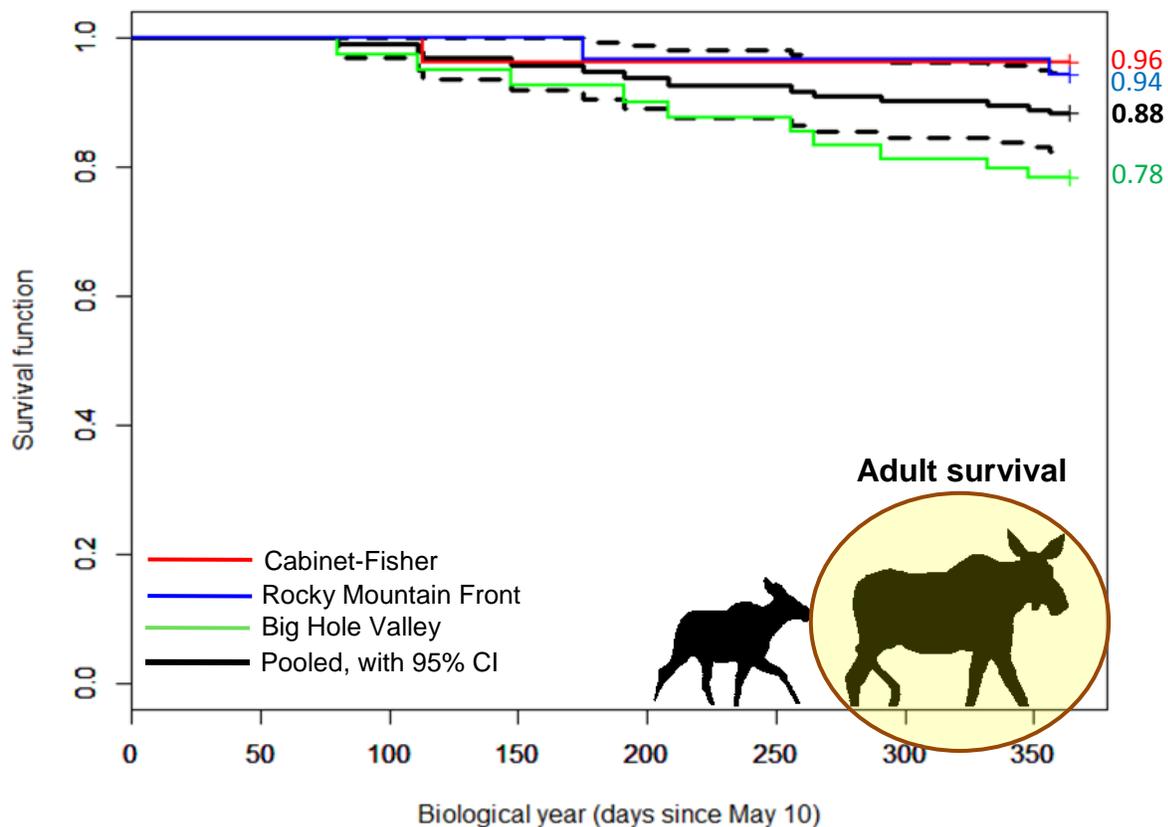


Figure 12. Kaplan-Meier estimates of annual adult female survival within each study area as well as pooled across study areas, during the past 2 biological years, Montana, 2013–2015.

Our monitoring is not currently designed to directly study cause-specific mortality, but we have opportunistically collected data at mortality sites. To date, we have documented 15 mortalities of collared adult moose across all study areas: 2 in the Cabinet-Fisher, 11 in the Big Hole and 2 in the Rocky Mountain Front areas (Table 2). The Big Hole has experienced relatively high mortality due to disease or non-predation causes (Figure 13). Ongoing research will attempt to better understand the causes and consequences of this mortality.

Table 2. *Numbers of mortalities by cause for radio-collared adult female moose documented during February 2013–July 2015, Montana.*

Cause of Mortality	Study area		
	Cabinet-Fisher	Big Hole Valley	Rocky Mountain Front
Disease, non-predation	0	10	0
Hunter harvest	0	1	0
Poaching	0	0	1
Predation, wolf	1	0	1
Unknown	1	0	0



Figure 13. *An example mortality site of F334 in the Big Hole study area, 2015. The full carcass was transported to the Montana Veterinary Diagnostic Lab and necropsied by a veterinary pathologist. Cause of death was determined to be multifactorial, including poor overall condition and infection by 20–30 adult arterial worms in each carotid artery.*

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 a mix of fixed-wing and rotary-wing aircraft depending on terrain and forest cover, with exclusively fixed-wing in the Big Hole Valley and 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 and 41 calves from 40 litters in 2014. In our current 2015-2016 biological year, we have documented 55 calves from 52 litters. We then monitor the fates of these calves by visually locating them with their dams throughout their first year of life (Figure 14).

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 16), and in the future we may consider applying nest success models developed to accommodate such unobserved mortality (Dinsmore et al. 2002).



Figure 14. 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 two biological years (May 2013 – April 2015), the pooled Kaplan-Meier survival estimate of calves-at-heel was 0.394 with a 95% confidence interval of ([0.29, 0.54]; Figure 15). 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 15), but mortalities during fall and winter have also occurred.

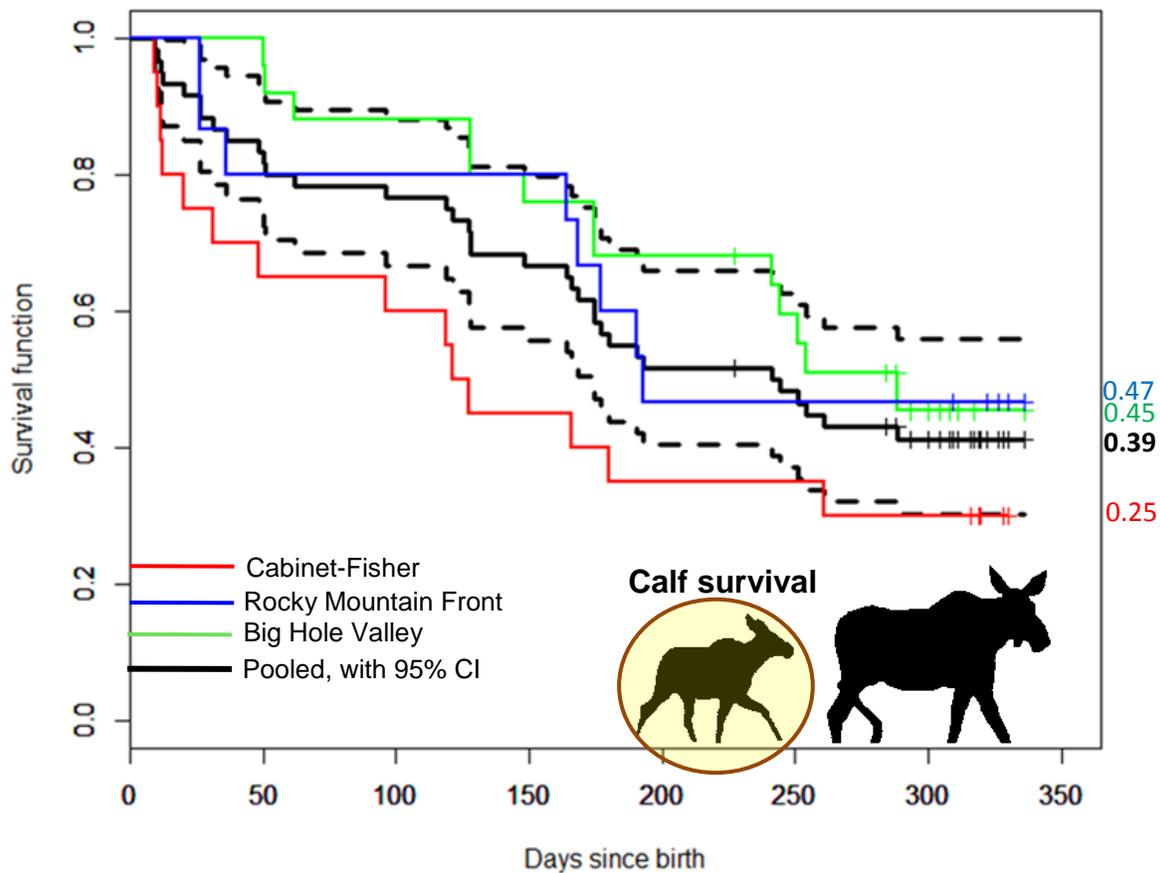
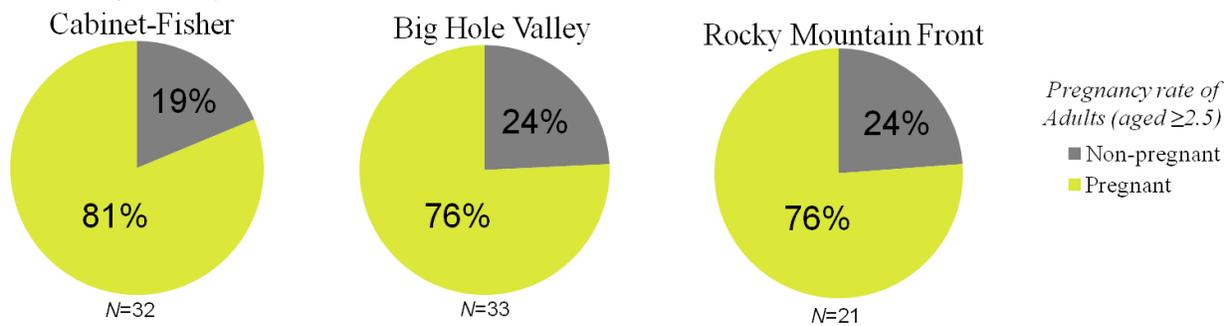


Figure 15. Kaplan-Meier estimates of annual calf survival for the first year of life within each study area as well as pooled across study areas, during the past 2 biological years, Montana, 2013–2015.

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). As reported by the commercial lab offering this test (BioTracking, Moscow, Idaho), a 5–7% rate of false positives can be expected from PSPB-based diagnoses. Pooled across 3 study areas and 3 years of winter captures (2013–2015), our PSPB-based results thus far have suggested an average adult (ages ≥ 2.5) pregnancy rate of 77.9% and a yearling (age 1.5) pregnancy rate of 28.6% (Figure 16A).

Following winter pregnancy testing, we monitor all radio-collared cows with weekly aerial telemetry flights during the birthing season to document the presence and timing of birthed calves. We use flights to estimate an “apparent parturition” rate, representing the proportion of cows with which we detected calves each spring. Thus far our average parturition rate is 24% lower than the corresponding pregnancy rate (range 6%–34%; Figure 16B). We refer to this as an “apparent” rate because of the potential for false negatives when calves are born but die before we are able to detect them. Thus, the difference between pregnancy and parturition rates reflects calves lost both during pregnancy (fetal loss or reabsorption) and soon after birth.

A) Pregnancy rate



B) (Apparent) Parturition rate

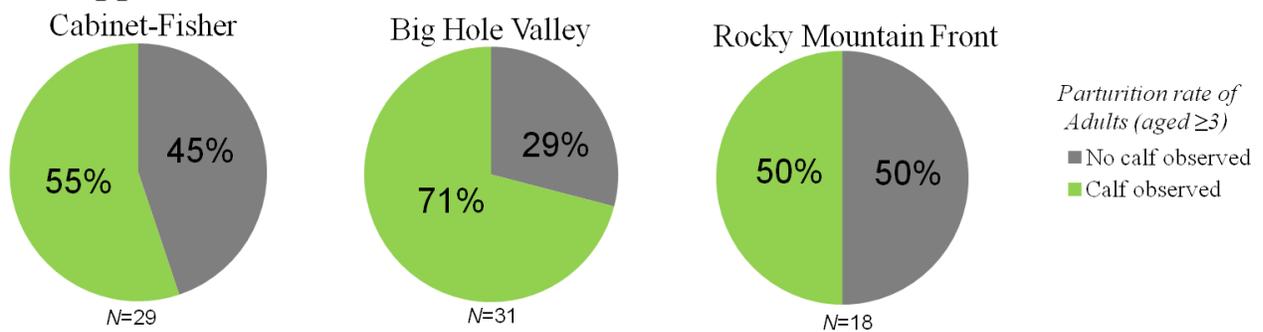


Figure 16. Estimated adult (aged ≥ 2.5) (A) pregnancy rates according to PSPB tests of serum and (B) apparent parturition rates according to calves-at-heel with cows during weekly May–June aerial telemetry flights, from a paired set of 86 adult (age ≥ 2.5) female moose captured during winters of 2013–15 in the Cabinet-Fisher, Big Hole Valley, and Rocky Mountain Front study areas, Montana. Note: Adult females that died before the spring birth pulse were withheld from estimation of parturition rates.

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 17).

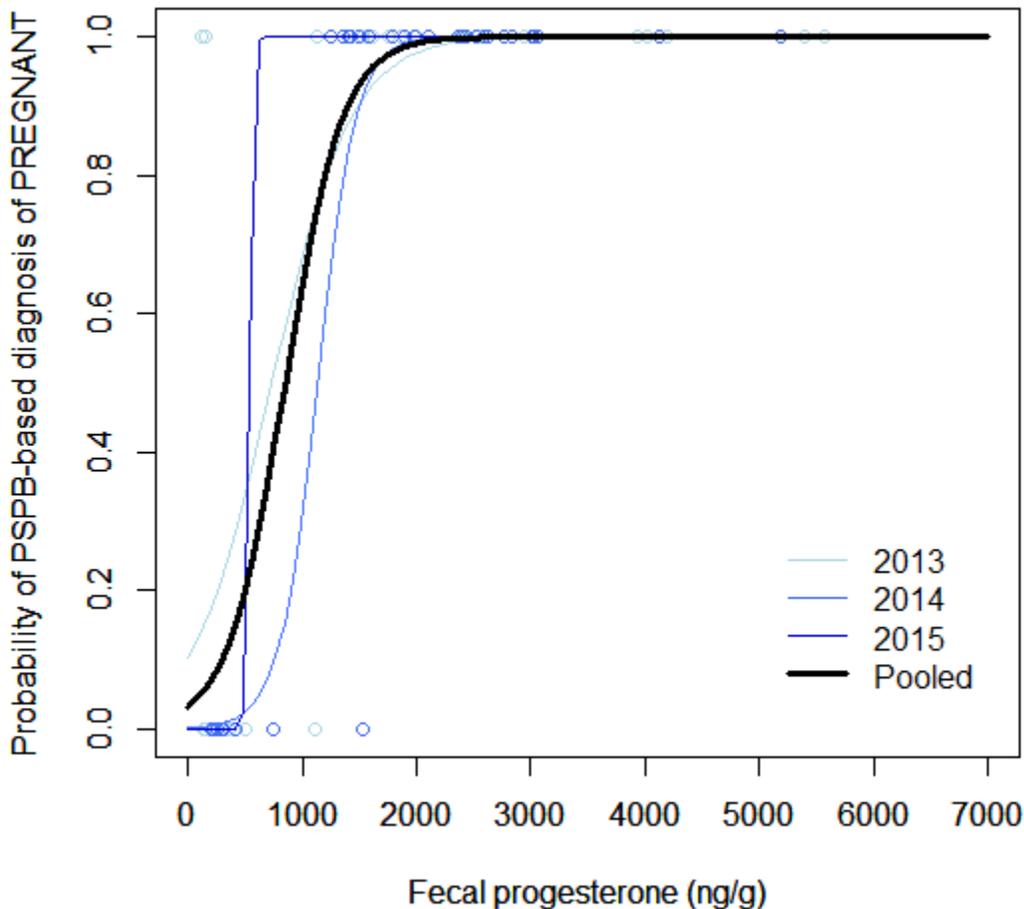


Figure 17. Observed (points) and modeled (lines) relationship between fecal progesterone concentrations and pregnancy diagnoses (according to PSPB in serum) for moose captured in 2013–2015, Montana.

Restricting results to the PSPB sampling, our overall pregnancy rate was 77.9% of adults, which is below the 84.2% average of adult moose pregnancy rates across North American (Boer 1992). When we compare predicted pregnancy with observed litters, the realized parturition rate has been 6–34% lower than this pregnancy rate. This is similar to results of other studies (e.g., Becker 2008) where parturition rates are lower than earlier winter pregnancy rates due to presumed fetal losses throughout winter and/or death of neonatal calves prior to their detection during spring. 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.

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 percent 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 observed for Shiras moose appear to be relatively low (e.g., <15%; Peek 1962, Stevens 1970, Schladweiler and Stevens 1973, Becker 2008), though it is unclear if this reflects a general difference in nutrition or other locally adapted trait. Thus far our observed twinning rates, pooled across 3 birth pulses of 2013–2015, 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).



Figure 18. Adult female moose F116, a 3-year-old at the time, seen in the Cabinet-Fisher study area, April 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 recruitment of new animals into the population after being born and surviving their first year of life. 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 two biological years, 2013–2015 (Figure 19).

While moose on the Cabinet-Fisher study area have seen the lowest calf-survival rate of the 3 areas thus far, they have also encountered the highest adult survival rate. 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 population growth rate of 1.08, or an 8% increase per year. Similarly, the Rocky Mountain Front moose have also seen high survival rates, and an estimated growth rate of 1.06. To the contrary, the Big Hole Valley population has shown the highest calf survival, but the lowest adult survival rate, which resulted in an estimated population growth rate of 0.92, or an 8% decline per year.

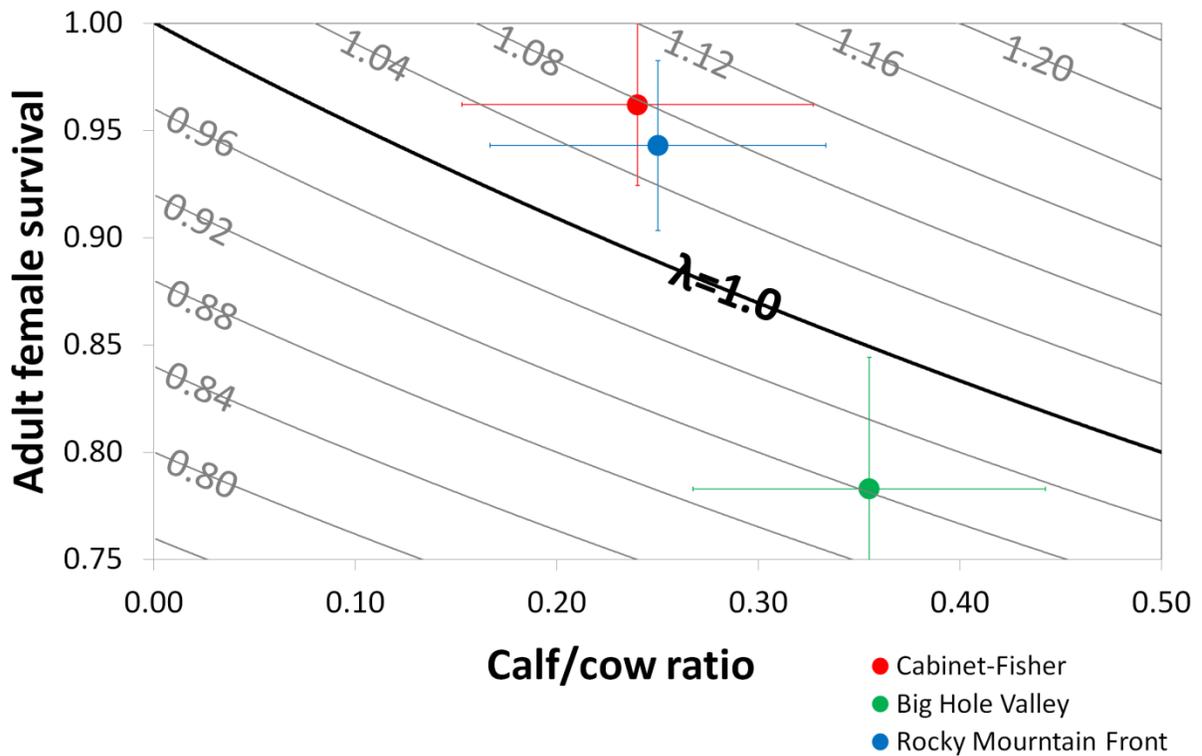


Figure 19. Contour plot showing the estimated annual population growth rates (λ , represented as lines) resulting from two-dimensional combinations of adult female survival and calf:cow ratios, and the annual means and standard errors of these vital rates for 3 moose populations in Montana during two pooled biological years, 2013–2015. Growth rates above the bold line where $\lambda = 1$ indicate a growing population, growth rates below $\lambda = 1$ indicate declining populations.

2.3.5 Age composition. During the 2012–2014 hunting seasons we have asked moose hunters to voluntarily submit incisor teeth for cementum aging. These 3 years of sampling have yielded 328 aged teeth (293 males, 35 females), with ages ranging from <1 to 16 years old (Figure 20). Average age was significantly different between males (5.5 years) and females (4.0 years, $P=0.003$), which is likely the result of hunter selection for older trophy males. The mean age of this sample was statistically similar to that of our sample of 100 live-captured adult females (5.6 years) from portions of Regions 1, 3, and 4.

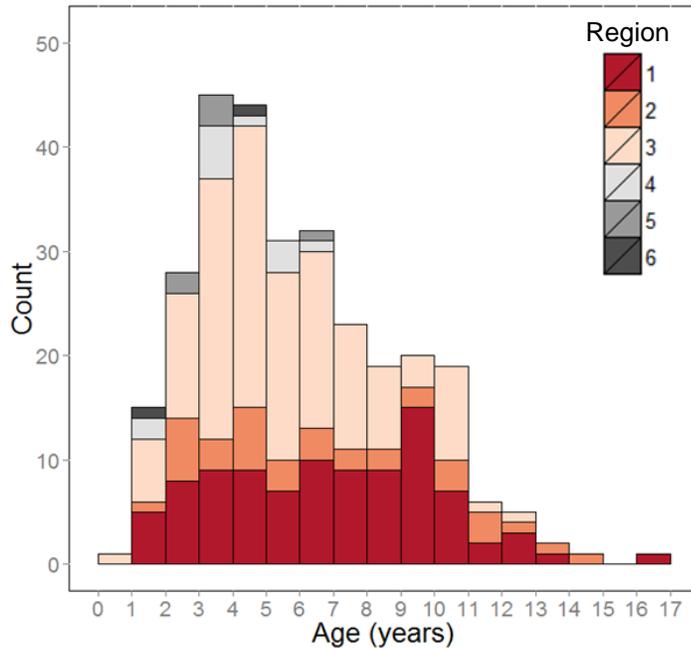


Figure 19. Age distribution of 293 hunter-killed bull moose across all regions of Montana, 2012–2014.

Comparing the age distributions of bulls (excluding cows) harvested between the two regions with the largest samples size, Regions 1 ($N=95$) and 3 ($N=176$), suggests the potential for an older distribution in Region 1 (Figure 21). This pattern is corroborated by that in our live-captured adult female moose, where Cabinet-Fisher (R1) moose have been the oldest, averaging 7.3 years, followed by the Big Hole Valley (R3) at 5.2 years, and the Rocky Mountain Front (R4) at 4.1 years old.

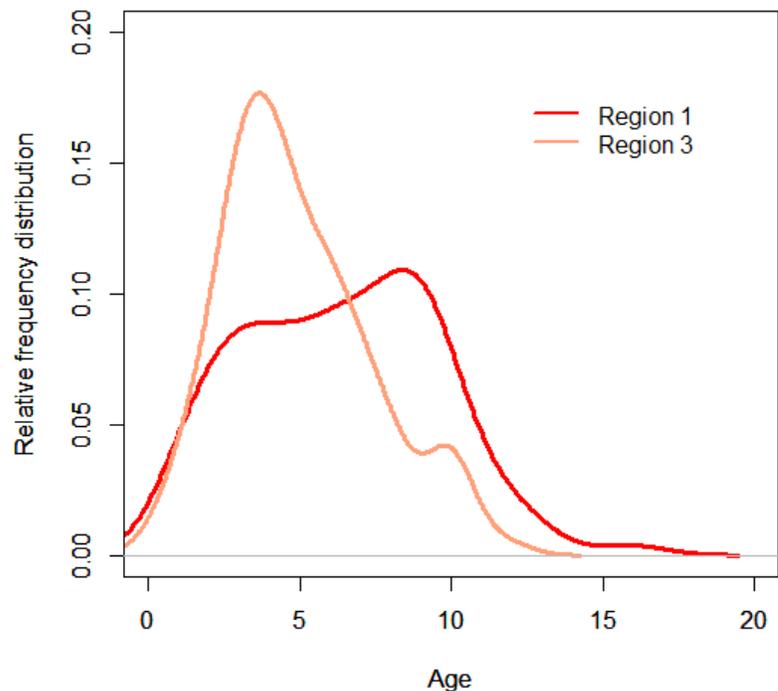


Figure 20. Age distributions of bull moose harvested in Regions 1 (northwest) and 3 (southwest), 2012–2014, Montana.

2.4. 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 drives ungulate dynamics (Franzmann and Schwartz 1985, Bertram and Vivion 2002, Becker 2008). Rump fat thickness has been shown to have a strong linear relationship ($r^2=0.96$) with total body fat in moose (Stephenson et al. 1998). In addition to collecting precise measurements of rump fat among all captured adult female moose, we have asked hunters to measure rump fat of harvested moose, beginning in 2013. Here we present preliminary analyses of these hunter-collected data, specifically comparing estimates of fat on bull moose over time and among regions.

Moose hunters measured rump fat by marking a toothpick within provided sampling kits for 201 bull and 26 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 did find a significant loss in rump fat depth among bull moose across both years (Figure 22).

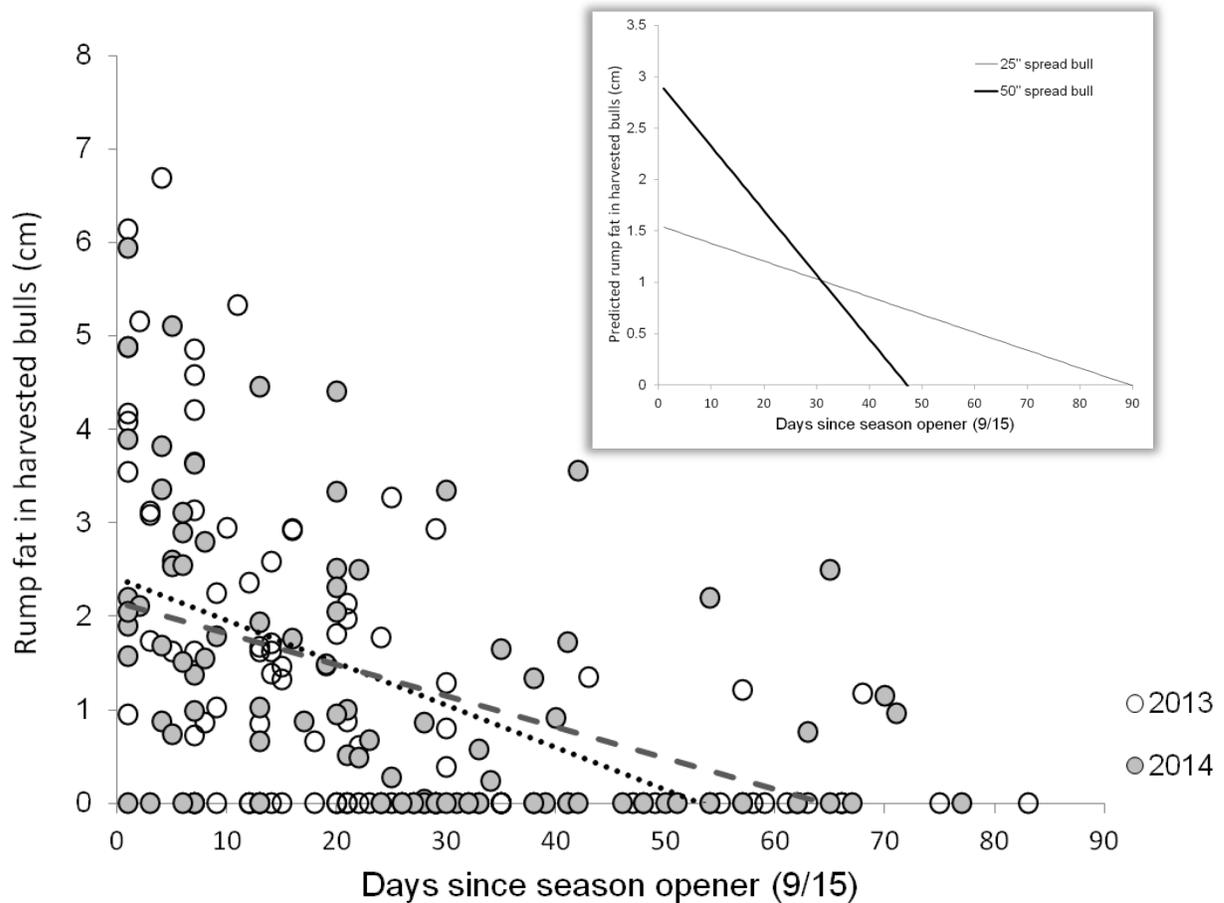


Figure 21. Depth of rump fat declined among harvested bull moose according to the date of harvest during the 2013 and 2014 hunting seasons, and on average declined faster for larger bulls than for smaller ones (inset), Montana.

We also found preliminary evidence that the loss of fat throughout the hunting season was stronger in moose with larger antler spreads (modeled with an interaction between date and spread), which corroborates general life history of ungulates for which reproductive effort is greatest among prime-aged males (Figure 22; Mysterud et al. 2004).

We compared observed measurements of fat for each moose to the average expected amount of fat following the trend lines in Figure 22, and estimated the residuals, 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 then 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 23).

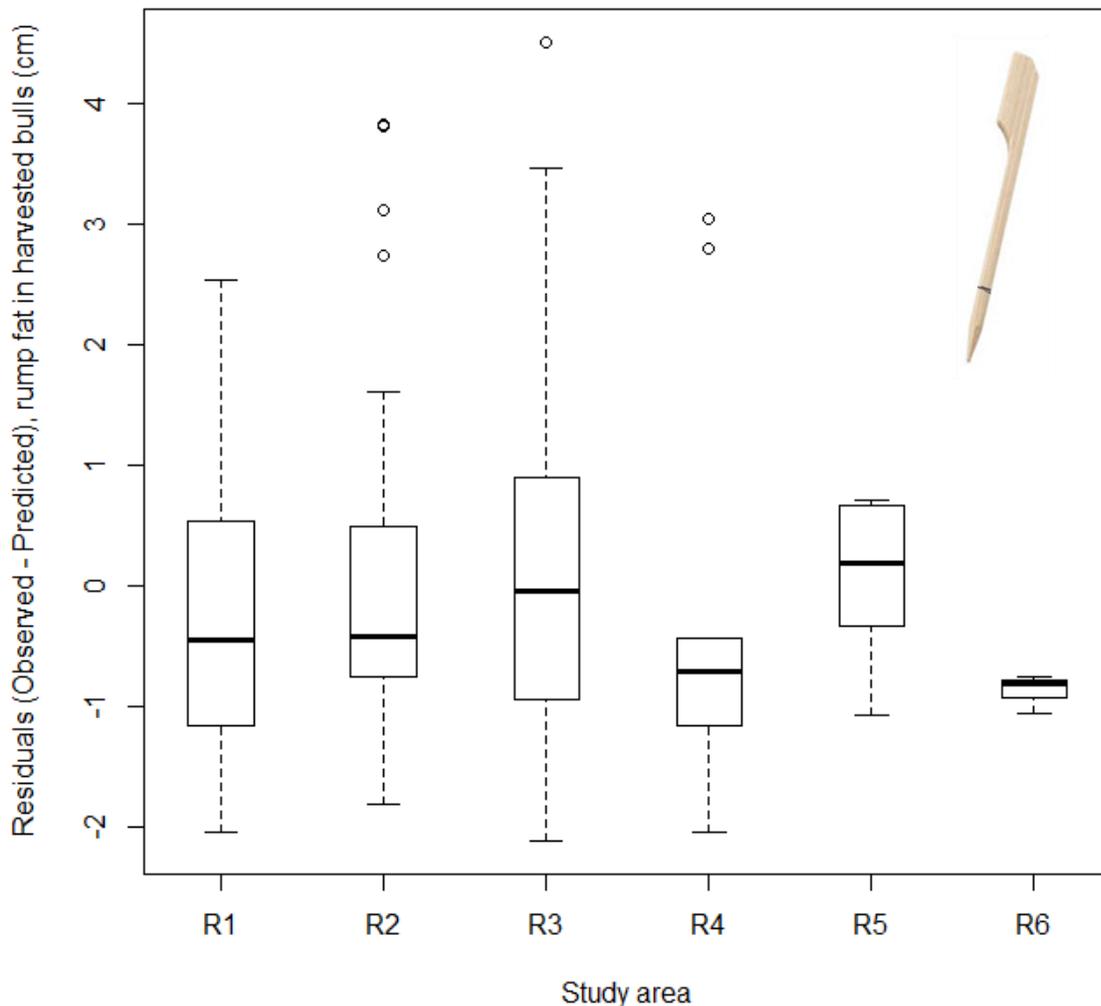


Figure 22. Average residual values comparing the thickness of rump fat in hunter-killed moose to the predicted amount of fat given the date of the hunting season during which each moose was harvested. These data were collected by hunters by marking a toothpick (inset photo) included in sampling kits mailed to all license-holders, Montana, 2013–2014.

2.5. Parasite and disease prevalence

Disease and parasite sampling provide valuable baseline information concerning the health and environmental stressors of moose (and other ungulates) across the state. This information is especially relevant given concerns about the effects of several parasites on moose along the southern extent of their range (Samuel 2004, Murray et al. 2006, Henningsen et al. 2012).

As an example of one parasite being monitored, we count ticks across hair transects in the coats of each captured moose (Sine et al. 2009), and estimated a range of winter tick (*Dermacentor albipictus*) densities from 0 to 0.5 ticks per cm², translating (coarsely) to estimated total tick loads of 0–20,000 ticks per individual moose. There appeared to be differences among study areas that were consistent across years (Figure 24). Tick-induced hair loss is commonly experienced by moose during March–April when ticks reach their adult life form (Mooring and Samuel 1999), though some moose showed evidence of 10-60% hair loss in February.

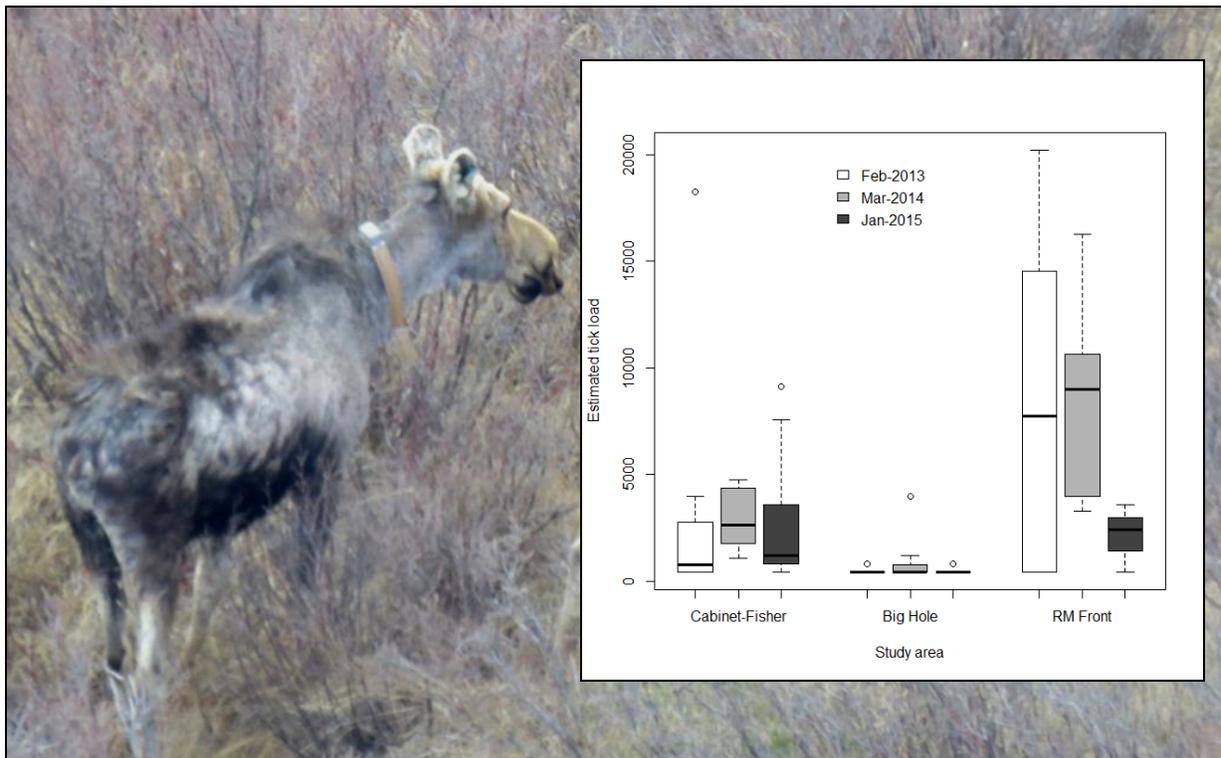


Figure 23. We searched linear transects along the rump and shoulder to estimate the density of winter ticks within the coats of captured moose. Moose on the Rocky Mountain Front have consistently exhibited the highest tick densities and levels of hair loss. Note both the hair loss (symptom of ticks) and ear cropping (symptom of arterial worm) exhibited in the photo of moose F413 on the Rocky Mountain Front, April 2015.

2.6. Temperature and snow conditions

Climate and weather conditions can directly and indirectly influence moose populations (Karns 2007, Van Ballenberghe and Ballard 2007). Climatic patterns determining the timing of spring green up, summer precipitation and winter snow conditions can influence survival and recruitment indirectly through effects on forage availability and quality (Van Ballenberghe and Ballard 2007, Brown 2011) and through climate-mediate effects on parasite densities, such as winter ticks (Samuel 2007). Direct effects of climate on moose can be seen in their metabolic response to temperatures (Renecker and Hudson 1986) and the energetic costs of traveling through deep snow.

In 2013, we began monitoring spatio-temporal variation in ambient temperature using field-deployed temperature data loggers (Thermochrom ibuttons, DS1921G-F5; Dallas Maxim Corporation, Dallas, Texas) in each study area (Figure 25). Thermo-loggers were housed within custom radiation shields following Holden et al. (2013) and placed on North side of tree/shrub at 2 m height (Holden et al. 2011). In January, 2013 we also began monitoring snow conditions at moose telemetry locations to document snow depth, snow conditions, and moose sinking depth. Data from these data-loggers and field measurements will be used to validate GIS models developed by the University of Montana Climate Office (Holden et al. 2011) and National Operational Hydrologic Remote Sensing Center (Brennan et al. 2013), respectively. Calibrated model estimates will be used to test the potential effects of climactic factors on moose vital rates.

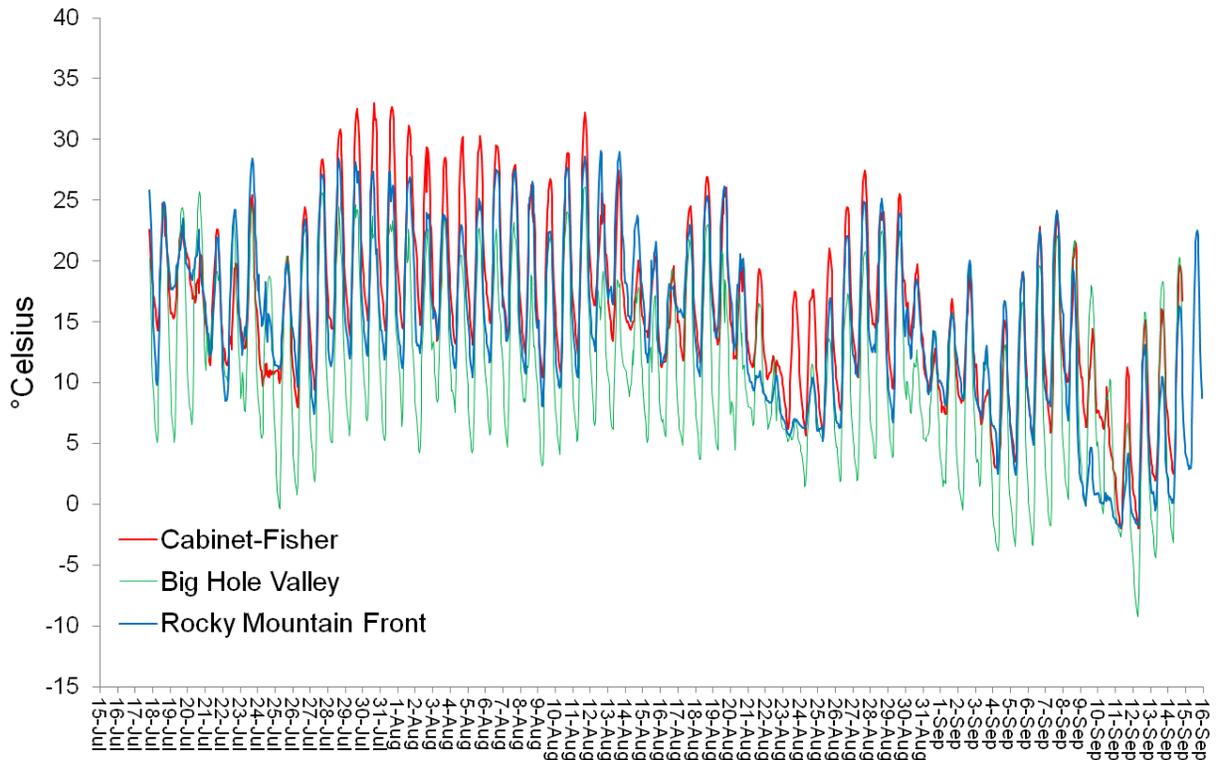


Figure 24. Hourly average ambient temperatures during summer 2014 from temperature sensors deployed within moose research study areas.

Deliverables

Below we list project deliverables (publications, reports, presentations, media communications, and value-added collaborations) stemming from this moose research project, during FYs 13–15 (July 2012–June 2015). In addition to those communications listed below, are frequent discussions with moose hunters statewide.

1. Annual Reports:

2013, 2014, 2015. 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-3.

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.

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, 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
Sheridan Wildlife Speaker Series (<i>DeCesare</i>)	Sheridan, 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	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
2015	Summit Daily (CO)	Moose research	Newspaper
	UM Science Source (MT)	Moose research	Newspaper
	KOFI (MT)	Moose research	Radio
	MFWP Outdoor Report (MT)	Moose research	Television
	Western News (MT)	Moose research	Newspaper

7. Other Project-related Collaborations

Partners	Title	Activities during FY15
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 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 *Lab results from first round of analyses (185 samples) are pending
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

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Literature cited

- 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.
- 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.
- 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.
- Boer, A. H. 1992. Fecundity of North American moose. *Alces (Supplement)* 1:1–10.
- Bontaities, K. M., K. A. Gustafson, and R. Makin. 2000. A Gasaway-type moose survey in New Hampshire using infrared thermal imagery: preliminary results. *Alces* 36:69–75.
- Brennan, A., P. C. Cross, M. Higgs, J. P. Beckmann, R. W. Klaver, B. M. Scurlock, and S. Creel. 2013. Inferential consequences of modeling rather than measuring snow accumulation in studies of animal ecology. *Ecological Applications* 23:643–653.
- Brown, G. S. 2011. Patterns and causes of demographic variation in a harvested moose population: evidence for the effects of climate and density-dependent drivers. *Journal of Animal Ecology* 80:1288–1298.
- 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.
- 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.
- DeCesare, N. J., T. D. Smucker, R. A. Garrott, and J. A. Gude. 2014. Moose status and management in Montana. *Alces* 50:35–51.
- 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.
- Eberhardt, L. L., and M. A. Simmons. 1992. Assessing rates of increase from trend data. *Journal of Wildlife Management* 56:603–610.
- Ericsson, G., and K. Wallin. 1999. Hunter observations as an index of moose *Alces alces* population parameters. *Wildlife Biology* 5:177–185.
- 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.
- Erisman, B. E., L. G. Allen, J. T. Claisse, D. J. Pondella, E. F. Miller, J. H. Murray, and C. Walters. 2011. The illusion of plenty: hyperstability masks collapses in two recreational fisheries that target fish spawning aggregations. *Canadian Journal of Fisheries and Aquatic Sciences* 68:1705–1716.
- Franzmann, A. W., and C. C. Schwartz. 1985. Moose twinning rates: a possible population condition assessment. *The Journal of wildlife management* 49:394–396.
- 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.
- 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.
- Harris, R. B. 1986. Reliability of trend lines obtained from variable counts. *Journal of Wildlife Management* 50:165–171.
- Henningson, J. C., A. L. Williams, C. M. Tate, S. A. Kilpatrick, and W. D. Walter. 2012. Distribution and prevalence of *Elaeophora schneideri* in moose in Wyoming. *Alces* 48:35–44.
- 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.
- Holden, Z. A., J. T. Abatzoglou, C. H. Luce, and L. S. Baggett. 2011. Empirical downscaling of daily minimum air temperature at very fine resolutions in complex terrain. *Agricultural and Forest Meteorology* 151:1066–1073.
- Holden, Z. A., A. E. Klene, R. F. Keefe, and G. G. Moisen. 2013. Design and evaluation of an inexpensive radiation shield for monitoring surface air temperatures. *Agricultural and Forest Meteorology* 180:281–286.
- 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.
- Humbert, J.-Y., L. Scott Mills, J. S. Horne, and B. Dennis. 2009. A better way to estimate population trends. *Oikos* 118:1940–1946.
- Karns, P. D. 2007. Population distribution, density, and trends. Pages 125–140 Ecology and management of the North American moose. 2nd edition. University Press of Colorado, Boulder, Colorado.
- 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.
- Legendre, P. 2013. *lmodel2: Model II Regression*.

- 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.
- 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.
- Monteith, K. L., V. C. Bleich, T. R. Stephenson, B. M. Pierce, M. M. Conner, J. G. Kie, and R. T. Bowyer. 2014. Life-history characteristics of mule deer: Effects of nutrition in a variable environment. *Wildlife Monographs* 186:1–62.
- Mooring, M. S., and W. M. Samuel. 1999. Premature loss of winter hair in free-ranging moose (*Alces alces*) infested with winter ticks (*Dermacentor albipictus*) is correlated with grooming rate. *Canadian Journal of Zoology* 77:148–156.
- Murray, D. L., E. W. Cox, W. B. Ballard, H. A. Whitlaw, M. S. Lenarz, T. W. Custer, T. Barnett, and T. K. Fuller. 2006. Pathogens, nutritional deficiency, and climate influences on a declining moose population. *Wildlife Monographs* 166:1–30.
- 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.
- Mysterud, A., R. Langvatn, and N. C. Stenseth. 2004. Patterns of reproductive effort in male ungulates. *Journal of Zoology* 264:209–215.
- 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.
- Peek, J. M. 1962. Studies of moose in the Gravelly and Snowcrest Mountains, Montana. *The Journal of Wildlife Management* 26:360–365.
- Pritchard, J. K., M. Stephens, and P. Donnelly. 2000. Inference of population structure using multilocus genotype data. *Genetics* 155:945–959.
- Renecker, L. A., and R. J. Hudson. 1986. Seasonal energy expenditures and thermoregulatory responses of moose. *Canadian Journal of Zoology* 64:322–327.
- 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.
- Roffe, T. J., K. Coffin, and J. Berger. 2001. Survival and immobilizing moose with carfentanil and xylazine. *Wildlife Society Bulletin* 29:1140–1146.
- Samuel, B. 2004. White as a ghost: winter ticks & moose. *Federation of Alberta naturalists*.
- Samuel, W. M. 2007. Factors affecting epizootics of winter ticks and mortality of moose. *Alces* 43:39–48.
- Schladweiler, P., and D. R. Stevens. 1973. Reproduction of Shiras moose in Montana. *The Journal of Wildlife Management*:535–544.
- Sine, M., K. Morris, and D. Knupp. 2009. Assessment of a line transect field method to determine winter tick abundance on moose. *Alces* 45:143–146.
- 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*.
- Spoelma, T. P., T. A. Morgan, T. Dillon, A. L. Chase, C. E. Keegan, and L. T. DeBlander. 2004. Montana's forest products industry and timber harvest, 2004. Page 36. *Resource Bulletin*, USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado.
- 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.
- Stevens, D. R. 1970. Winter ecology of moose in the Gallatin Mountains, Montana. *The Journal of Wildlife Management*:37–46.
- 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.
- 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.
- Ueno, M., E. J. Solberg, H. Iijima, C. M. Rolandsen, and L. E. Gangsei. 2014. Performance of hunting statistics as spatiotemporal density indices of moose (*Alces alces*) in Norway. *Ecosphere* 5:art13.