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OVERWINTER SURVIVAL RATE OF MOOSE (ALCES ALCES) CALVES IN RELATION TO HABITAT COMPOSITION

by

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A Thesis Submitted in Partial Fulfillment
of the Requirements for a Degree with Honors
(Wildlife Fisheries and Conservation Biology)

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ABSTRACT

Naturally occurring resource scarcity and limited foraging in winter habitats of northern New England moose (*Alces alces*) calves result in an energetic strain—particularly for individuals experiencing winter tick (*Dermacentor albipictus*) parasitism. Recent collaborative studies conducted between Maine's Department of Inland Fisheries and Wildlife (MIFW) and the University of New Hampshire have attributed the decline of winter survival in moose (*Alces alces*) calves to be closely linked to winter tick (*Dermacentor albipictus*) parasitism (Jones et al 2018, Ellingwood et al. 2018, Healy et al. 2018, Pekins 2018). In addition to winter tick abundance on individuals, we analyzed how winter habitat composition along with other environmental and biological factors impact survival in two climatically distinct regions in Maine. Of the measured parameters, the western moose population had a more significance response in survival than the northern population, which appeared to be less sensitive to the parameters. Survival in the western population was negatively correlated with winter tick abundance (β = -0.130, 95% CI: -0.206 – -0.054) and percent of open habitat (β = -9.273, 95% CI: -14.954 – -3.593), and positively correlated with average snowfall (β = 15.705, 95% CI: 7.644 – 23.766) and capture weight (β = 0.032, 95% CI: 0.013 – 0.051). Model selection results suggest an influence of sex, capture weight, winter tick abundance, average snowfall and percent of deciduous forest within winter home ranges on survival in the northern population. However, there was high variance associated with parameter estimates, making it difficult to precisely identify the covariate effects. This suggests that there may be a more complex dynamic occurring the northern region that we were unable to detect, given the suite of variables we measured

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INTRODUCTION

As climate change continually impacts ecosystem dynamics it is subsequently affecting the survival of species, particularly those found in colder climates. Biological and environmental factors within a species habitat are crucial to understand as they contribute to the survival and persistence of populations. Along the lower extent of their North American range, many moose (*Alces alces)* populations in the northeastern United States are experiencing declines (Jones et al. 2018). Moose exhibit a K-selected life history strategy with generally low reproductive rates (most cows produce either a single or twin calves, but triplets have been observed) and high maternal investment (Franzman and Schwartz 2007). Moose breed annually from late September to October, giving birth to calves the following spring between May and early June after a gestation period of 216-240 days (Stegemann 2006, Franzman and Schwartz 2007). Calves often stay with their mother for approximately one year after birth, but are usually weaned in mid-September as the cow prepares for the next breeding season and upcoming winter months (Franzman and Schwartz 2007, Stegemann 2006).

Growth in moose is divided into three basic periods: (1) the prenatal phase, ending at birth (May to June); (2) the suckling phase, ending at weaning (October to November); and (3) the maturity phases, from postweaning until mortality, reaching sexual maturity at two years of age (Franzman and Schwartz 2007). The calf is either wholly or partially dependent on its mother during the first two periods, during which body size and mass are changing rapidly with average weight gains ranging from 1.3 – 1.6% per day (Franzman and Schwartz 2007). Lactation is energetically costly, requiring

2 – 3 times more energy than gestation (Robbins 1993), but the limited mobility of calves forces lactating cows to balance nutritional requirements with predator avoidance (McLaren et al. 2017). Habitat selection for females post-parturition is heavily influenced by available forage (Severud et al. 2019). However, females have been observed to select habitat that will provide adequate protection from predation during the spring and summer (Dussault et al. 2005). As autumn brings about a decline in forage quality, which corresponds with the weaning period, forage may become more important than predator avoidance for both the calf and cow (Severud et al. 2019).

Winter habitat selection for moose in northern New England is influenced by snow depth, forage availability, and foraging intensity (Andreozzi 2009). Conifer stands shelter moose from snow, thus increasing the presence of moose in such stands during periods of increased snow depth (Coady 1974, Timmerman and McNicol 1988, Courtois et al. 2002, Dussault et al. 2006). The energetic cost of movement increases exponentially in snow accumulation greater than 60 cm (Franzmann and Schwartz 2007). Researchers have found that as snow levels accumulate over 60cm, there is a decrease in open habitat foraging and an increase in use of closed canopy forests and edge habitats (Eastman 1974, Peek et al 1976, McNicol and Gilbert 1980, Doeer 1983, Schwab 1985, Hundertmark et al. 1990, Ardea Biological Consulting 2004). Conifer stands also provide protection from predators (Dussault et al. 2006) due to the visual obstruction from lateral cover (Mysterud and Ostbye 1999, Altendorf et al. 2001, White and Berger 2001, Dussault et al. 2005).

Moose are less active during the winter months to conserve energy (Gao 2013). Therefore, finding suitable forage to help them meet energetic demands is crucial during the winter (Gao 2013). While conifer stands offer protective shelter, they provide the lowest food availability (Courtois et al. 2002). Renecker and Hudson (1989b) and Schwartz (1992a) found spring and summer diets to be 150 to 300 percent more nutritious than winter diets—primarily comprised of deciduous tree and shrub woody twigs and conifers—due to the higher abundance of forage (Franzman and Schwartz 2007). A compilation of North American studies reviewed by Franzmann and Schwartz (2007), found that moose sampled a total of 221 different plant species, but ate high quantities of aspen, birch, and willow throughout their range year-round. Moose have "preferred" and "principle" foods, the former of which are consumed in high proportions when available (Franzmann and Schwartz 2007). Adults are more resilient to habitats with scarce resource availability throughout the winter months (Gaillard et al. 2000 and Monteith et al. 2015). Schwartz et al. (1987a), found that when calves are fed supplement diets during the winter, they do not experience a decline in weight and body dimension loss, suggesting that their growth process is restricted by environmental constraints during the winter (Franzmann and Schwartz 2007). The food scarcity and limiting nutrients associated with occupying conifer stands and the subsequent incurred energy deficit may be impacting calf survival.

Recent studies have suggested that North American moose populations are declining due to high calf mortality related to winter tick (*Dermacentor albipictus*) parasitism (Jones et al 2018, Ellingwood et al. 2018, Healy et al. 2018, Pekins 2018). Winter tick larvae will attach in September to November, with peak engorgement occurring during this time. Nymphal development occurs from December to February with peak engorgement of adult ticks occurring at the tail-end of winter from late

February to mid-March (Franzmann and Schwartz 2007). Consequences of blood loss from winter ticks include excessive grooming that damages the winter coat (Franzmann and Schwartz 2007), restlessness, chronic anemia and low serum protein, mortal weight loss, and reduced visceral fat (Franzmann and Schwartz 2007 citing McLaughlin and Addison 1986, Glines and Samuel 1986, Samuel 1991a, Ellingwood et al. 2018). The naturally deficient diet of moose calves during the winter due to limited foraging resources puts a strain on their energy deficit and protein imbalances (Schwartz et al. 1988). The added physiological strain of replenishing blood lost to winter tick feeding this time intensifies these effects (Ellingwood et al. 2018). Ellingwood et al. (2018) estimated that a 150kg calf with moderate to severe infestations of winter tick lose 64–149% of their total blood volume in early March to late April when adult ticks are in their engorgement period ready to drop off. Over this engorgement period, metabolic demands of calves increase 2.7–6.4% of their daily energy requirements which accrues a protein loss of 33–114% of the daily protein requirement (Ellingwood et al. 2018). In one day, a calf infested with winter tick can lose 2–4 weeks of daily metabolic requirements (Ellingwood et al. 2018), co-occurring when calves are already in their poorest body conditions during late winter (Musante et al. 2007).

Understanding how moose balance energetic demands throughout the winter, such as poor forage quality, high tick loads, and variable weather condition, can provided insight to the resilience of Maine’s moose population. More specifically, studying whether habitat using during the winter can help or hurt the survival of calves in two climatically distinct regions is imperative as the influence of climate change is more heavily felt. The objectives of our study were to assess the influence of winter habitat composition on overwinter survival of moose calves in relation to other biological and environmental factors. GPS data from calves previously collared by MDIFW was used to determine 1) biological and environmental factors that affect overwinter survival of calves, with a focus on winter tick abundance, body condition, weather and habitat composition, and 2) if the effect of these variables differ between the two climatic and geographically distinct regions.

METHODS

Study Area

Data was collected by the Maine Department of Inland Fisheries and Wildlife as part of a larger study on moose survival and recruitment in Maine. Data was collected in two study areas, Wildlife Management District (WMD) 8 from 2013 to 2018 and WMD 2 from 2014 to 2018. The boundaries of these areas were previously defined by state wildlife agencies based on similar biological, geophysical, and hunting characteristics (Jones et al 2018).

WMD 8 is located in western Maine (Jackman) which encompasses portions of Somerset and Piscataquis Counties (Healy et al. 2018) and is north and west of Greenville to the Quebec border (Jones et al. 2018) (Figure 1). Previous vegetation analyses determined that the dominate cover type is hardwood forest comprised of red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), paper birch (*Betula papyrifera*), and American beech (*Fagus grandifolia*) (McCaskill et al. 2016, Jones et al. 2018, Healy et al. 2018). Balsam fir (*Abies balsamae*) was the dominant softwood found at high elevations alongside norther white-cedar (*Thuja occidentalis*) and red spruce (*Picea rubens*) (McCaskill et al. 2016, Jones et al. 2018, Healy et al. 2018).

WMD 2 is located in northern Maine within Aroostook County (Healy et al 2018). The eastern boundary is Route 11, the southern boundary is the American Realty Road, and the Allagash River borders the western boundary (Figure 1). A vegetation analysis by McCaskill et al. (2016) found the area to be dominated by spruce-fir and maple-beech-birch forests. Softwood stands in the area were dominated by balsam fir, northern white-cedar, red spruce, and black spruce (*Picea mariana*) (McCaskill et al. 2016, Healy et al. 2018).

Background

In WMD 8, moose density for 2014–2016 was estimated as 0.97–1.35 moose/km^2 (Jones et al. 2018), whereas 2011–2012 winter aerial surveys estimated a density of 1.7 moose/km^2 (Kantar and Cumberland 2013). For WMD 2, moose density in 2011–2012 was estimated to be 3.0–3.1 moose/km^2 (Kantar and Cumberland 2013), but has decreased to 2.5 moose/km^2 in recent surveys (Healy et al. 2018, L. E. Kantar, MDIFW, unpublished data).

As part of a collaborative study with New Hampshire, >200 adult cow and calf moose were fitted with GPS radio-collars from 2014–2018 within WMD 8 (Healy et al. 2018). WMD 2 was added to this study in 2016; >120 GPS radio-collars were deployed from 2016–2018 (Healy et al. 2018). Captures occurs via aerial net-gunning, upon which calves—roughly 8 months old—were removed from the net, restrained, and blindfolded (Jones et al. 2019). Calves were weighted at capture (Jones et al. 2019). Additionally, they were fitted with a Vectronic GPS radio collar (GPS Plus Vertex Survey Collar: Vectronic Aerospace GmbH, Berlin, Germany) which allowed for growth (Jones et al. 2019 citing Musante et al. 2010). The GPS radio collars were set to take two daily fixes at 0000 and 1200 EST (Jones et al. 2019). After a 4-hour period without movement, detected by a motion sensor within the collar, a mortality was presumed; the collar sent a "mortality message" via email after 6-hours of nonmovement (Jones et al. 2019).

Winter tick were counted using a 10 cm x 10 cm plot on the upper edge of the shoulder blade and on the rump between the hipbone and tail base (Jones et al. 2019). Visible ticks were counted along four parallel 10 cm transects, spaced 2 cm apart, after the hair was parted down to the skin by the capture crew (Jones et al. 2019). The average across all measurements per moose was calculated and used for an individual winter tick abundance in subsequent model testing.

Calculating winter conditions

Winter year was defined from November to April in the respective year of the study the individual was a yearling—i.e. a moose who was calf in winter year one (W1) had a corresponding winter year defined from November 2013 to April 2014. The average monthly maximum and minimum temperature, precipitation, snowfall, and snow depth were calculated for each winter year using historical online weather data from the National Oceanic and Atmospheric Administration (NOAA) National Weather Service (NWS). Weather taken from stations in Fort Kent, Maine and Jackman, Maine were used to attain monthly values for WMD 2 and WMD 8 respectively. Monthly values were then averaged to obtain an overall average for each parameter associated with its respective winter year. Each calf was assigned a winter year (W1, W2, W3, W4, or W5) with the associated parameters in order to assess differences in winter conditions throughout the study.

Given the high correlation of maximum temperature and minimum temperature, and average snow depth with average precipitation and snowfall, minimum temperature and average snowfall were better supported given their lower AIC scores and used for analyses (Appendix 1). While winter year improved model fit overall, it was removed from the models because it lacked stability and consistency due to its correlation with average snowfall ($r = 0.767$) (Appendix 1). Furthermore, the decision of removal was attributed to the overall effect of winter year absorbing all annual variation—masking the effect of the weather covariates. The top model for each area was implemented with the inclusion of winter year for comparison (Table 3, 4, and 5).

Characterizing habitat composition

Following methods similar to Healy et al. (2018), National Land Cover Data (NLCD 2014) was used to determine the habitat composition of winter home ranges for each individual. Based on NLCD classification description, habitat composition was broken into four categories: 1) Deciduous Forest; areas dominated by trees >5m tall with over 20% total vegetation cover and over 75% of the species simultaneously shedding foliage during seasonal changes, 2) Evergreen Forest; areas dominated by trees >5m tall with over 20% total vegetation cover and over 75% of the species maintaining their leaves year round making the canopy never without green foliage, 3) Mixed Forest; areas dominated by trees >5m tall with over 20% total vegetation cover and neither deciduous or evergreen species attribute to more than 75% of the total tree cover, and 4) Open; encompasses all other categories found in WMD 2 and 8 including Shrub/Scrub, Open Water, Cultivated Crops, Emergent Wetlands, Woody Wetlands, and Barren Lands (NLCD 2014). Open encompass a broad range of vegetation types under the assumption that these areas lack structural over story cover which could lead to greater snow levels and less foraging opportunities during the winter months. Shrub/Scrub, the regenerating forest, was found to be the dominant vegetation type in the open category. Woody Wetlands is believed to be where moose's primary food source—aspen, birch, and willow—is classified in the NLCD. Each vegetation class was masked into a thematic raster layer within ArcGIS and projected in UTM 19 N coordinates for subsequent analysis (Version 10.3; ESRI 2011).

Calculating winter home range polygons

GPS Plus X (Vectronic Aerospace GmbH, Berlin, Germany) was used to log GPS transmissions from the collard individuals by MIFW. This data was truncated to obtain GPS points for the duration of the study (November–April) or until the collar received a mortality signal for the individual. Due to collar malfunctions, 11 moose were excluded from analysis (Appendix 2). Based on justification provided by previous studies, a 95% Kernel Density Estimator was used to generate winter home range polygons for each individual (Worton 1995, Seaman et al. 1999, Healy et al. 2018) (Appendix 5). Geospatial Modeling Environment v. 0.7.4.0 (Beyer 2015) was used to obtain the amount of each vegetation class—Deciduous, Evergreen, Mixed, and Open—for each individual winter home range polygon. The percent cover of each vegetation class was calculated from these values and used for analysis.

Statistical analysis

General linear models (GLM) were built and used for model selection within R (R Core Team 2018). Model selection was conducted in a multistep process using Akaike’s Information Criterion (AIC) values to identify top GLM depicting overwinter survival for each data set. Models were constructed for pooled data as well as subset into districts. Individual characteristics (district, winter year, sex, capture weight, body condition, and winter tick abundance) were first compared against a null model to gauge whether they were influencing survival. A quadratic term was added to winter tick abundance to assess if there was a threshold for winter tick abundance on calves that was not being described adequately by a linear relationship. However, the resulting model did worse, and therefore we retained the singular term for winter tick abundance. “District” was only applied for the pooled data and was not used during individual analysis of WMD 2 and 8. The parameter found to have the lowest AIC value was used as a base model, upon which individual characteristics were added to produce the best fit model before assessing the influence of winter conditions and habitat characteristics. Next, we considered variables related to winter conditions (winter year, minimum temperature, and average snowfall) and were added or removed to the base model depending on the resulting AIC score. Finally, we considered habitat composition (%Deciduous, %Evergreen, %Mixed, and %Open) and added or removed to the model depending on the resulting AIC score. Variables, previously excluded, that we were interested in testing for support, were added to see how they changed the top model. Delta AIC scores were generated from our best model for each analysis. From our best model we then assessed the relative importance of each coefficient based on the magnitude of the effect, and whether β-estimates and their 95% confidence interval overlapped zero.

RESULTS

Of the 270 calves used for this study, 103 were collared in WMD 2 and 167 were collared in WMD8—36 and 106 died respectively throughout the winter years (Table 1). The average winter home range size of individuals was 7.01 km^2 (SD = 7.36 km^2). WMD 2 was primarily comprised of mixed, evergreen, and deciduous forest with an average minimum temperature of 8.71°F and an average monthly snowfall of 0.653 inches (Table 1 and Table 2). WMD 8 was primarily comprised of mixed, evergreen, and deciduous forest, and shrub/scrub habitat with an average minimum temperature of 8.54°F and an average snowfall of 0.603 inches (Table 1 and Table 2). Winter home ranges in WMD 2 lacked any areas of medium to high intensity development, whereas these were found in a small fraction of WMD 8 (Table 2). Calves in WMD 2 had an average of 10.36 winter ticks while calves in WMD 8 had an average of 13.84 winter ticks, but values were highly variable throughout years in the study (Table 1).

Models for pooled data

Among the individual characteristic parameters for the pooled data, capture weight drastically improved model fit and was used as a base model. We identified support for an effect of sex on survival (Table 3). The resulting base model containing, sex, capture weight and winter tick abundance, was then used to assess the influence of winter conditions and habitat composition. Average snowfall, minimum temperature, and district were important predictors of calf survival. The percent of open habitat was the most important predictor among habitat composition types. The addition of the evergreen and deciduous initially overcame the >2 ΔAIC penalty, but when the three habitat terms were put together the model did worse. Evergreen was removed, but the percent of deciduous forest was kept due to the higher AIC score (Table 3). The best resulting model coefficients from the pooled data indicate that capture weight (β = 0.013, 95% CI: 0.005 – 0.022), percent of open habitat (β = -3.909, 95% CI: -6.707 – -1.11), sex (β = -0.805, 95% CI: -1.525 – -0.085), and minimum temperature (β = -0.156, 95% CI: -0.296 – 0.015) were most influential on overwinter calf survival ($r^2 = 0.194$) (Table 6). Winter tick abundance, district, average snowfall, and percent of deciduous habitat improved model fit, but the 95% confidence intervals overlapped zero indicating greater variability in the strength and direction of the effect (Table 6).

Models for Wildlife Management District 8

The same base model from the previous analysis of the pooled data containing sex, capture weight, and winter tick abundance was used for WMD 8. We assessed the influence of weather conditions and found that an effect of average snowfall was supported. The percent of open habitat was the most important predictor among habitat composition types. Addition of other habitat factors reduced the models fit and were therefore removed. The best resulting model coefficients indicated that average snowfall (β = 15.705, 95% CI: 7.644 – 23.766), capture weight (β = 0.032, 95% CI: 0.013 – 0.051), winter tick abundance (β = -0.130, 95% CI: -0.206 – -0.054), and percent of open habitat (β = -9.273, 95% CI: -14.954 – -3.593) significantly influenced overwinter calf survival ($r^2 = 0.416$) (Table 4). There was support for an effect of sex on survival with males having lower survival than females, however the 95% confidence intervals overlapped zero indicating that there was variability in the strength and direction of the effect (Table 7).

Models for Wildlife Management District 2

The same base model from the previous analysis of the pooled data containing sex, capture weight, and winter tick abundance was used for WMD 2. We assessed the influence of weather conditions and found that an effect of average snowfall was supported. The percent of deciduous habitat was the most important predictor among habitat composition types. Addition of other habitat factors reduced the models fit and were therefore removed (Table 5). The best resulting model coefficients indicated that sex (β = -1.161, 95% CI: -2.155– -0.168) was the only supported factor on overwinter calf survival ($r^2 = 0.091$) (Table 8). There was support for an effect of capture weight, winter tick, average snowfall, and percent of deciduous habitat on survival, however the 95% confidence intervals overlapped zero indicating that there was variability in the strength and direction of the effect (Table 8).

Survival trends of Wildlife Management District 8

Among the measured variable, there was greater support for covariate effects on survival for the sub-population in WMD 8. Winter tick abundance negatively impacted survival rate, with close to a 50% decline in survival for individuals with very high tick loads (approx. 20 ticks; Figure 2). Capture weight was shown to have a positive relationship with predicted survival (Figure 2). Individuals with a higher percent of open habitat within their winter home range had a lower predicted survival rate, decreases to a near 0% survival after more than 50% of their winter home range was comprised of open habitat (Figure 2). Higher average snowfall during the winter increased the predicted survival rate of calves (Figure 2). Mortality rates were consistently higher in the western district through out the study resulting in lower overwinter survival.

DISCUSSION

The best supported model for the entire data set suggests that capture weight and sex are important biological factors contributing to overwinter survival. Minimum temperature and the percent of open habitat within a calf's winter home range were found to be important environmental factors. As weight increased both female and male calves had a higher predicted survival rate. These results parallel previous studies which indicate that yearlings commonly lose weight and body dimension as a direct result of negative energy balances during the winter (Franzmann and Schwartz 2007). For moose, energy— defined as the capacity for activity and function—is virtually all obtained via plant consumption (Franzmann and Schwartz 2007). As energic demands increase during the winter, larger yearlings may be more resilient due to higher fat deposits that can act as an energic reserve increasing their chance of survival as seen through this positive relationship.

Additionally, larger calves may be better adapted to cope with the high energetic demands associated with large tick loads. Recent studies have found calves with a higher winter tick abundance to have a lower survival rate (Samuel 2004, Ellingwood et al. 2018, Healy et al. 2018, Jones et al 2018, Pekins 2018). An experimental design of moose with extensive hair-loss infested with winter tick had lower average weight gain and fat stores than moose not infested (Bergeron 2011). The best supported model for WMD 8 showed that weight and winter tick abundance had a larger effect size given the beta estimates and associated variance. This is suggestive that the added effect of winter tick abundance on top of lower body conditions is contributing to lower survival rates, as previous studies have indicated. As forage effort and intake over winter are reduced due to excessive grooming associated with high winter tick infestations, calves are incurring a greater energy deficit leading to lower survival.

This is co-occurring during a period of low-quality forage as seen through the negative association of having more open habitat within a calf's winter home range. Open habitat was defined less conservatively, with the inclusion of multiple habitat types (e.g. barren, wetlands, developed areas, etc) we believed to have insufficient forage during the winter months, subsequently resulting in lower food rich environments. A calf with a higher percent of open habitat would consequently have to travel farther to find sufficient forage necessary to meet the demands of maintenance and growth for yearlings. A limited amount of high-quality foraging within the winter home range, may force calves to consume plants with low nutritive values. Moose are unable to meet minimum energy requirements when consuming these foods and would have to eat a larger volume of them (Franzmann and Schwartz 2007).

An infested calf covering greater distances and foraging on poor quality foods would be unable to meet the exacerbated energy requirements resulting in a net negative loss of energy, and potential weight loss, further lowering survival rate. As previously demonstrated, adults are better adapted to withstanding scare resource availability (Gaillard et al. 2000, Franzmann and Schwartz 2007), whereas growth vital to calf winter survival is restricted by environmental constraints (Monteith et al. 2015). During the winter months, open areas are covered by snow and most likely lack sufficient browse. This could be leading to the observed negative trend of open areas on calf survival.

Open habitat is likely providing less overstory cover resulting in greater snowfall, and snow depth throughout an individual's over winter home range. As a result, this could contribute to increased energetic demands for movement. Along with insufficient forage, open areas during the winter have higher snow accumulation due to less forest cover. This could lead to a negative compounding effect of energetic demands on moose calves due to the difficulty associated with movement at high snow depths. However, our results found snow depth to be positively association with predicated overwinter survival rates (Figure 2 and 3). This relationship was particularly strong in WMD 8 ($\beta = 15.705$, 95% CI: 7.644–23.766). We suspect this is due to the influence snow depth has on winter tick populations, which we were unable to parse out within our models.

A higher percent of deciduous forest within the winter home range appeared to have a negative impact on overwinter survival, but given the variance of the beta estimates no sound conclusion could be stated. However, these results are suggestive that there is a relationship between the percent of deciduous forest in winter home ranges and survival. While deciduous forest type might contain a greater amount of forage, it has less canopy cover in the winter which is likely leading to similar problems described with open habitat. The addition of more available forage is not enough to overcome the net negative energetic demands associated with snow depth and winter tick loads leading to a potential negative effect on survival.

Both mixed and coniferous vegetation types were not found to have an effect on survival. We expected coniferous forests to an effect on survival given the shelter it provides as snow accumulates (Coady 1974, Timmerman and McNicol 1988, Courtois et al. 2002, Dussault et al. 2006), but lack of food availability it provides (Courtois et al.

2002). Moose may have had enough protective conifer stands within their winter home ranges, but were able to utilize other types of forest for foraging purposes, resulting in conifer stands showing no definitive effect on survival. Variation in the amount and distribution of all cover types within a home range could cumulatively provide enough resources for an individual. Within their winter home ranges, moose were most likely able to make use of variation in habitat structure among the categorized landcover types resulting in our inability to identify an effect on survival.

We found support for strong covariate effects of winter tick abundance negatively impacting the sub-population in WMD 8, but there was more variation in the parameter estimates for WMD 2 (Figure 2 and 3). We believe this variability influenced the parameter estimates for the pooled data as well. Other dynamic influences in the northern sub-population could be occurring that are not being effectively captured in our model. For example, this difference could be a result of the geographic differences of these two districts. Being that WMD 8 is in western Maine, the resulting winters are more likely to be shorter and less severe. This trend could be exacerbated in the coming years due to climate change. An increase in shorter winters favors winter tick abundance resulting in a negative impact on moose populations at the periphery of their southern ranges (Jones et al. 2018). Another explanation could be the difference in average tick loads found on calves between the two study sites (Table 1). While it may appear to be a small difference, the measurements were only taken on two small areas of the individual. When applied to the entire body of an individual, this would result in calves in the western district having exponentially higher winter tick abundances compared to the northern district (Figure 5). Given that sex was found to be the only statistically significant predictor of survival in WMD 2, we were most likely unable to capture variation in survival within the model coefficients that we measured. However, this study emphasizes the importance of considering both environmental conditions and biological factors when assessing impacts on survival rates.

Suggestions for future avenues of study

The lack of support in weather variables used in this study suggest that they are not fully capturing annual variation. The winter data is coarse at best, resulting in unexplained variation. There were most likely other dynamics occurring that we were unable to tease apart. For example, the impact of weather on winter tick populations or how summer resources might influence survival. We suggest a more rigorous approach that captures snow depth in relation to the structure of winter vegetation and forest composition. This could prove helpful when thinking about both available forage and the energetic cost of moving through the landscape. This will become increasingly important as climate change's effects on winter length and severity become more pronounced.

Furthermore, the available habitat data used provided a rough estimate of what each winter home range was comprised of. By using generalized landcover types, vital information is not accounted for. For example, vegetation structure could be influencing habitat selection by females post-parturition leading into the resulting winter home range as forage becomes increasingly important. We suggest the use of Lidar data, or more detailed vegetation information, moving forward as it would be able to capture these discrepancies and provide a more detailed description of vegetation composition within an individual's home range.

The weight of calves during the winter was found to be a very important parameter in predicting overwinter survival. There is likely a carryover effect from summer conditions—particularly in relation to the female being able to provision for her growing offspring—that is influencing this dynamic. Other important seasonal dynamics such as the condition of females and available resources during gestation, and summer months when calves are nursing were not accounted for in this study. These factors will influence the growth rate of offspring which helps prepare them for the upcoming winter, and are therefore important dynamics to study more intensely. Understanding how seasonal dynamics effect populations is becoming increasingly important as climate change continues to alter species habitat.

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TABLES AND FIGURES

Table 1. Summary of the total number of individuals (Male and Female) used in the study, the number of respective winter mortalities (Mortalities), average capture weight (kg), average count of winter ticks, average minimum temperature (°F), and average snowfall (in.) subdivided for each winter year in Wildlife Management District (WMD) 2 and 8, Maine, USA, winters of 2013 – 2018. Winter year is defined as November through April for snowfall, but captures took place from December to January.

Winter Year	Total	Male	Female	Mortalities	Capture Weight (kg)	Winter tick	Min temp (°F)	Snowfall (in.)
WMD 2	**103**	**44**	**59**	**44**	**411.7**	**11**	**8**	**18**
2014-2015	8	3	5	4	395.7	9	3	14
2015-2016	34	14	20	19	422.9	10	11	16
2016-2017	26	12	14	9	430.9	22	9	19
2017-2018	35	15	20	12	409.4	3	8	21
WMD 8	**167**	**75**	**92**	**113**	**411.9**	**14**	**9**	**16**
2013-2014	32	15	17	25	NA	23	6	17
2014-2015	33	12	21	25	NA	15	6	18
2015-2016	36	16	20	27	427.9	9	14	11
2016-2017	33	17	16	20	407.1	21	11	19
2017-2018	33	15	18	16	400.7	3	6	15
Total	**270**	**119**	**151**	**157**				

Table 2. The composition of landcover type within each study area and the average percent of landcover within the of used landcover for winter home ranges of moose within their respective districts, Maine, USA, 2014. Classification based on the National Land Cover Data (NLCD 2014).

Landcover type	Composition of study area	Composition of winter home range
WMD 2		
Deciduous	0.1867	0.1511
Evergreen	0.2040	0.2202
Mixed	0.3932	0.3919
Open	0.2161	0.1717
WMD 8		
Deciduous	0.1952	0.1680
Evergreen	0.2307	0.2395
Mixed	0.2358	0.2400
Open	0.3383	0.2560

Table 3. Comparison of generalized linear models, number of parameters (K), Akaike's Information Criterion value (AIC), and change in AIC value from the top model (ΔAIC) of moose calf overwinter survival model selection, Wildlife Management District (WMD) 2 and 8, Maine, USA, winters of 2013 – 2018.

Model grouping	**Model parameters**	**K**	**AIC**	**ΔAIC**
Habitat composition				
Model.20	Survival3~Sex + Cap.weight + Winter.tick + District + Min.temp + Ave.snow + Open + Deciduous	9	226.48	0.00
Model.19	Survival3~Sex + Cap.weight + Winter.tick + District + Min.temp + Ave.snow + Open + Deciduous + Evergreen	10	228.45	1.82
Model.18	Survival3~Sex + Cap.weight + Winter.tick + District + Min.temp + Ave.snow + Open + Mixed	9	228.56	2.08
Model.17	Survival3~Sex + Cap.weight + Winter.tick + District + Min.temp + Ave.snow + Open + Evergreen	9	228.20	1.72
Model.16	Survival3~Sex + Cap.weight + Winter.tick + District + Min.temp + Ave.snow + Open	8	226.63	0.15
Model.15	Survival3~Sex + Cap.weight + Winter.tick + District + Min.temp + Ave.snow + Mixed	8	232.70	6.23
Model.14	Survival3~Sex + Cap.weight + Winter.tick + District + Min.temp + Ave.snow + Evergreen	8	231.29	4.82
Model.13	Survival3~Sex + Cap.weight + Winter.tick + District + Min.temp + Ave.snow + Deciduous	8	232.39	5.91
Winter conditions				
Model.12	Survival3~Sex + Cap.weight + Winter.tick + District + Min.temp + Ave.snow	7	241.80	15.32
Model.11	Survival3~Sex + Cap.weight + Winter.tick +Min.temp + Ave.snow	6	241.28	14.655
Model.10	Survival3~Sex + Cap.weight + Winter.tick + Ave.snow	5	244.72	18.24
Model.9	Survival3~Sex + Cap.weight + Winter.tick + Min.temp	5	244.64	18.16
Model.8	Survival3~Sex + Cap.weight + Winter.tick + Winter.year	7	241.65	15.17
Winter tick				
Model.7	Survival3~Sex + Cap.weight + Winter.tick + (I(Winter.tick^2))	5	255.97	29.49
Model.6	Survival3~Sex + Cap.weight + Winter.tick	4	254.06	27.58
Individual biological characteristics				
Model.5	Survival3~Winter.tick	2	376.77	150.29
Model.4	Survival3~Body.cond	2	377.97	151.49
Model.3	Survival3~Cap.weight	2	256.93	30.45
Model.2	Survival3~Sex	2	383.19	156.71
Model.1	Survival3~District	2	368.44	141.96
Null Model	Survival3~1	1	384.41	157.93

Table 4. Comparison of generalized linear models, number of parameters (K), Akaike's Information Criterion value (AIC), and change in AIC value from the top model (ΔAIC) of moose calf overwinter survival model selection, Wildlife Management District (WMD) 8, Maine, USA, winters of 2013 – 2018.

Model number	**Model parameters**	**K**	**AIC**	**ΔAIC**
Habitat composition				
WD15	Survival3~Sex + Cap.weight + Winter.tick + Ave.snow + Open	6	85.97	0.00
WD19	Survival3~Sex + Cap.weight + Winter.tick + Ave.snow + Open + Deciduous + Evergreen + Mixed	9	88.24	2.27
WD18	Survival3~Sex + Cap.weight + Winter.tick + Ave.snow + Open + Mixed	7	87.35	1.39
WD17	Survival3~Sex + Cap.weight + Winter.tick + Ave.snow + Open + Evergreen	7	87.94	1.98
WD16	Survival3~Sex + Cap.weight + Winter.tick + Ave.snow + Open + Deciduous	7	87.75	1.79
WD14	Survival3~Sex + Cap.weight + Winter.tick + Ave.snow + Mixed	6	98.90	12.93
WD13	Survival3~Sex + Cap.weight + Winter.tick + Ave.snow + Evergreen	6	96.95	10.99
WD12	Survival3~Sex + Cap.weight + Winter.tick + Ave.snow + Deciduous	6	99.38	13.42
Winter conditions				
WD11	Survival3~Sex + Cap.weight + Winter.tick + Min.temp + Ave.snow	6	100.71	14.75
WD10	Survival3~Sex + Cap.weight + Winter.tick + Ave.snow	5	98.87	12.91
WD9	Survival3~Sex + Cap.weight + Winter.tick + Min.temp	5	109.31	23.35
WD8	Survival3~Sex + Cap.weight + Winter.tick + Winter.year	6	100.71	14.75
Winter tick				
WD7	Survival3~Sex + Cap.weight + Winter.tick + (I(Winter.tick^2))	5	115.60	29.64
WD6	Survival3~Sex + Cap.weight + Winter.tick	4	114.15	28.18
Individual biological characteristics				
WD5	Survival3~Winter.tick	2	218.15	132.19
WD4	Survival3~Body.cond	2	220.17	134.21
WD3	Survival3~Cap.weight	2	114.86	28.89
WD2	Survival3~Sex	2	224.05	138.09
WD1	Survival3~Winter.year	5	220.94	134.97
Null Model	Survival3~1	1	223.04	137.07

Table 5. Comparison of generalized linear models, number of parameters (K), Akaike's Information Criterion value (AIC), and change in AIC value from the top model (ΔAIC) of moose calf overwinter survival model selection, Wildlife Management District (WMD) 2, Maine, USA, winters of 2014 – 2018.

Model number	**Model parameters**	**K**	**AIC**	**ΔAIC**
Habitat composition				
ND12	Survival3~Sex + Cap.weight + Winter.tick + Ave.snow + Deciduous	6	124.21	0.00
ND19	Survival3~Sex + Cap.weight + Winter.tick + Ave.snow + Deciduous + Open + Mixed + Evergreen	9	129.31	5.11
ND18	Survival3~Sex + Cap.weight + Winter.tick + Ave.snow + Deciduous + Mixed	7	126.11	1.90
ND17	Survival3~Sex + Cap.weight + Winter.tick + Ave.snow + Deciduous + Evergreen	7	126.20	1.99
ND16	Survival3~Sex + Cap.weight + Winter.tick + Ave.snow + Deciduous + Open	7	125.48	1.27
ND15	Survival3~Sex + Cap.weight + Winter.tick + Ave.snow + Open	6	126.48	2.27
ND14	Survival3~Sex + Cap.weight + Winter.tick + Ave.snow + Mixed	6	126.28	2.07
ND13	Survival3~Sex + Cap.weight + Winter.tick + Ave.snow + Evergreen	6	126.20	1.99
Weather conditions				
ND11	Survival3~Sex + Cap.weight + Winter.tick + Min.temp + Ave.snow	6	134.59	10.38
ND10	Survival3~Sex + Cap.weight + Winter.tick + Ave.snow	5	133.86	9.65
ND9	Survival3~Sex + Cap.weight + Winter.tick + Min.temp	5	134.04	9.83
ND8	Survival3~Sex + Cap.weight + Winter.tick + Winter.year	7	132.55	8.34
Winter tick				
ND7	Survival3~Sex + Cap.weight + Winter.tick + (I(Winter.tick^2))	5	135.03	10.82
ND6	Survival3~Sex + Cap.weight + Winter.tick	4	133.73	9.52
Individual biological characteristics				
ND5	Survival3~Winter.tick	2	146.92	22.72
ND4	Survival3~Body.cond	2	146.08	21.87
ND3	Survival3~Cap.weight	2	134.87	10.66
ND2	Survival3~Sex	2	144.64	20.43
ND1	Survival3~Winter.year	4	146.06	21.85
Null Model	Survival3~1	1	145.40	21.19

Table 6. Logistic regression β-coefficients and p-value with resulting significance level from the best model describing overwinter survival for moose calves, Wildlife Management District (WMD) 2 and 8, Maine, USA, winters of 2013 – 2018.

Parameters	**β estimate**	**Std. Error**	**Lower CI**	**Upper CI**	**P-value**[a]
Intercept	-3.729	2.290	-8.217	0.759	0.103
Sex (MALE)	-0.805	0.367	-1.525	-0.085	0.02843 *
Capture weight	0.013	0.004	0.005	0.022	0.00242 **
Winter tick	-0.021	0.017	-0.055	0.014	0.239
District (8)	-0.152	0.370	-0.878	0.573	0.681
Min Temperature	-0.156	0.072	-0.296	-0.015	0.02965 *
Average Snowfall	2.581	1.617	-0.588	5.751	0.110
% Open	-3.909	1.427	-6.707	-1.111	0.00617 **
% Deciduous	-2.026	1.388	-4.746	0.694	0.144

[a] Values without an asterisk indicate insignificant results. Values with one or more asterisk have the following significance at an α = 0.05: ‘**’ 0.01 and ‘*’ 0.05.

Table 7. Logistic regression β-coefficients and p-value with resulting significance level from the best model describing overwinter survival for moose calves, Wildlife Management District (WMD) 8, Maine, USA, winters of 2013 – 2018.

Parameters	**β estimate**	**Std. Error**	**Lower CI**	**Upper CI**	**P-value**[a]
Intercept	-18.672	5.228	-28.920	-8.425	0.000355 ***
Sex (MALE)	-0.350	0.617	-1.560	0.860	0.570885
Capture weight	0.032	0.010	0.013	0.051	0.000798 ***
Winter tick	-0.130	0.039	-0.206	-0.054	0.000809 ***
Average snowfall	15.705	4.113	7.644	23.766	0.000134 ***
% Open	-9.273	2.898	-14.954	-3.593	0.001375 **

[a] Values without an asterisk indicate insignificant results. Values with one or more asterisk have the following significance at an α = 0.05: ‘***’ 0.001, ‘**’ 0.01, and ‘*’ 0.05.

Table 8. Logistic regression β-coefficients and p-value with resulting significance level from the best model describing overwinter survival for moose calves, Wildlife Management District (WMD) 2, Maine, USA, winters of 2014 – 2018.

Parameters	**β estimate**	**Std. Error**	**Lower CI**	**Upper CI**	**P-value**[a]
Intercept	-1.950	2.624	-7.094	3.194	0.457
Sex (MALE)	-1.161	0.507	-2.155	-0.168	0.022 *
Capture weight	0.005	0.006	-0.006	0.016	0.416
Winter tick	0.013	0.025	-0.036	0.062	0.598
Average snowfall	2.271	1.925	-1.503	6.045	0.238
% Deciduous	-2.909	1.925	-6.682	0.864	0.131

[a] Values without an asterisk indicate insignificant results. Values with one or more asterisk have the following significance at an α = 0.05: ‘*’ 0.05.

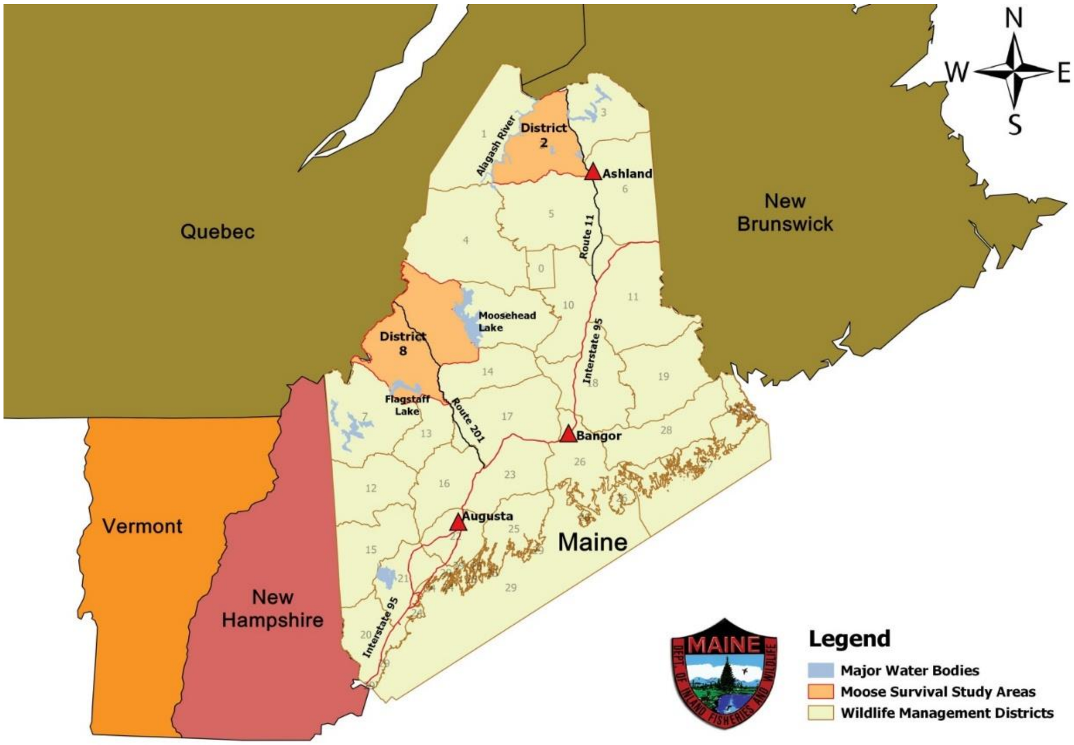


Figure 1. Locations of moose survival study areas and names of important surrounding landmarks, Maine, USA. Figure taken from Maine's Inland Fisheries and Wildlife Department Moose Survival Project Progress Report 2018 (Kantar 2018).

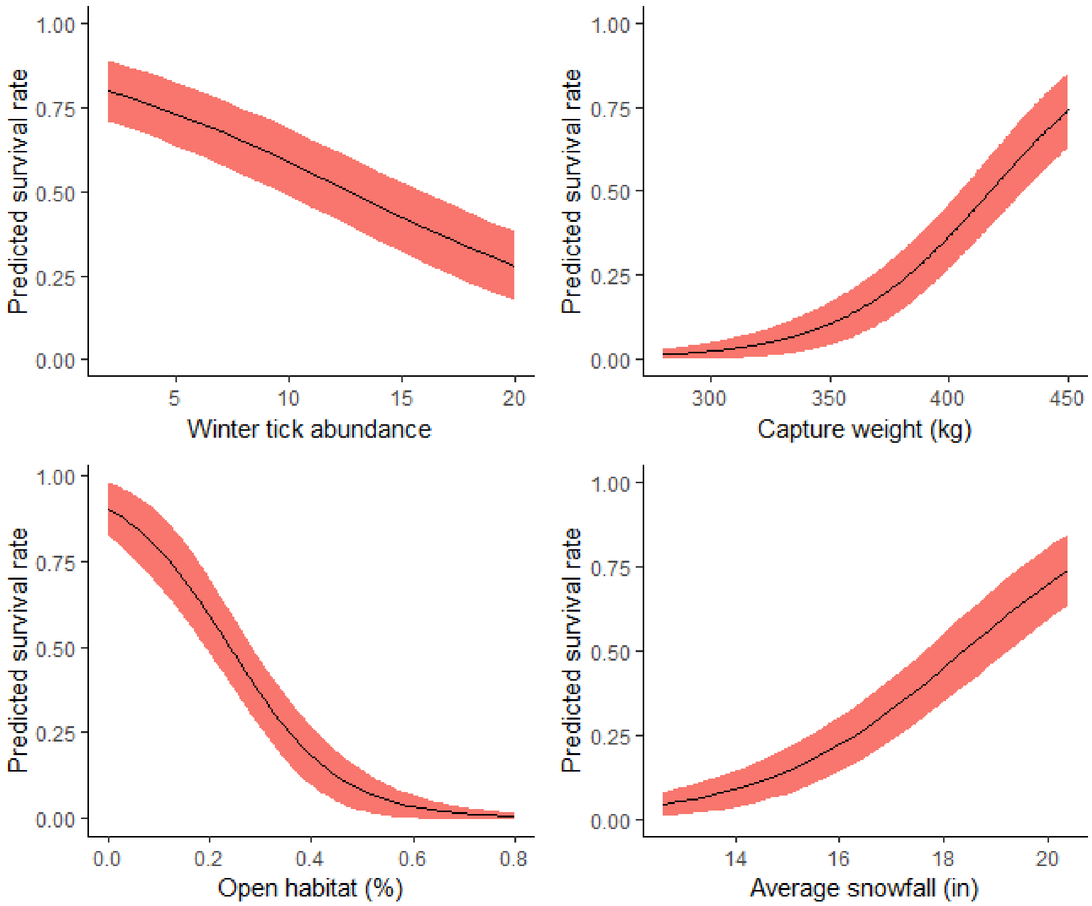


Figure 2. Predicted survival rate female calves, with a 95% confidence interval, given the abundance of winter tick at capture, their weight at capture (kg), the percent of open habitat within their winter home range, and the average snowfall (in) during their first winter as a yearling, in Wildlife Management District (WMD) 8, Maine, USA, winters of 2013 – 2018. Male calves consistently had a 16% lower chance of survival.

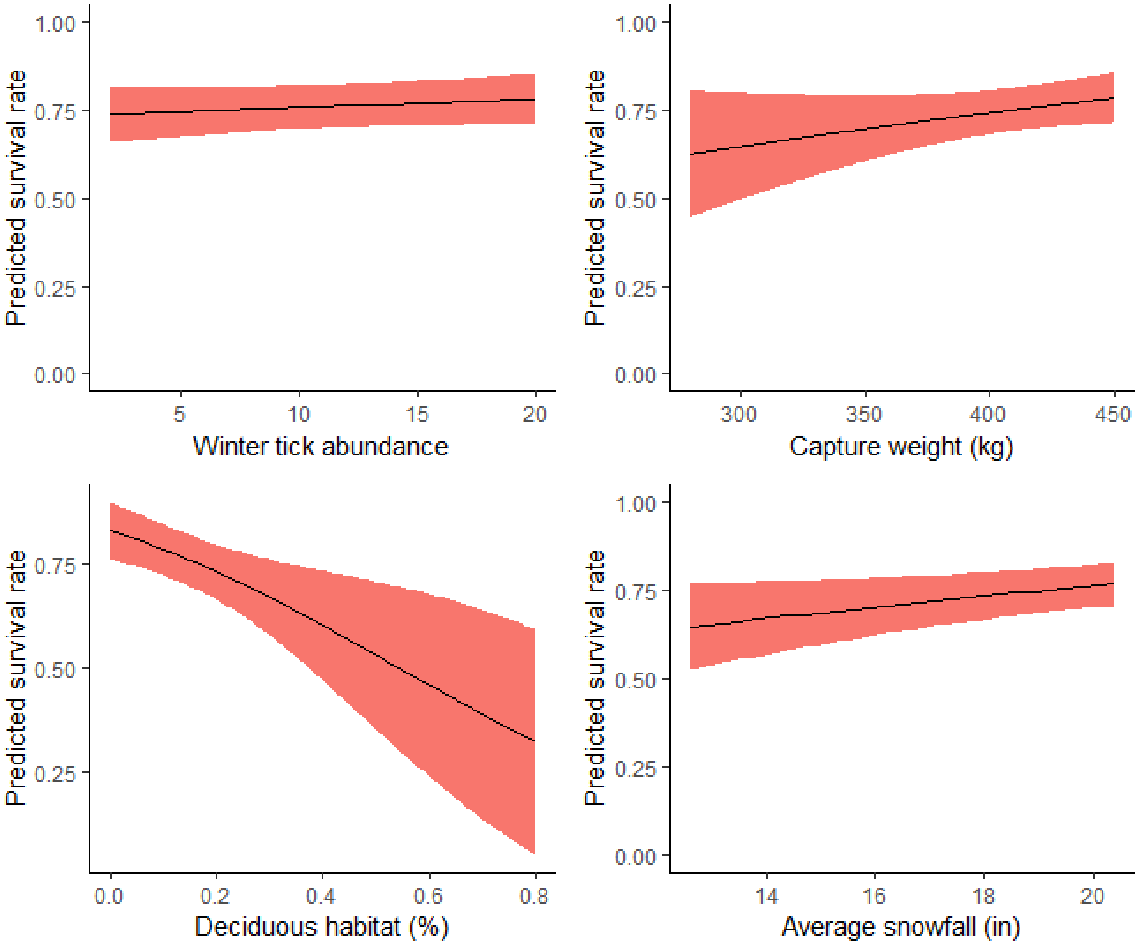


Figure 3. Predicted survival rate female calves, with a 95% confidence interval, given the abundance of winter tick at capture, their weight at capture (kg), the percent of deciduous habitat within their winter home range, and the average snowfall (in) during their first winter as a yearling, in Wildlife Management District (WMD) 2, Maine, USA, winters of 2013 – 2018. Male calves consistently had a 16% lower chance of survival.

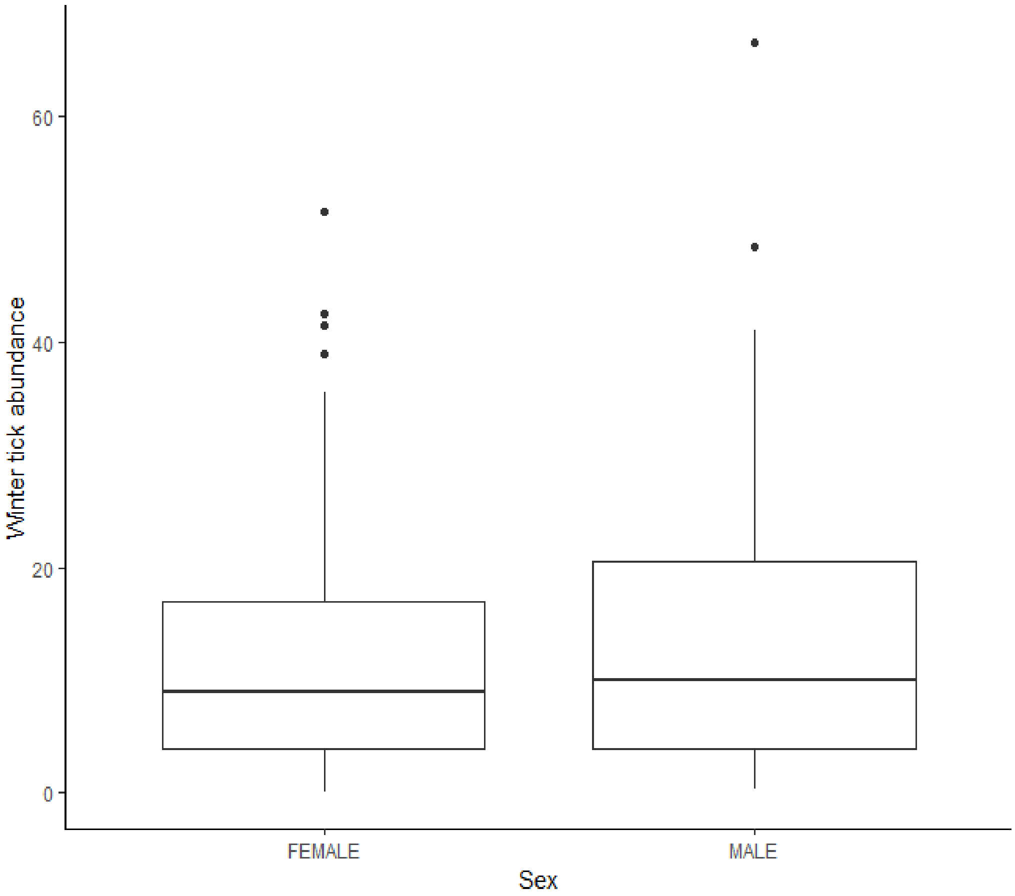


Figure 4. Distribution of winter tick infestations for female and male yearlings upon capture, in
Wildlife Management District (WMD) 2 and 8, Maine, USA, winters of 2013 – 2018.

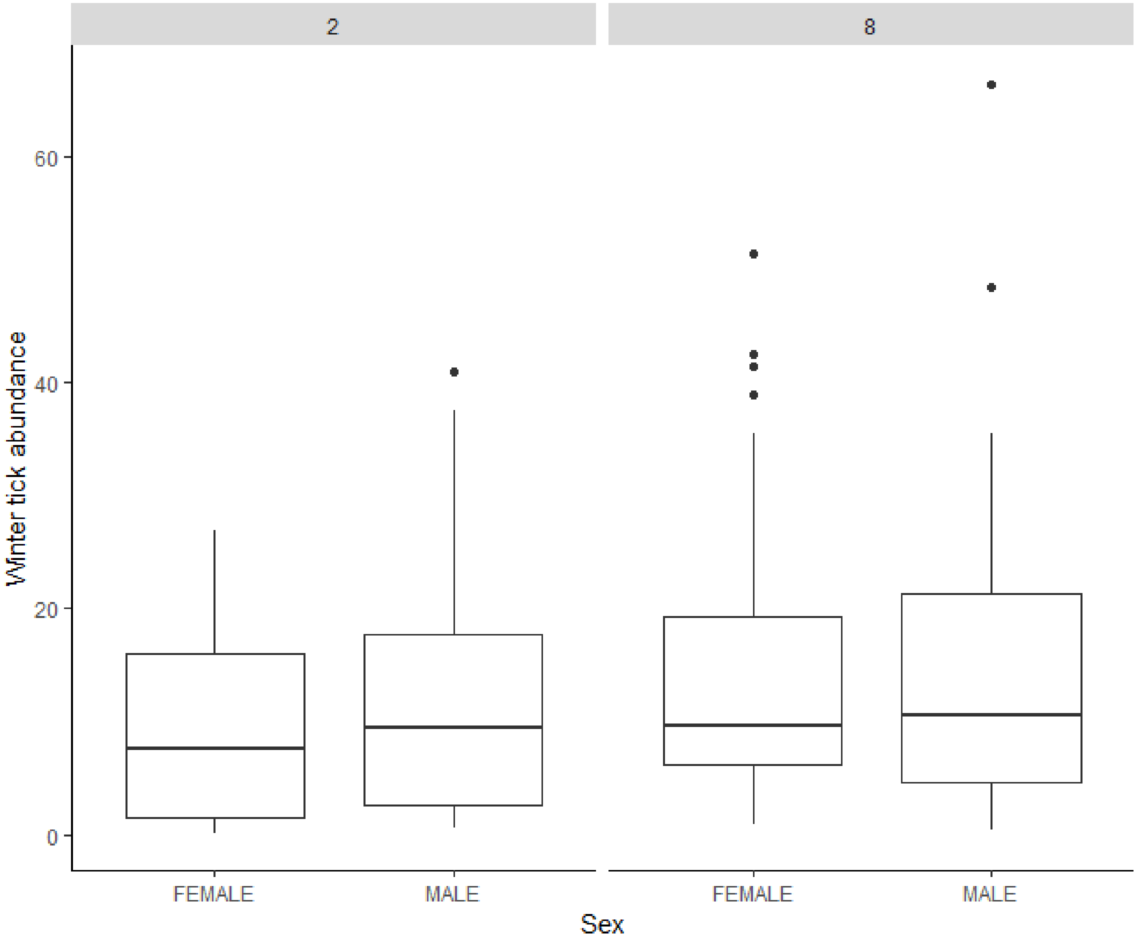


Figure 5. Distribution of winter tick infestations for female and male yearlings upon capture divided by Wildlife Management District (WMD) 2 and 8, Maine, USA, winters of 2013 – 2018.

APPENDICES

Appendix 1. Correlation of parameters used for model selection in Wildlife Management District (WMD) 2 and 8, Maine, USA, winters of 2013 – 2018. Bolded values indicate variables that were closely correlated (>0.7).

Coefficient	Winter year	Winter tick	Capture weight	Body condition	Max temp	Min temp	Ave rain	Ave snow	Ave Snow-depth	% Mixed	% Decid-uous	% Ever-green	% Open
Winter year	1.000	-0.247	-0.144	0.067	-0.466	-0.508	0.085	**0.767**	0.553	-0.716	-0.129	0.142	0.007
Winter tick	-0.247	1.000	0.150	-0.015	0.173	0.293	-0.034	-0.039	-0.113	0.132	-0.037	-0.046	-0.019
Cap.weight	-0.144	0.150	1.000	-0.473	0.130	0.186	0.138	-0.102	-0.032	0.169	0.068	-0.145	-0.086
Body.cond	0.067	-0.015	-0.473	1.000	-0.132	-0.130	-0.056	0.089	0.071	-0.046	0.050	0.005	-0.017
Max.temp	-0.466	0.173	0.130	-0.132	1.000	**0.918**	-0.251	-0.560	**-0.771**	-0.256	0.172	-0.047	0.155
Min.temp	-0.508	0.293	0.186	-0.130	**0.918**	1.000	0.070	-0.371	-0.508	-0.069	0.134	-0.040	0.003
Ave.rain	0.085	-0.034	0.138	-0.056	-0.251	0.070	1.000	0.399	**0.717**	0.480	0.002	-0.090	-0.347
Ave.snow	**0.767**	-0.039	-0.102	0.089	-0.560	-0.371	**0.399**	1.000	**0.830**	0.156	-0.238	0.172	-0.147
Ave.snowdepth	0.553	-0.113	-0.032	0.071	**-0.771**	-0.508	**0.717**	**0.830**	1.000	0.393	-0.176	0.063	-0.294
X.Mixed	-0.072	0.132	0.169	-0.046	-0.256	-0.069	0.480	0.156	0.393	1.000	-0.157	-0.360	-0.466
X.Deciduous	-0.129	-0.037	0.068	0.050	0.172	0.134	0.002	-0.238	-0.176	-0.157	1.000	-0.466	-0.163
X.Evergreen	0.142	-0.046	-0.145	0.005	-0.047	-0.040	-0.090	0.172	0.063	-0.360	-0.466	1.000	-0.234
X.Open	0.007	-0.019	-0.086	-0.017	0.155	0.003	-0.347	-0.147	-0.294	-0.466	-0.163	-0.234	1.000

Appendix 2. List of individuals excluded due to GPS collar malfunction from study in Wildlife Management District (WMD) 2 and 8, Maine, USA, winters of 2013 – 2018.

Moose ID	Collar ID	Count of Lon	Max of capDt	Max of mortDt	Max of dateUTC	Max of Winter1Dt1	notes	UTC Day till Winter1
17215	19122	60	1/0/1900	1/0/1900	4/3/2017	5/1/2017	Last loc 4/3/2017	28
17216	19126	107	1/0/1900	1/0/1900	3/24/2017	5/1/2017	Last loc 3/24/2017	38
17234	19176	183	1/0/1900	1/0/1900	4/25/2017	5/1/2017	Mort signal on 4/25/2017, normal 6/29/2017, last loc 10/3/2017	6
17238	19202	30	9/27/2018	9/27/2018	3/19/2017	5/1/2017	Last loc 3/19/2017 - hunter harvest 9/27/2018	43
17274	19191	1	1/0/1900	1/0/1900	1/9/2017	5/1/2017	Not getting locations - last loc 5/17/2017	112
18300	19142	5	1/0/1900	1/0/1900	1/6/2018	5/1/2018	Last loc 1/6/2018	115
18305	19182	59	4/9/2018	4/9/2018	2/12/2018	5/1/2018	Animal still alive last loc 1/13/2019 collar stuck in mort mode	78
18323	28914	NA	NA	1/2/2018	NA	NA	Euthanized	NA
18332	14331	29	1/0/1900	1/0/1900	2/24/2018	5/1/2018	Last loc - 2/24/2018	66
18333	14332	44	1/0/1900	1/0/1900	2/5/2018	5/1/2018	Last loc 2/5/2018	85
18337	14351	21	1/0/1900	1/0/1900	3/4/2018	5/1/2018	Last loc 3/30/2017	58
18339	14354	10	1/0/1900	1/0/1900	2/15/2018	5/1/2018	Last loc 2/15/18	75

Appendix 3. Logistic regression β-coefficients and p-value with resulting significance levels for model WD 19 with each landcover type for moose calves, Wildlife Management District (WMD) 8, Maine, USA, winters of 2013 – 2018.

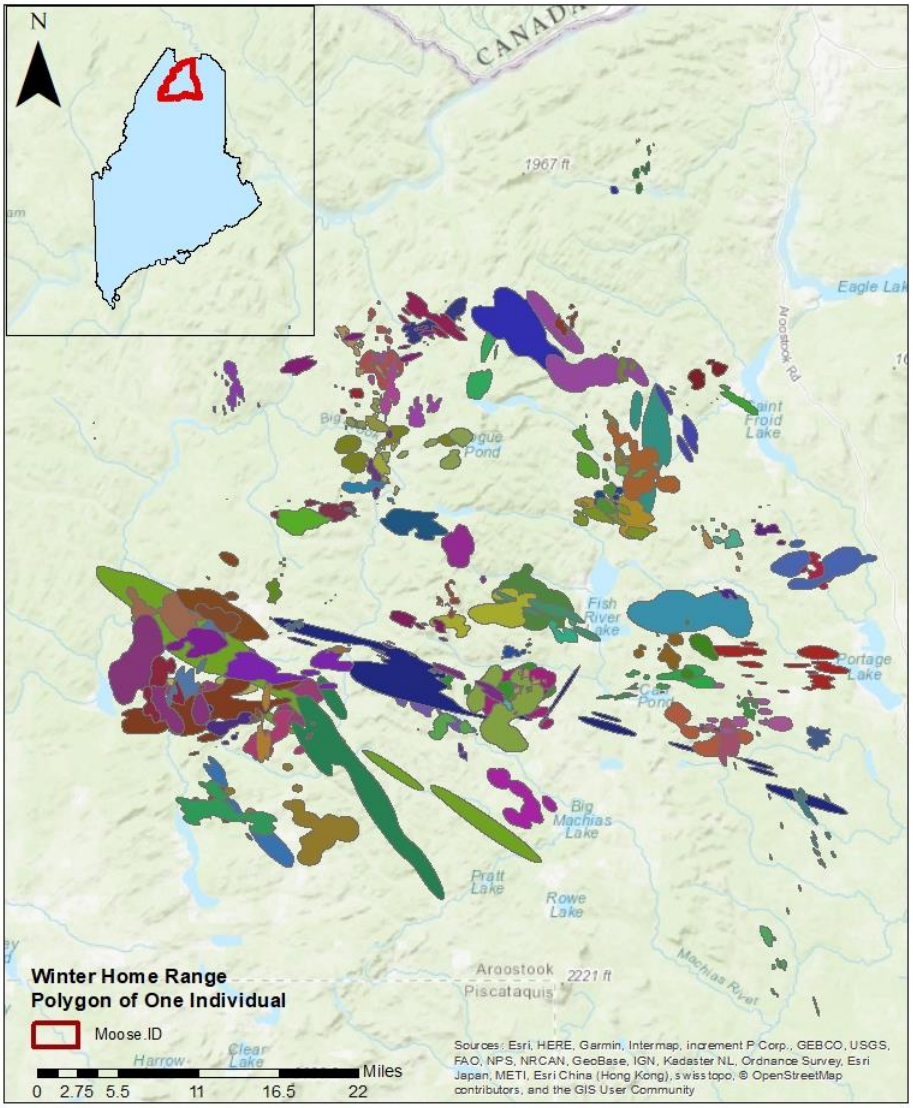
Parameters	**β estimate**	**Std. Error**	**Lower CI**	**Upper CI**	**P-value**[a]
Intercept	-11.886	6.222	-5.973	18.417	0.056096 .
Sex (MALE)	-0.453	0.662	-0.636	1.961	0.494065
Capture weight	0.035	0.010	-0.010	0.031	0.000685 ***
Winter tick	-0.133	0.040	-0.0380	0.117	0.000775 ***
Average snowfall	15.804	4.351	-4.177	12.880	0.000281 ***
% Deciduous	-8.800	5.123	-4.918	15.163	0.085827 .
% Open	-17.068	5.626	-5.401	16.652	0.002414 **
% Mixed	-10.732	5.993	-5.753	17.739	0.073317 .
% Evergreen	-8.402	5.527	-5.306	16.361	0.128475

[a] Values without an asterisk indicate insignificant results. Values with one or more asterisk have the following significance at an α = 0.05: '***' 0.001, '**' 0.01, and '*' 0.05.

Appendix 4. Logistic regression β-coefficients and p-value with resulting significance levels for model ND 19 with each landcover type for moose calves, Wildlife Management District (WMD) 2, Maine, USA, winters of 2013 – 2018.

Parameters	**β estimate**	**Std. Error**	**Lower CI**	**Upper CI**	**P-value**[a]
Intercept	-0.093	4.273	-8.468	8.282	0.9827
Sex (MALE)	-1.202	0.516	-2.213	-0.191	0.0198 *
Capture weight	0.005	0.006	-0.007	0.016	0.4323
Winter tick	0.011	0.026	-0.040	0.062	0.6699
Average snowfall	2.005	1.995	-1.905	5.916	0.3148
% Deciduous	-4.760	3.738	-12.086	2.567	0.2029
% Open	-2.932	3.756	-10.294	4.429	0.435
% Mixed	-1.266	3.486	-8.100	5.567	0.7164
% Evergreen	-1.616	4.030	-9.515	6.284	0.6885

[a] Values without an asterisk indicate insignificant results. Values with one or more asterisk have the following significance at an α = 0.05: '*' 0.05.



Appendix 5. Example of 95% kernel density estimator for winter home range polygons of individuals in Wildlife Management District (WMD) 2, Maine, USA, winters of 2013 – 2018.