MOOSE CALF SURVIVAL, CAUSE-SPECIFIC MORTALITY, AND HABITAT USE

William J. Severud[1], Glenn D. DelGiudice, and Tyler R. Obermoller[1]

SUMMARY OF FINDINGS

Adult survival and recruitment are important drivers of large herbivore population dynamics. The moose (*Alces alces*) population in northeastern Minnesota has exhibited a downward trend from 2006 to 2017. Our research was initiated because neonatal and seasonal survival rates and specific causes of mortality (e.g., predation, undernutrition, disease) of calves were largely unknown. Also unknown was habitat use of calves and their dams during vulnerable and energetically taxing life stages. We remotely monitored global positioning system (GPS)-collared adult female moose during the calving season to locate and GPS-collar neonates in 2013 and 2014 (n = 49 and 25, respectively). In 2015, we used behavioral cues of existing GPS-collared cows to identify calving behavior and calf mortality due to predation. We surveyed and compared habitat characteristics of pre-calving, calving, peak-lactation, and mortality sites to investigate important factors that predicted use at a fine and broad scale. Survival of calves dropped precipitously to 58% by 30 days of age in 2013 and 2014, and then to 34% by 9 months of age. Median age at death of calves that died before 1 year of age was 18.3 days. Hazard started low at birth and spiked at about 20 days old. Similar patterns were observed in 2015, with a 30-day survival rate of 63% and 10-month survival rate of 40.5% of uncollared calves. Over-winter survival was generally high in all 3 years. Predation was the leading cause of mortality in 2013 and 2014, with 84% of mortalities due to wolves (*Canis lupus*) or black bears (*Ursus americanus*). Predation was an important cause of mortality in 2015 as well, but the relative certainty in assigning cause was low. Calves were generally preyed upon once the dam and calves departed their calving sites. At a fine scale, canopy closure, total available forage, and calf concealment were important variables when distinguishing site types. Cows tended to move from areas of little concealment cover to areas of greater concealment but less forage to calve. During peak milk production, cows and their calves used areas with abundant forage and high concealment. At a broad scale, the amount of mixed and deciduous forest was lower around calving sites when compared to pre-calving and peak-lactation sites. Calf mortality sites also had less deciduous forest. Identifying specific causes of calf mortality and understanding their relations to various landscape characteristics and other extrinsic factors should yield insight into mechanisms contributing to the declining moose population in northeastern Minnesota and serve as a basis for an ecologically sound management response.

INTRODUCTION

Ungulate population declines have been attributed to poor juvenile survival (Pinard et al. 2012, Forrester and Wittmer 2013). Large herbivore population growth is most sensitive to variation in adult survival, but differences in temporal variation of juvenile survival may be important in

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[1] Graduate Research Assistant, University of Minnesota, Department of Fisheries, Wildlife, and Conservation Biology, 2003 Upper Buford Circle, Ste. 135, St. Paul, MN 55108

accounting for between-year variation in growth rates (Gaillard et al. 1998, 2000, Lenarz et al. 2010). When viable populations of predators are present, predation can be a primary cause of mortality of temperate ungulate neonates (Linnell et al. 1995, Carstensen et al. 2009, Severud et al. 2015*a*). Less is known about other specific ultimate and proximate sources of moose (*Alces alces*) calf mortality or contributing factors. It also is unclear when predation is compensatory or additive to other sources of mortality (Franzmann et al. 1980, Linnell et al. 1995), although a recent study documented additive effects of predation on moose calves in Alaska (Keech et al. 2011). The degree of predation's impact on population-wide calf survival rates depends on the extant predator guild and relative densities of predator and prey (Eriksen et al. 2011, Patterson et al. 2013). The moose population in northeastern Minnesota has declined 55% from 2005 to 2016 (DelGiudice 2016). Survival and cause-specific mortality of calves was largely unknown in this area, but recruitment had been estimated at 0.40 mostly before the population began its decline (Lenarz et al. 2010).

Selection of calving sites by ungulates may influence neonatal survival. Often females tradeoff access to forage for predator avoidance during this vulnerable life stage (Bowyer et al. 1999, Poole et al. 2007). Cover may affect vulnerability to predation (Griffith and Youtie 1988). As nutritional demands for lactation increase and calves begin to incorporate browse into their diet, forage becomes more important. Lactation is an energy-demanding phase of reproduction, requiring 2–3 times more energy than gestation (Robbins 1993). Milk production peaks 21–31 days post-parturition for moose cows (Schwartz and Renecker 2007).

OBJECTIVES

1. Estimate neonatal (30-day), seasonal, and annual survival of moose calves
2. Quantify cause-specific mortality of moose calves
3. Identify potentially important covariates that influence survival or cause-specific mortality
4. Compare habitat characteristics at pre-calving, calving, peak-lactation, and mortality sites at 2 different spatial scales

METHODS

Our study area is the same as that of the Environmental and Natural Resources Trust Fund (ENRTF)-supported study in the Arrowhead region of northeastern Minnesota focused on survival and cause-specific mortality of adult moose (Carstensen et al. 2015). White-tailed deer populations occurred at pre-fawning densities of ≤4 deer/km^2 (Grund 2014). Major predators of moose in the area included gray wolves (*Canis lupus,* 3 wolves/100 km^2, Erb et al. 2016) and black bears (*Ursus americanus,* 23 bears/100 km^2, Garshelis and Noyce 2011). Moose had not been harvested in the state since 2012 (DelGiudice 2014).

As part of the adult moose mortality study, 84, 25, and 20 female moose were captured and fitted with Iridium GPS collars (Vectronic Aerospace GmbH, Berlin, Germany) during January 2013, February 2014, and February 2015, respectively (Butler et al. 2013; Carstensen et al. 2014, 2015). Blood was collected and analyzed for serum progesterone; ≥2.0 ng/mL was indicative of pregnancy. We monitored cow movements during pre-parturition and calving, with particular attention given to pregnant cows, looking for calving movements (Bowyer et al. 1999, McGraw et al. 2014, Severud et al. 2015*a*).

In 2013 and 2014, calves were located and fitted with an expandable Globalstar GPS Calf Collar (Vectronic Aerospace, Berlin, Germany). Details of calf captures, handling protocols, and mortality investigations can be found in Severud et al. (2015*a*,*b*). In response to capture-induced abandonment of calves and capture-related mortality of adults (DelGiudice et al. 2014, 2015; Carstensen et al. 2015), the Governor of Minnesota issued Executive Order 15-10 (28 Apr 2015), barring state agencies from conducting or permitting any collaring of moose in the state. We then monitored existing collared adult females for calving movements, and tracked dam behavior for indications of mortality movements.

We estimated birth-dates of all calves (2013–2015) based on dams' calving movements. We assumed calves were born 12 hours after the cow localized. In 2013 and 2014, time of death was estimated using the mortality mode of collars, and calf and dam locations relative to the mortality site. In response to a high rate of collar slippage in 2014, we conducted an apparent survival check flight in March 2015. In 2015, dam behavior was used to indicate calf mortality (time and location from which the dam initially fled was also the estimated time of death). We conducted flights via helicopter to assess seasonal apparent survival rates in 2015 during late November and early December (about 190 days old) and late March 2016 (about 320 days old).

We calculated Kaplan-Meier survival, hazard, and Cox proportional hazard using the R packages *survival, KMsurv,* and *muhaz*. Since calf births were tightly synchronized (Severud et al. 2015*b*), we calculated survival by calf age, with day 0 meaning birth. For smoothed empirical hazard curves, we used a global bandwidth and the product-limit method. We calculated cause-specific mortality rates with a cumulative incidence function using the R package *wild1*. Dam and calf location data were screened for locations that were thought to be erroneous fixes. We then calculated proximity between cows and calves. Summer field tests demonstrated mean linear error (± standard error, range) of locations for adult collars of 3.7 m (± 0.3, 0–17) under open canopy and 7.0 m (± 0.3, 1–36) under dense canopy (≥80% closure), and for calf collars of 24.9 m (± 2.7, 1–274) under open canopy and 40.3 m (± 1.3, 0–367) under dense canopy (Obermoller et al., unpublished data).

We collected site characteristics at the pre-calving site (location immediately preceding the calving movement) and presumed calving site (averaged coordinates over a 40- to 48-hour time period immediately following the calving movement, adjusted on site as confirmed by calving evidence; Figure 1). We similarly surveyed locations where calf mortalities were indicated by GPS locations of the dam (2013 and 2014) or confirmed by site evidence (e.g., calf bone fragments, hooves, hair, or predator sign in 2015). Calf mortalities occurring at the calving site were treated as having identical habitat conditions. When calf mortalities occurred outside of the calving site, new habitat data were collected.

Peak lactation of moose dams occurs 21–31 days postpartum (Schwartz and Renecker 2007). In 2015, when we observed evidence indicating a calf had survived ≥26 days (pellets and tracks), we collected site characteristics at the corresponding cow's peak-lactation location. We used the nearest GPS location from each collared cow with a known calf at 26 days post-calving. If the location was in the middle of a long distance movement, we used the center of the nearest grouping of ≥3 locations, which were usually 1 hour apart. We conducted all habitat work to match phenological conditions (i.e., leaf off and leaf on) to the time the initial location was recorded.

Habitat plots were centered at each cow's GPS location closest to the time of interest, unless that location was refuted by visual evidence. This typically occurred at calving and mortality sites, when we were able to see where a cow had calved or where a calf had died. In these cases, plot centers were placed in the middle of the cow's calving bed or at the primary location of calf remains or sign of a struggle. In the center of each plot, we collected an averaged waypoint using a handheld GPS unit, recorded the elevation from the unit's base map, and used a spherical convex densiometer to estimate canopy density. We also measured the prevailing slope and aspect using a clinometer and compass.

Canopy density (in addition to being measured at the plot center) and horizontal visibility were recorded 15 m from the plot center in each cardinal direction. We used a 2-m cover pole to determine horizontal visibility, recording the visible percentage (0, 25, 50, 75, or 100%) of each of 19 bands from the center (Poole et al. 2007). To estimate calf hiding cover, we held a cardboard cut-out of a standing moose calf silhouette at the center of the plot and recorded the percentage of the cut-out that could be seen from 15 m away at a 1-m height in each cardinal direction. The observer then moved towards the cut-out, maintaining a 1-m height, and recorded their distance from the calf when visibility reached 25, 50, 75, and 100%.

We recorded trees, saplings, and shrubs within an 11-m radius from the central point. Trees were defined as any upright (<45° lean) woody plant with a DBH ≥10 cm. Saplings and shrubs were defined as DBH <10 cm. We determined the species and DBH of each tree, alive or dead, within the plots, and counted number of stems of saplings and shrubs by species. Trees <18 cm DBH and shrubs were further classified as forage or non-forage species (Peek et al. 1976, Portinga and Moen 2015).

We used binary logistic regression to compare pairs of pre-calving, calving, peak-lactation, and mortality sites. The response variable was coded as 1 of these 4 site types. To avoid multicollinearity caused by correlated habitat covariates, we conducted pairwise correlation analysis on all variables. We removed single variables from a highly correlated pair ($|r| > 0.5$), retaining the most parsimonious set of variables. We developed *a priori* models using all possible combinations of remaining variables, and evaluated model support using Akaike's Information Criterion corrected for small sample size (AIC_c); models within 2 AIC_c units of the best approximating model (i.e., $\Delta AIC_c \leq 2.0$) were considered to have strong support.

To investigate broad-scale patterns, we buffered pre-calving, calving, peak-lactation, and mortality sites from 2013–2015 (sites defined using the same criteria listed above) with a 565-m radius to yield polygons of about 100 ha (Poole et al. 2007, McGraw et al. 2012). We overlaid these polygons on a land cover classification layer (Minnesota Land Cover Classification and Impervious Surface Area by Landsat and Lidar) and calculated the area (ha) of each class per polygon, or buffered location. We then compared land cover types by our defined site types using analysis of variance (ANOVA) with Tukey's Honestly Significant Difference (HSD) as a *post hoc* analysis.

RESULTS

We collared 49 calves from 31 dams in 2013 and 25 calves from 19 dams in 2014 (58% and 32% twinning rates, respectively). The sex ratio of collared calves was 36 females: 38 males. Seven dams abandoned 9 calves in 2013 and 6 dams abandoned 9 calves in 2014 (DelGiudice et al. 2014, 2015). These calves, as well as 2 additional calves that died during or shortly after capture from trampling by the dam and not nursing due to unknown causes (DelGiudice and Severud 2016), were not included in survival analyses, leaving 54 calves. Of these 54 calves, 4 slipped their collars in 2013 and 10 in 2014, allowing the study of survival and natural cause-specific mortality in 40 calves. In 2015, we observed calving movements or localization of 50 cows and tracked those dams for mortality movements. Assuming a 30% twinning rate (M. Schrage, Fond du Lac Natural Resource Management Division, unpublished data), this yielded about 65 uncollared calves under observation during 2015. Median calving dates for 2013, 2014, and 2015 were May 14, 19, and 10, respectively.

Blood profiles of calves sampled in 2013 were reported elsewhere (DelGiudice and Severud 2016). For the sample of all collared calves from 2013 and 2014, mean total body mass at capture was 15.8 kg (± 0.3, 12–20.5, $n = 38$) and mean hind foot length (HFL) was 45.9 cm (± 0.3, 42–49, $n = 42$). Body mass and HFL were weakly correlated ($r^2 = 0.31$, $P < 0.001$). There were no differences in mass or HFL by sex or between twins versus singletons. Mean rectal temperature was 101.6 °F (± 0.12, 99.9–103.4, $n = 43$). Mean dam age of all collared calves was 6.4 years old (± 0.5, 1–14, *n* = 43). Mean dam age of calves that died was 6.7 years old (± 0.7, 1–12, *n* = 23).

For pooled 2013 and 2014 collared calves, 30-day survival was 0.584 (95% Confidence Interval [CI] = 0.461–0.740, Figure 2) and declined to 0.341 (95% CI = 0.226–0.516) by 206 days of age (6–10 February 2014), when all remaining collars were removed (Figure 3). Incorporating data from winter survey flights to look for calves that slipped collars, survival is further adjusted to 0.285 (95% CI = 0.178–0.457). Nearly 80% of mortalities occurred by 1 July (about 50 days old) and 95% by mid-August (about 100 days old).

In 2015, we observed calf mortalities during the first 30 days of life, as indicated by mortality movements of dams. We were successful in confirming calf mortality in cases when the dam fled and made 1–7 return trips. Based on suspected and confirmed calf mortalities, 30-day survival was 0.632 (95% CI = 0.518–0.770, *n* = 54, Figure 2). For the uncollared 2015 cohort of calves, flights in early winter (30 Nov–3 Dec 2015) and late winter (28–29 Mar 2016) indicated an apparent survival rate of 0.442 and 0.405, respectively. In all 3 years, survival dropped dramatically from birth to age 50 days (Figures 2 and 3).

For collared calves in 2013 and 2014, dam age, HFL, mass, sex, and twin status did not meet the assumptions of proportionality, so we could not run Cox proportional hazard models. The empirical hazard function was low initially, and then peaked at about 15 days old before declining, with a second spike in hazard around 90 days of age (Figure 4). Mean age of death of calves that died before 1 year of age was 35 days old (± 7, 3–205, *n* = 31), but the median age was 18.3 days, very close to the peak in hazard. Mortalities from predation (*n* = 26) occurred 31.6 days (± 6.5, median = 17, range = 0–120.5) after leaving the calving site and occurred 1,553 m (± 289, median = 1,142, range = 107–5,788) from the calving site.

We documented 31 natural mortalities of collared calves in 2013 and 2014. Specific causes of mortality included 20 wolf-kills, 5 bear-kills, 2 natural abandonments, and 1 each of the following: drowning, abandonment of unknown cause, unknown predation, and an infection resulting from wolf bites (Figure 5). The cause-specific mortality curves rose rapidly from birth to 50 days of age. Over the first 9 months of age, the cumulative probability of being preyed upon by wolves was 50.2% (90% CI = 37.1–63.5), 11.7% (90% CI = 3.5–19.9) for bear predation, and 9.6% (90% CI = 2.9–16.3) for other causes. Predation accounted for 84% of all natural mortalities, with wolves having the greatest impact overall (77% of the predation events).

For uncollared calves born during 2015 we documented 11 natural mortalities, with 4 additional cases pending (no direct evidence of calf mortality, but predator scat [1 wolf, 5 bear] will be analyzed for presence of calf hair). We documented 8 wolf-kills, 1 bear-kill, and 2 unknown predator-kills (saliva evidence pending, calf remains located).

Most dams and their offspring (one outlier cow-calf pair excluded) were a mean of 101 m (± 1.5, 0–6,083) apart throughout the year. Much variation by individual and fate was apparent (Figure 6). The outlier was a twin that separated from its mother and twin in November. With this outlier included, the mean proximity of all dams and their offspring was 3,736 m (Figure 7).

We measured fine scale habitat characteristics at 34 pre-calving, 37 calving, 25 peak-lactation, and 5 mortality sites in 2015. For fine scale analysis, remaining habitat variables after removal of highly correlated variables included: slope, mean calf model visibility at 15 m (15 m vis), mean canopy closure, and total forage. We then evaluated 15 models of all possible combinations of variables.

There was high model uncertainty when comparing characteristics of pre-calving and calving sites; however, 15-m visibility was in 5 of 6 top models (Table 1). Median percentage of the calf model visible from 15 m was 40% less at calving sites when compared to pre-calving sites

(Figure 8). Canopy and forage were both significant predictors that distinguished calving from peak-lactation sites (Table 1). Peak-lactation sites had higher canopy closure and higher total amount of forage compared to calving sites (Figures 9 and 10). There was also high model uncertainty when predicting characteristics of calving and mortality sites, yet canopy or forage appeared in 5 of the top 7 models. Mortality sites had more open canopy and more forage than calving sites (Figures 9 and 10).

We analyzed 150 pre-calving, 155 calving, 73 peak-lactation, and 36 mortality sites from 2013 to 2015 at a broad scale. The discrepancy between pre-calving and calving sites is because not all cows made a calving movement. Only cows that still had a calf at heel 26 days postpartum were included. There were no differences by site type in the amount of open water, emergent wetlands, forested wetlands, conifer forest, regenerated forest, developed/urban, row crop, or grassland land cover types. However, pre-calving and peak-lactation sites both had more mixed and deciduous forest land cover compared with calving sites ($P < 0.03$; Figure 11). Mortality sites also had less deciduous forest compared to pre-calving and peak-lactation sites ($P < 0.03$; Figure 11).

DISCUSSION

We documented high mortality rates of moose neonates in this declining population. However, the mortalities tended to occur once the dams and their calves departed from calving sites. Peak energetic demands for dams due to lactation occur 21–31 days postpartum (Schwartz and Renecker 2007), which coincides with the highest hazard calves experienced. This suggests that dams seeking out high quality or quantities of forage to meet this demand may be travelling in risky areas or that movement to new foraging patches is itself risky, potentially exposing dams with young calves to predation. Our habitat surveys found that calving sites contained less forage, lower concealment, and decreased land cover types containing optimal foraging habitat than peak-lactation sites.

Our near-recruitment rates for 2013–2014 and 2015, although estimated in different ways (via collaring of calves versus observing cow movements and subsequent aerial surveys), were similar. Both methods required collars on adult cows, yet without calf collars extensive field searches and helicopter flight time were required. Tracking GPS-collared cow movements was a highly reliable way to estimate calving rates and to a lesser degree calf mortality. Due to the Governor of Minnesota's Executive Order 15-10, we were unable to confirm presence of calves shortly after birth, nor handle or collar calves in 2015. Without observing neonates at calving sites, we could not estimate twinning rates. We also did not know when a calf had died, but used dam movements as an indication of calf mortality. This also delayed site investigations, frequently making assignment of mortality cause difficult. Only in cases where the calf was ≤23 days old and the dam fled and made 1–7 return trips were we successful in confirming calf mortality. In a subset of those cases we could assign cause of death. This technique may serve as a method to estimate early neonatal mortality, but it has less power to detect mortality as calves age beyond 3 weeks (but see Obermoller et al. 2017). This method will not reliably detect calves that succumb to forms of mortality other than predation, because we have not documented cows fleeing from and returning to other mortality events (e.g., disease, drowning, abandonment, but see Obermoller et al. 2017).

Wolves accounted for the largest proportion of mortalities in all 3 years of the study. Wolf predation has been partially implicated in the decline of this population (Mech and Fieberg 2014) and has been shown to account for adult mortalities as well (Carstensen et al. 2015). However, adults have typically exhibited predisposing factors when preyed upon by wolves. The overall poor health of the northeastern Minnesota moose population (Carstensen et al. 2015, DelGiudice and Severud 2017) could potentially explain not only the high number of capture-induced abandonments we observed (DelGiudice et al. 2014, 2015), but also the high rates of predation on calves. Dams in other studies and study areas defended their calves less vigorously following harsh winters or if in poor nutritional condition (Keech et al. 2011, Patterson et al. 2013).

Dams and calves often were in close proximity throughout the first year of life. One outlier was a twin that did not follow its dam and twin across a large lake at about 175 days old. The lone twin returned to where the group had spent time and survived until mid-winter when she was captured to have her collar removed.

At a fine scale, pre-calving sites were relatively open (less concealment cover) with moderate levels of canopy closure and forage availability. Calving sites had more concealment cover but less forage, aligning with other findings that moose tradeoff forage for safety during calving (Bowyer et al. 1999, Poole et al. 2007). Peak-lactation sites had a more closed canopy and abundant forage, leading to high calf concealment cover. However, this cover also may cause dams to be unable to detect approaching predators (Poole et al. 2007). Mortality sites tended to be more open in both concealment cover and canopy, resulting in less forage available. Some of these habitat metrics could be influenced by phenology. Pre-calving and calving typically occurred pre-leaf-out, whereas peak-lactation and mortality sites occurred post-leaf-out. Indeed, horizontal cover and canopy closure increase dramatically in deciduous-dominated over- and understory after leaf-out.

At a broad scale, we observed calving sites surrounded by less mixed and deciduous forest cover types, which are important foraging habitat (Mabille et al. 2012), indicating again that cows are forfeiting forage availability when choosing calving sites. By examining land cover types as well as fine scale measurements, we can infer that the increased concealment and canopy closure we observed at peak-lactation sites were not only an artifact of phenology, but also a result of the habitat itself. Collared moose in Finland showed a similar pattern—cows calved in areas with minimal vegetation <5 m in height, but cows and their calves moved to areas with dense vegetation shortly thereafter, ostensibly to seek out high quality and quantities of forage (Melin et al. 2015).

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Table 1. Highest ranking *a priori* models for distinguishing pre-calving, calving, peak-lactation, and mortality sites of moose calves in northeastern Minnesota, May–July 2013. Statistically significant variables are marked with an asterisk (*). Only models within 2 units of the Akaike's Information Criterion for small sample size (AIC_c) for the best approximating model (i.e., $\Delta AIC_c \leq 2$) are presented. Canopy = mean canopy closure, Forage = total number of stems of forage species, 15m Vis = amount of calf silhouette visible from 15 m away from focal site (concealment cover).

Site comparison	Model	AIC_c	ΔAIC_c
Pre-calving vs. calving	15m Vis	99.185	0.000
	15m Vis + Forage	100.02	0.835
	15m Vis + Canopy	100.19	1.005
	Slope + 15m Vis	100.61	1.425
	Canopy	100.71	1.525
	15m Vis + Canopy + Forage	101.02	1.835
Calving vs. peak-lactation	Canopy* + Forage*	72.567	0.000
	15m Vis + Canopy* + Forage*	72.572	0.005
	Slope + Canopy* + Forage*	74.016	1.449
	Slope + 15m Vis + Canopy* + Forage*	74.131	1.564
Calving vs. mortality	Forage	33.172	0.000
	Canopy	34.196	1.024
	Slope	34.301	1.129
	15m Vis	34.641	1.469
	Slope + Forage	34.684	1.512
	15m Vis + Forage	35.104	1.932
	Canopy + Forage	35.117	1.945
Peak-lactation vs. mortality	Canopy*	23.042	0.000
	15m Vis + Canopy*	23.569	0.527
	Slope + Canopy*	24.165	1.123
	Slope + 15m Vis + Canopy*	24.27	1.228
	Canopy* + Forage	24.54	1.498

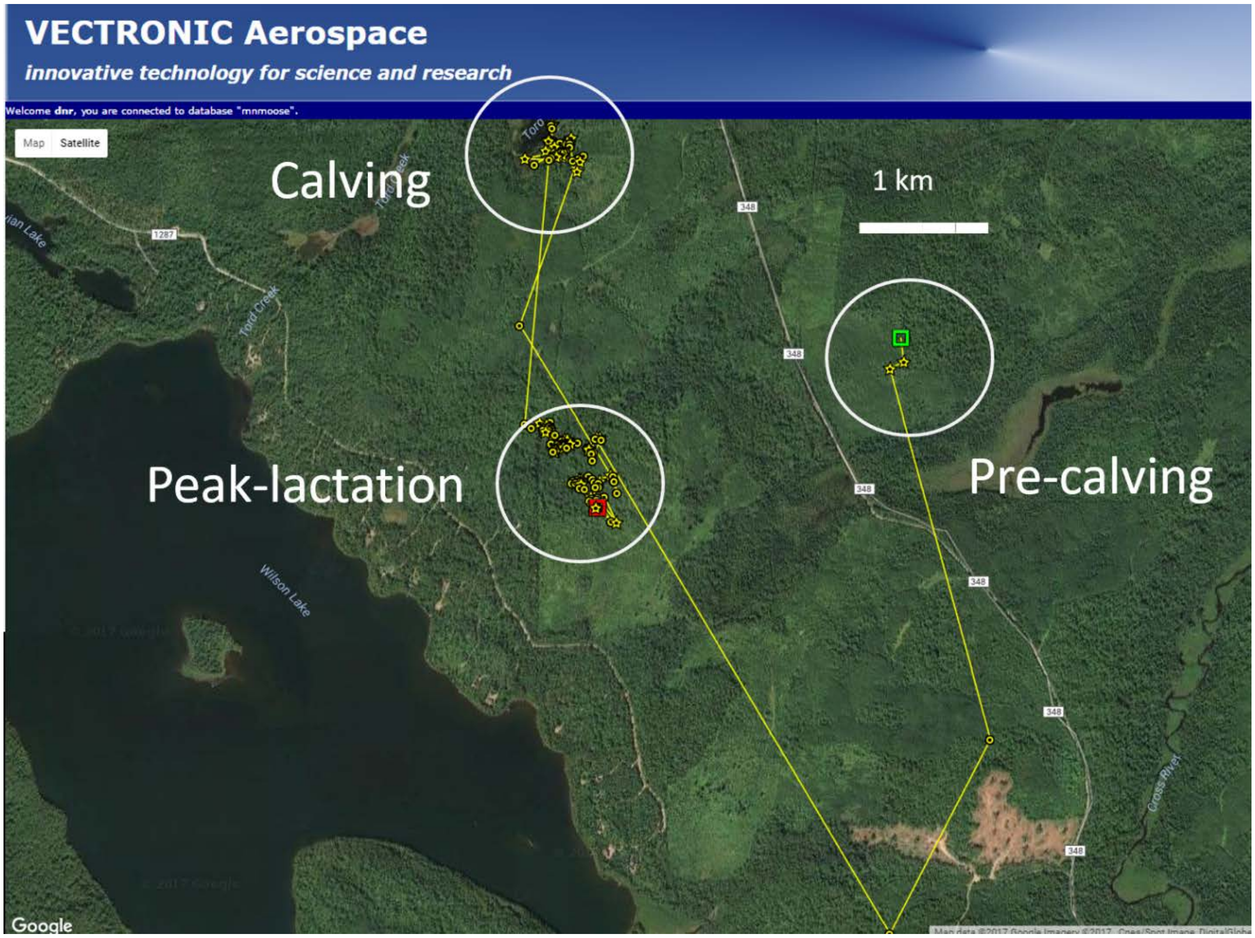

Figure 1. Example of moose pre-calving, calving, and peak-lactation sites, northeastern Minnesota, May–July 2013–2015. Pre-calving sites were defined as being where the calving movement originated. Peak-lactation sites were defined as locations of dams at 26 days from calving (milk production peaks 21–31 days postpartum).

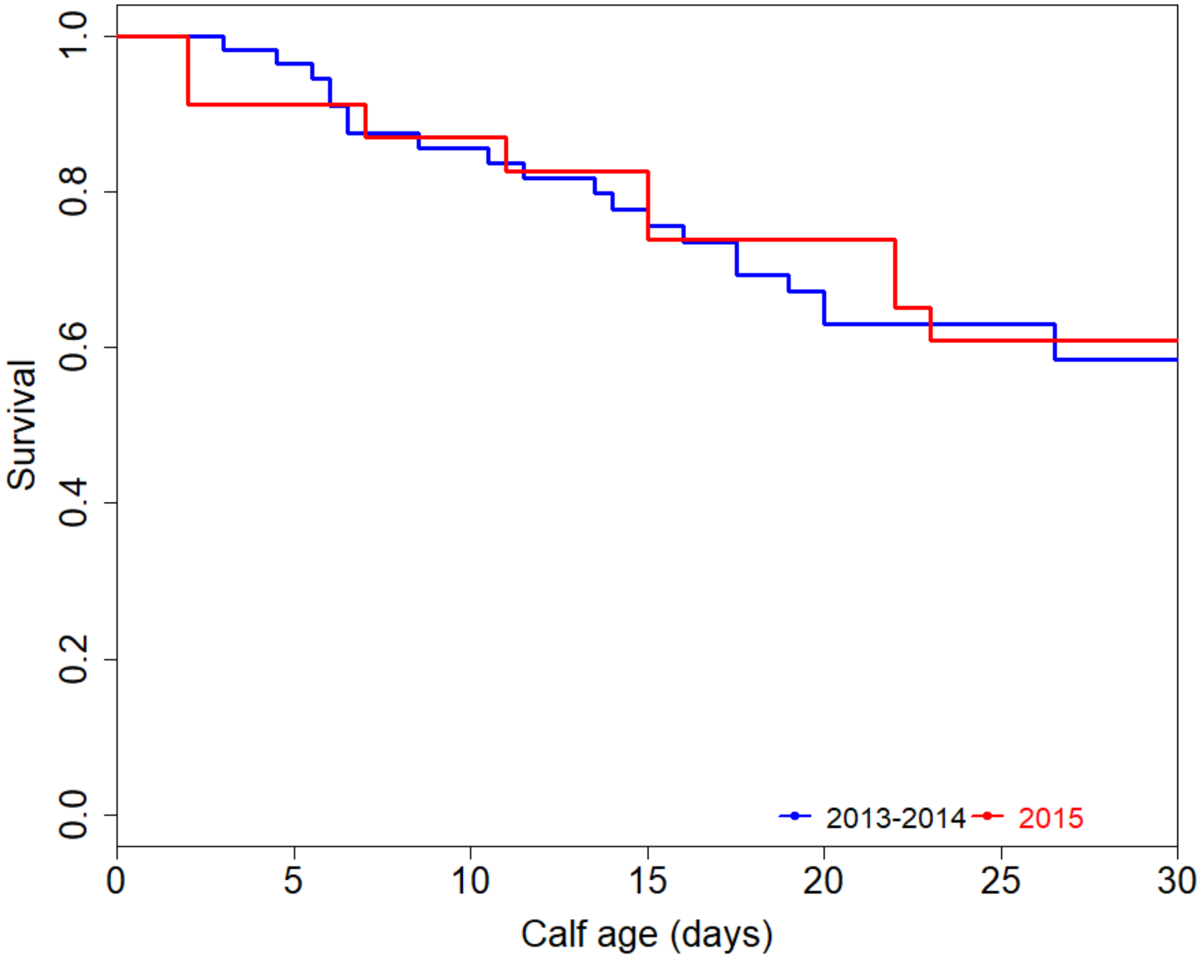

Figure 2. Kaplan-Meier 30-day survival for known moose calf mortalities, northeastern Minnesota, May–June 2013–2015. Mortality was confirmed by GPS collars (pooled 2013 and 2014, blue line, *n* = 54 calves) or through investigations triggered by dam movement patterns and observation of calf remains (2015, red line, *n* = 65 calves).

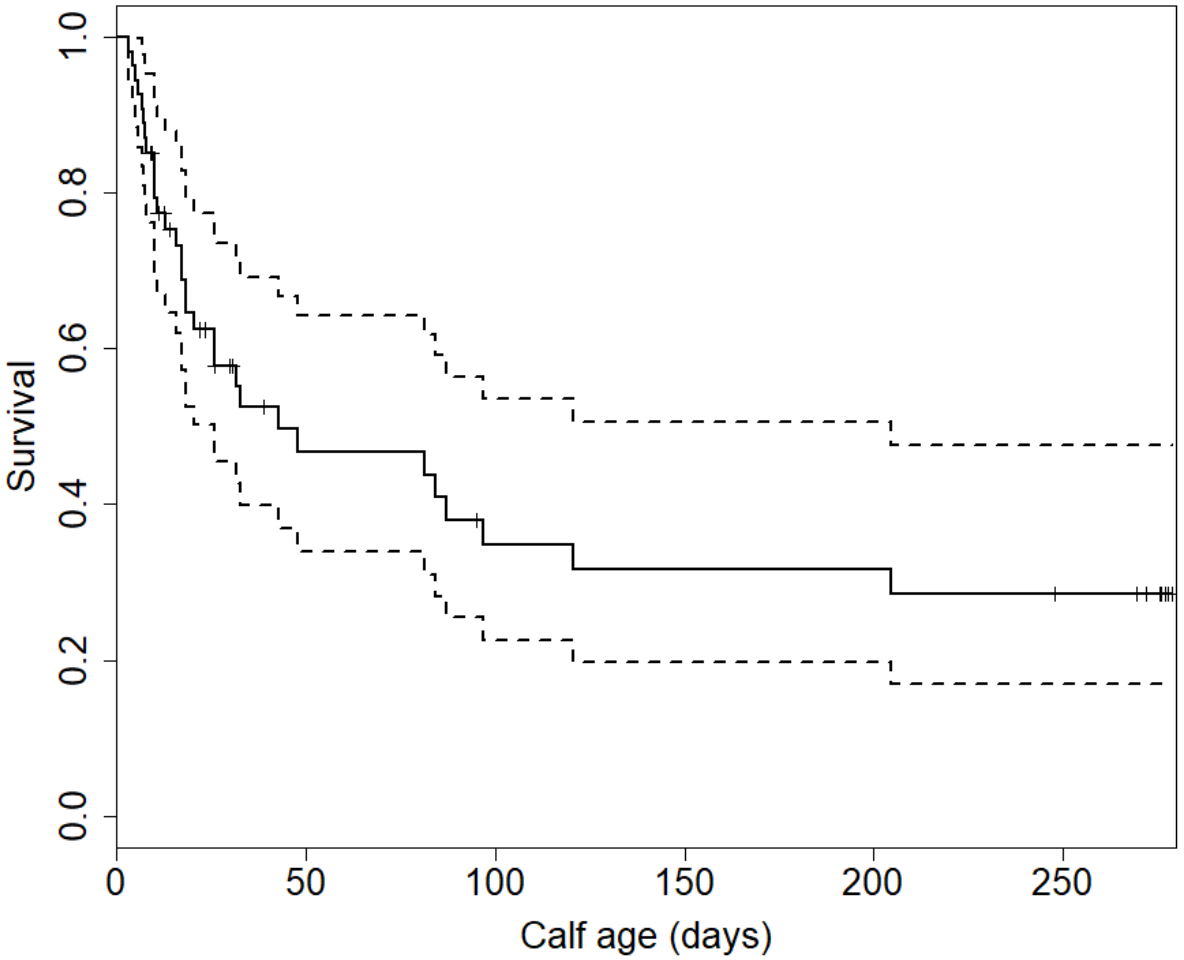

Figure 3. Kaplan-Meier 250-day survival for known moose calf mortalities (*n* = 54 calves), northeastern Minnesota, May–February 2013–2015. Tick marks indicate individuals censored due to slipped or removed collars. Dashed lines represent 95% confidence intervals.

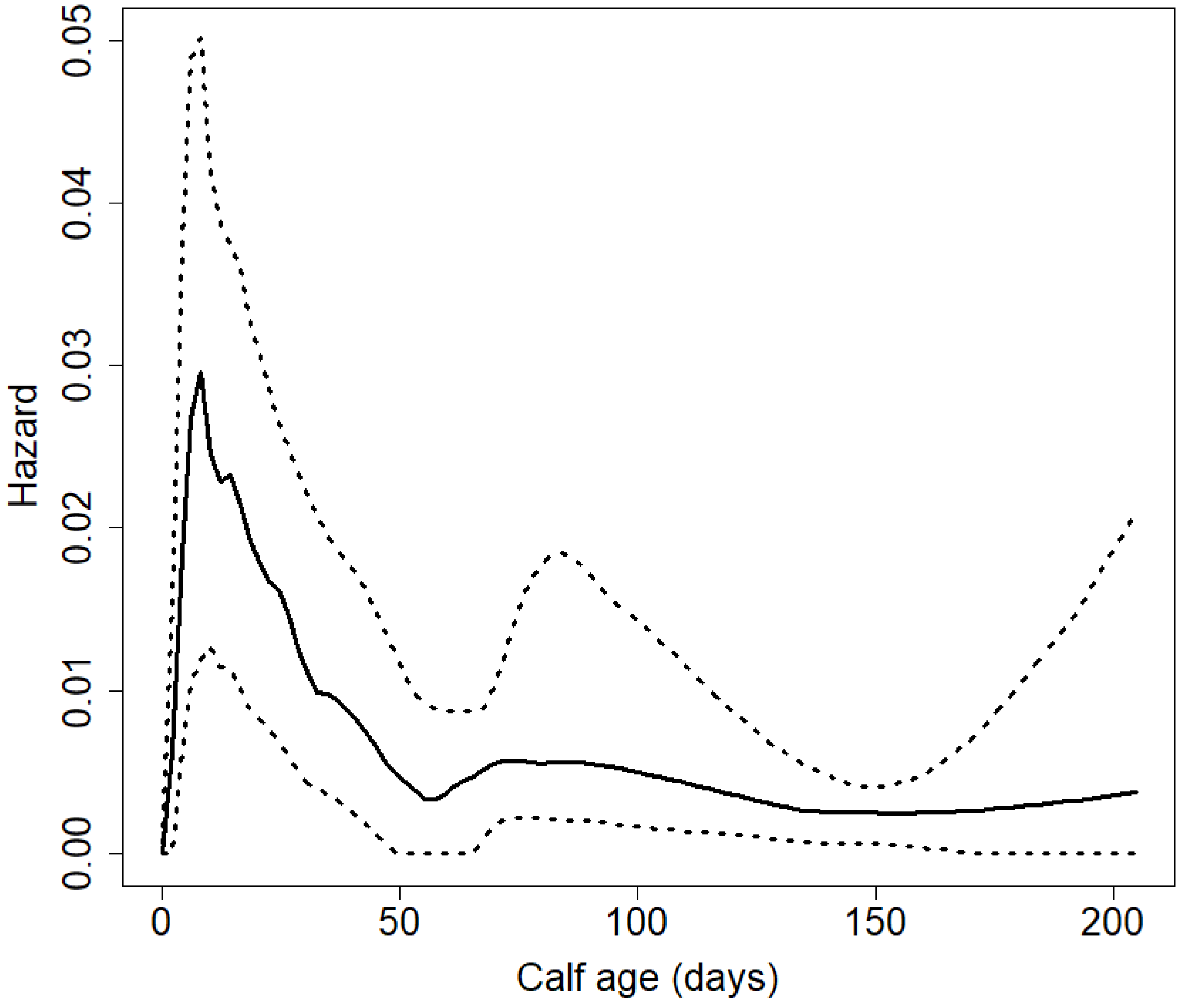

Figure 4. Empirical hazard function for known moose calf mortalities (*n* = 31 calves), northeastern Minnesota, May–February 2013–2015. Dashed lines represent 95% confidence intervals.

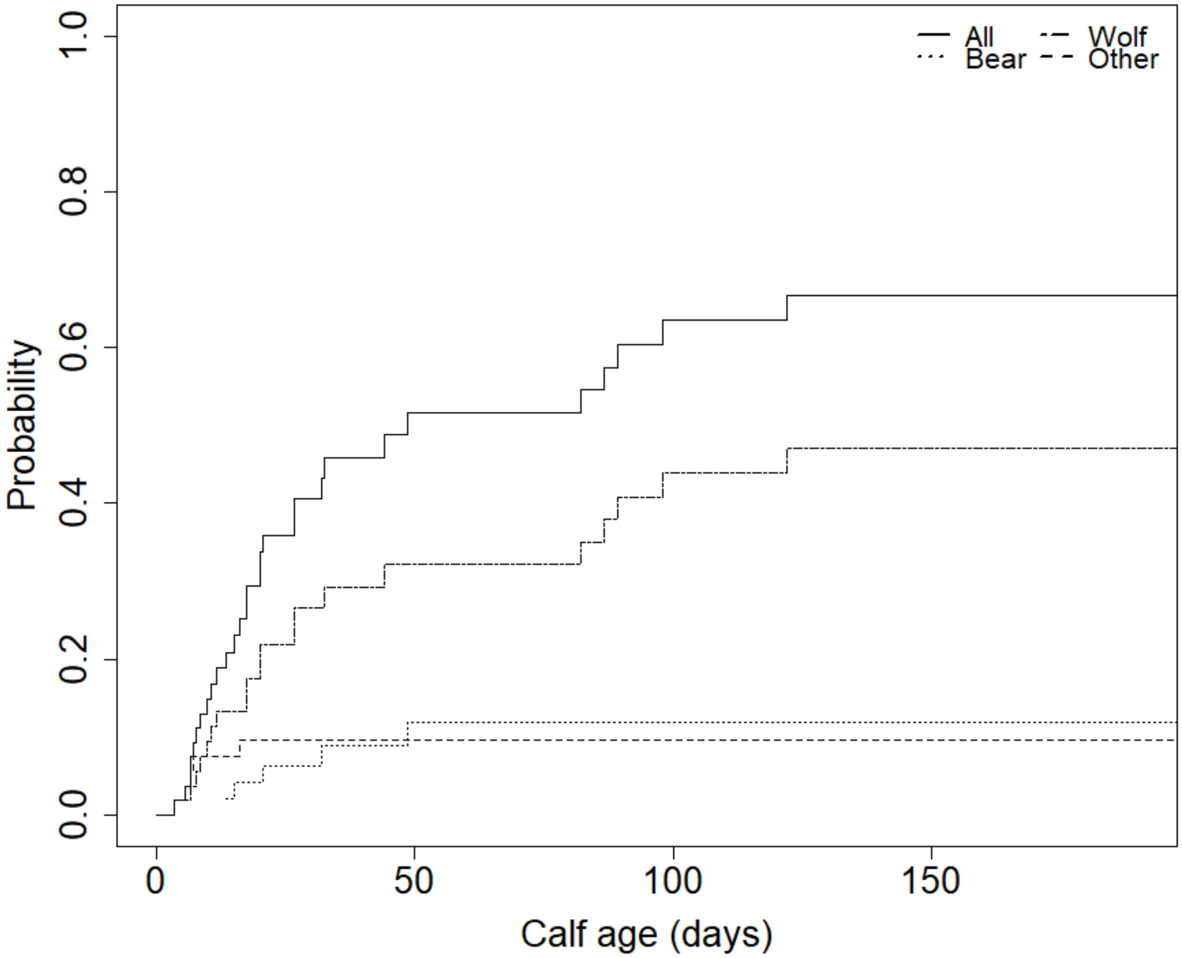

Figure 5. Cumulative incidence function for cause-specific mortality of moose calves in northeastern Minnesota (*n* = 40 calves), May–February 2013–2015. Causes of mortality were wolf predation (20), black bear predation (5), and other [natural abandonment (2), drowning (1), abandonment of unknown cause (1), unknown predator (1), and infection resulting from wolf attack (1)].

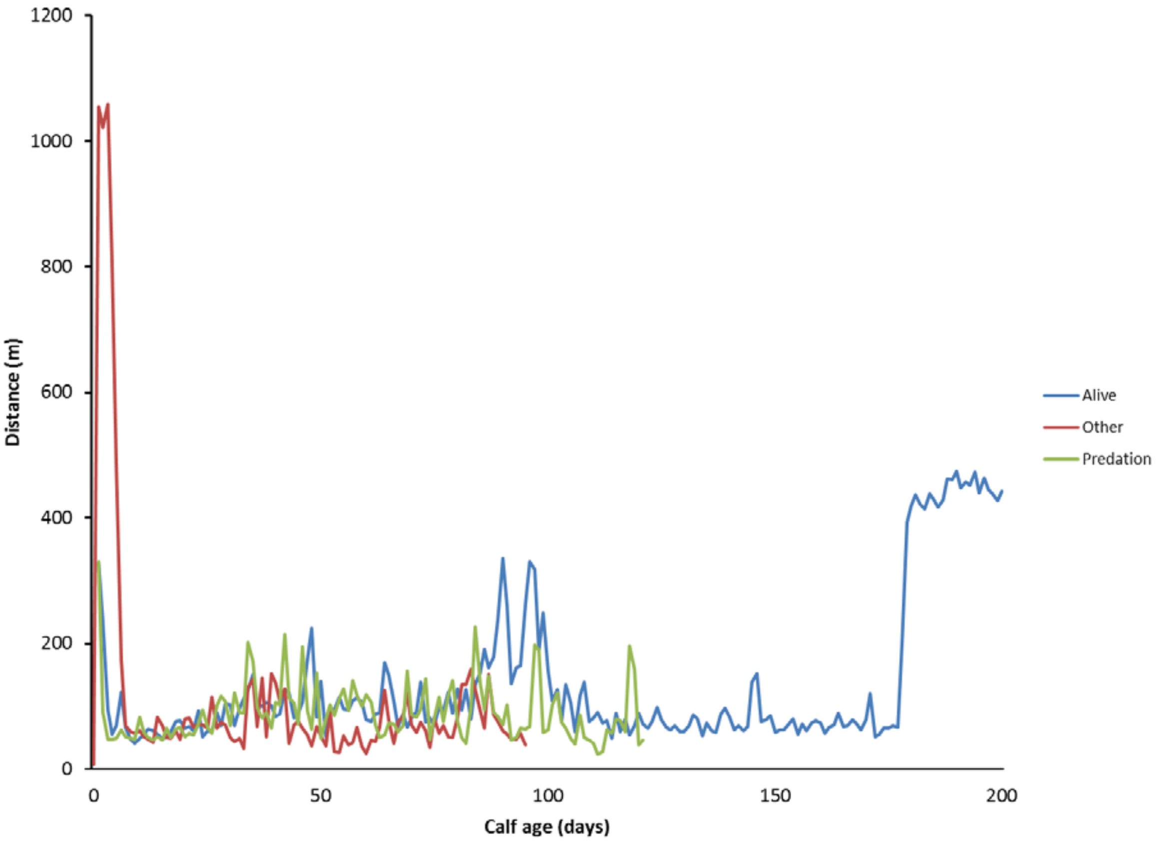

Figure 6. Mean daily distance between moose dams and their calves, excluding an outlier calf that moved up to 28,595 m from its dam, by calf age (up to 200 days old) and fate type (alive, other [non-predation mortality], and predation), northeastern Minnesota, May–February 2013–2015. Spikes in distance during the first 5 days were due to capture and handling.

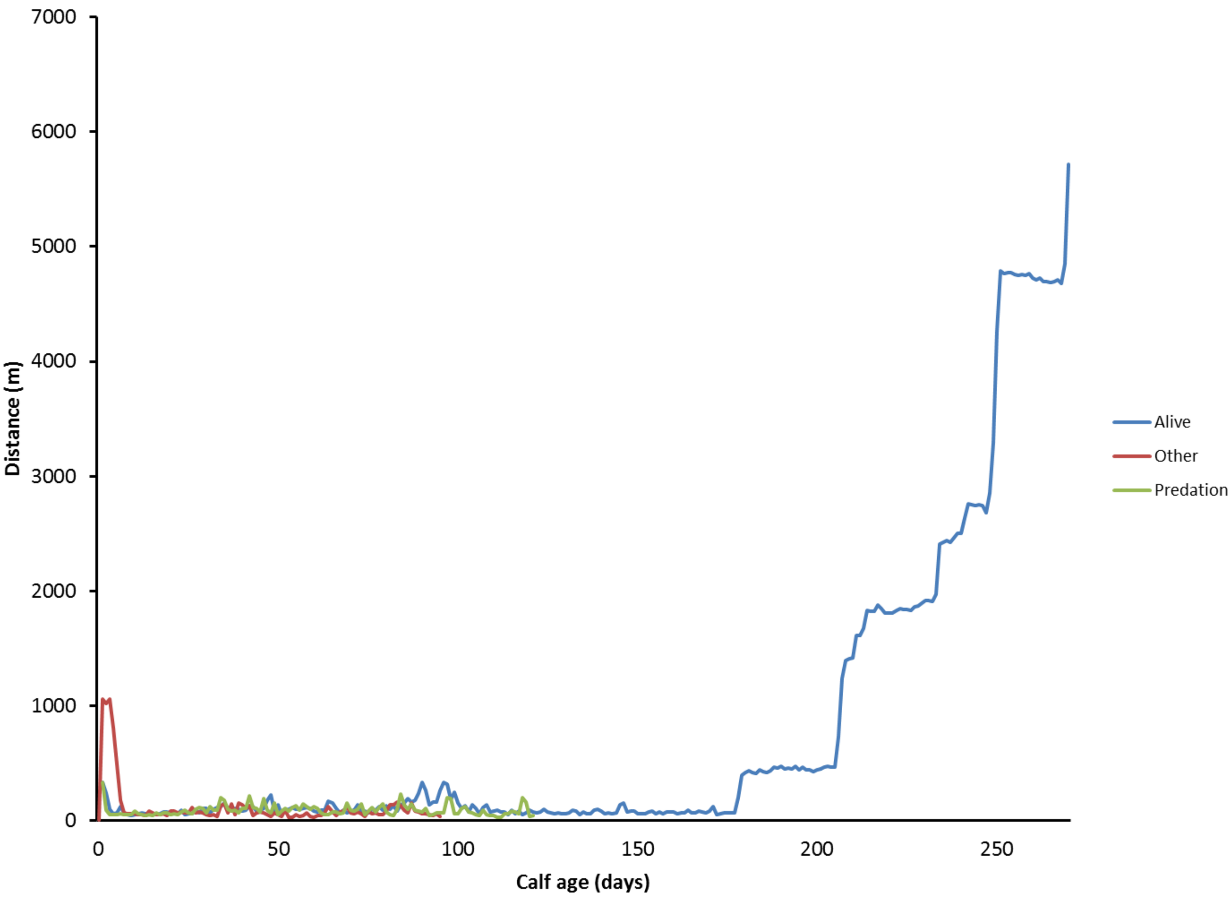

Figure 7. Mean daily distance between moose dams and their calves, including an outlier calf that moved much further from its dam than any other collared calf (up to 28,595 m), by calf age (up to 270 days old) and fate type (alive, other [non-predation mortality], and predation), northeastern Minnesota, May–February 2013–2015.

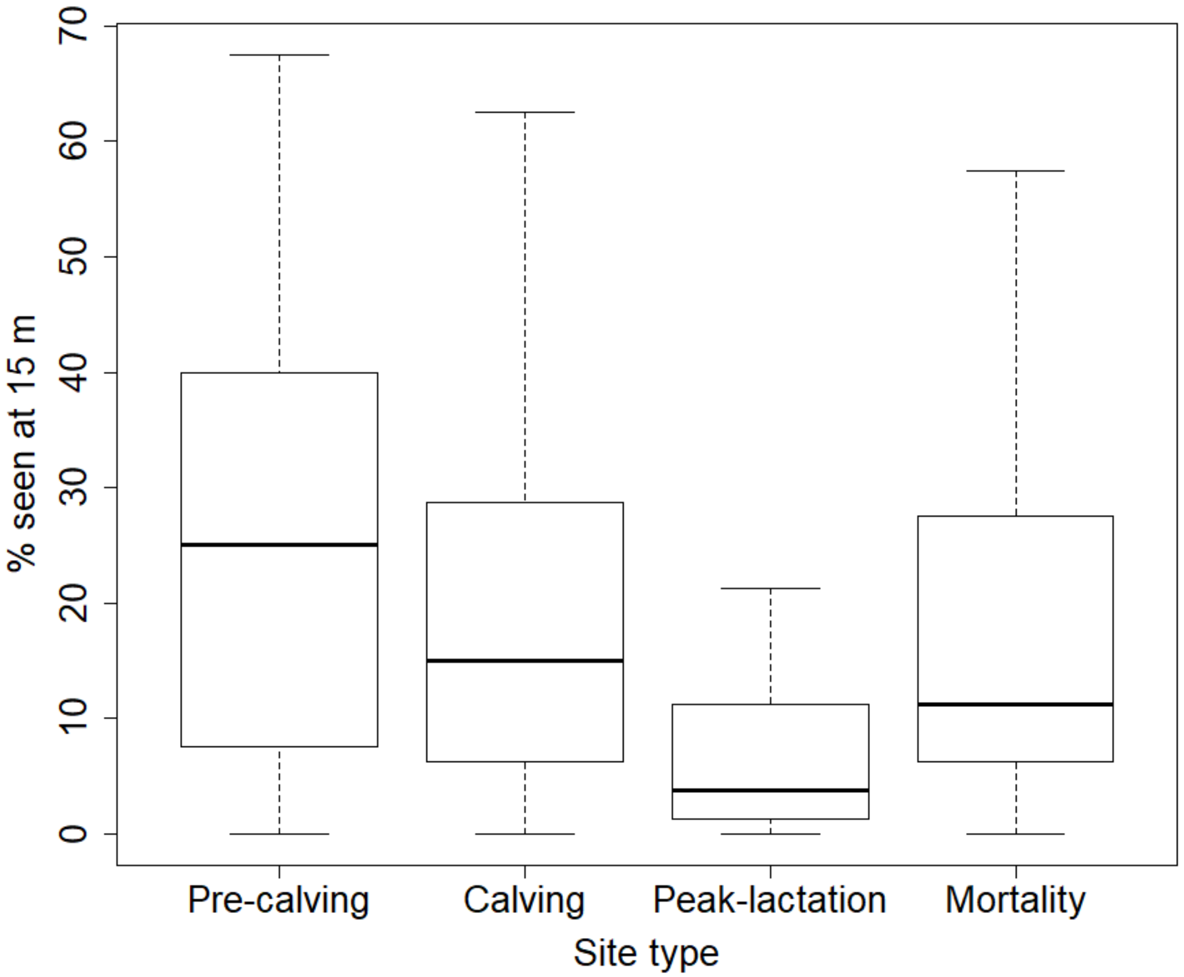

Figure 8. Percentage of calf silhouette visible from 15 m at pre-calving, calving, peak-lactation, and mortality sites (*n* = 34, 37, 25, and 5, respectively) of moose calves in northeastern Minnesota, May–July 2015. Boxes depict interquartile range and dark lines are median values.

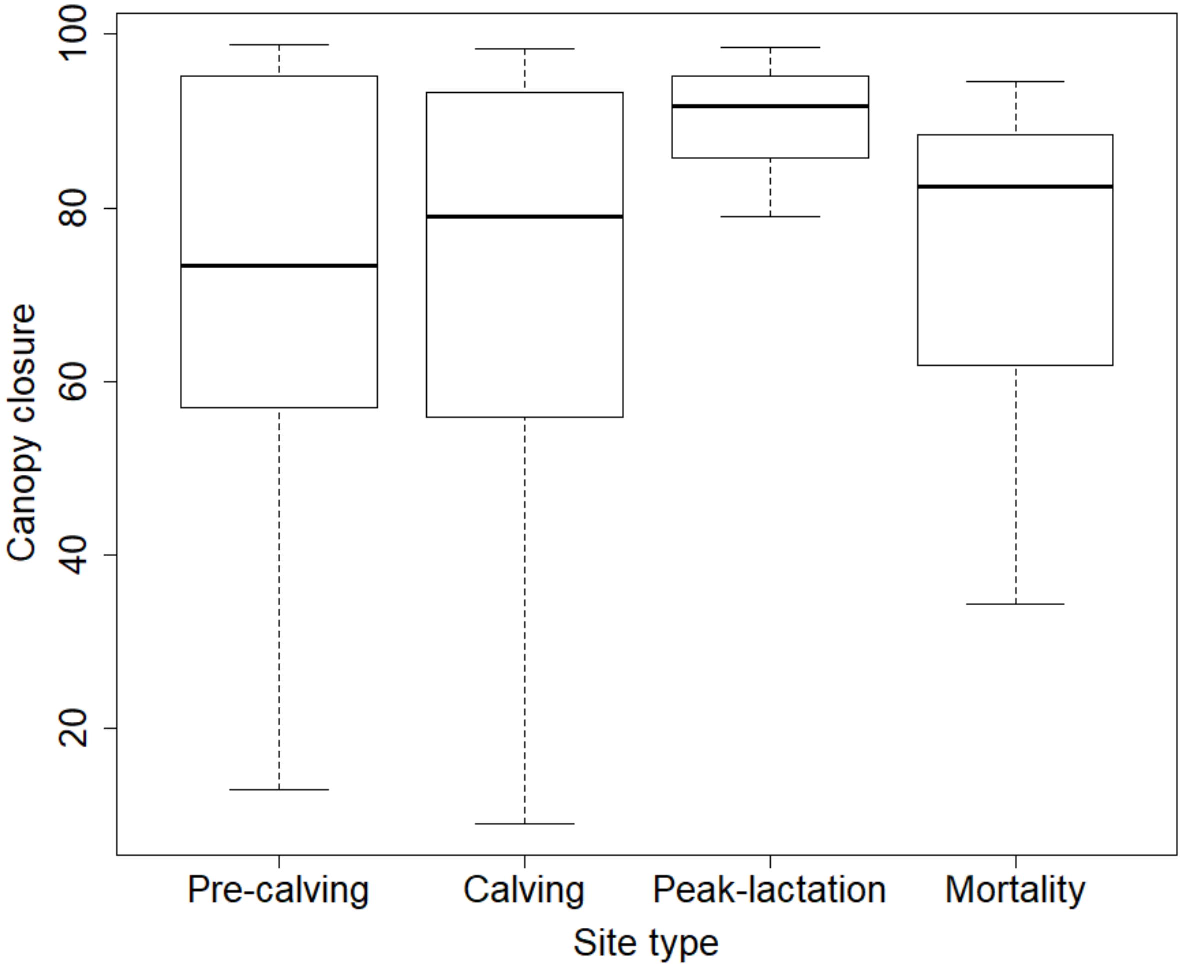

Figure 9. Canopy closure at pre-calving, calving, peak-lactation, and mortality sites (*n* = 34, 37, 25, and 5, respectively) of moose calves in northeastern Minnesota, May–July 2015. Boxes depict interquartile range and dark lines are median values.

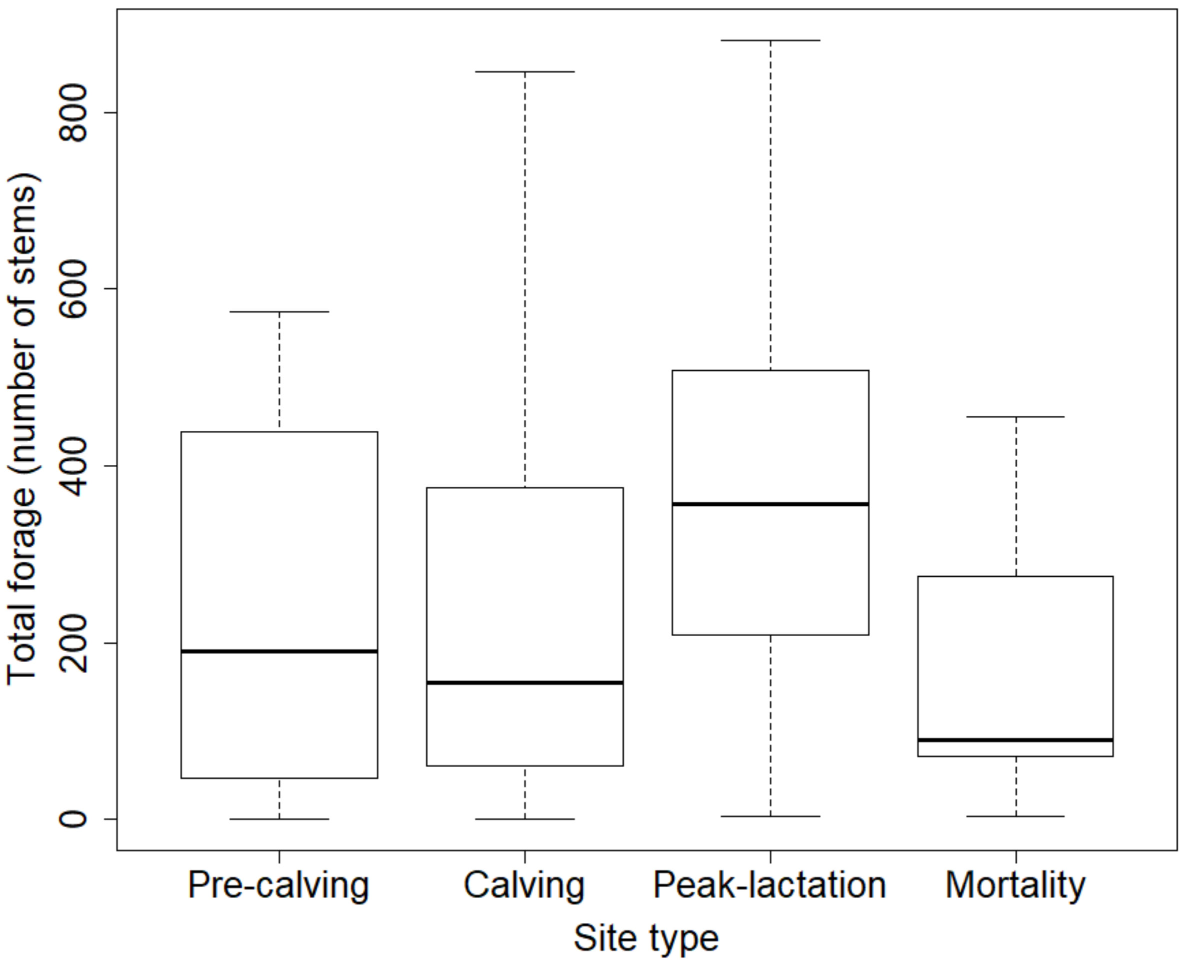

Figure 10. Number of forage stems at pre-calving, calving, peak-lactation, and mortality sites (*n* = 34, 37, 25, and 5, respectively) of moose calves in northeastern Minnesota, May–July 2015. Boxes depict interquartile range and dark lines are median values.

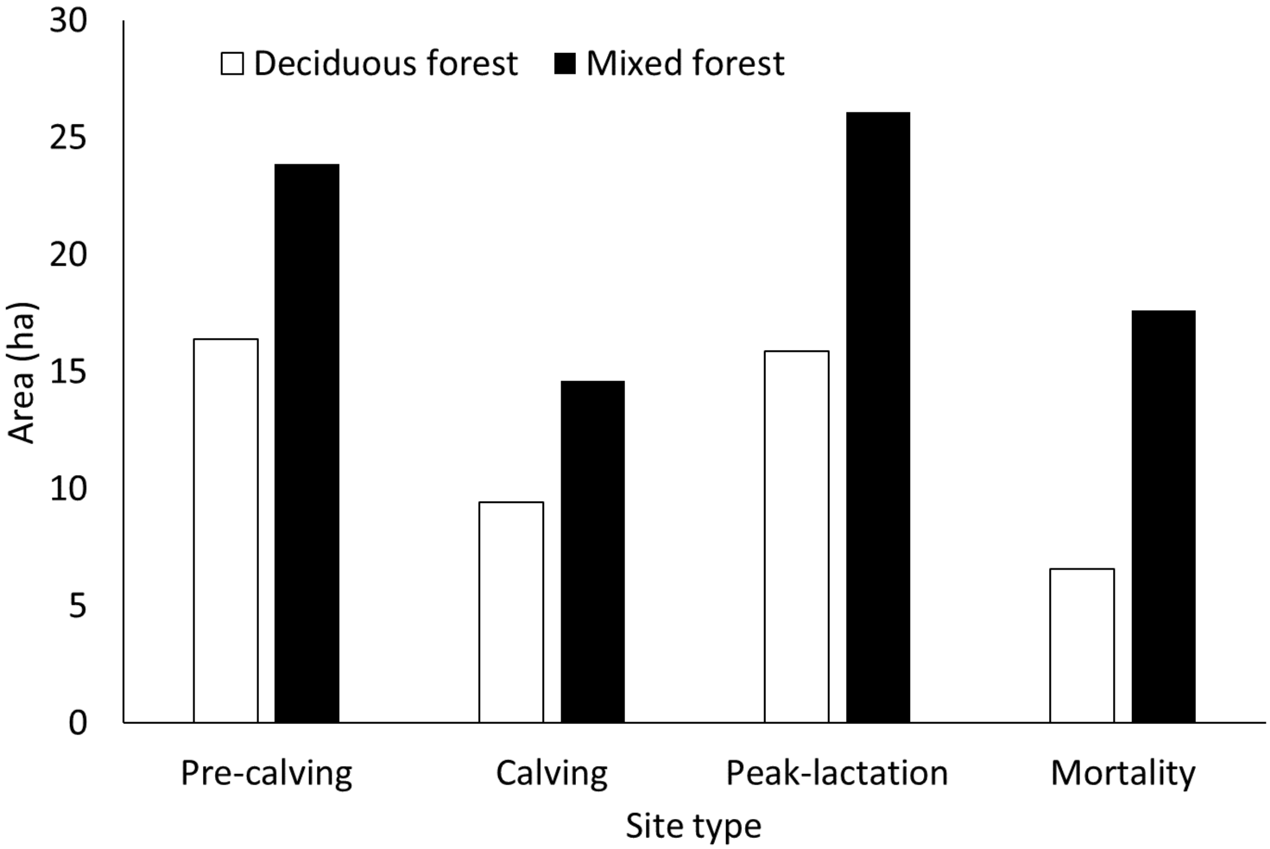

Figure 11. Amount (area in hectares) of deciduous forest (white) and mixed forest (black) within 100-ha buffers around pre-calving, calving, peak-lactation, and mortality sites of moose calves in northeastern Minnesota, May–July 2013–2015.