



Research Article

# Association of Moose Parturition and Post-Parturition Habitat With Calf Survival

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**ABSTRACT** Habitat use during calving and the energetically demanding post-parturition period can be an important determinant of neonatal survival. The moose (*Alces alces*) population in northeastern Minnesota, USA declined 65% from 2006 to 2018. During 2013–2015, annual survival of calves was estimated as low as 28%. We remotely monitored global positioning system (GPS)-collared adult female moose and their neonates during the calving and post-parturition seasons to examine calving movements, birth-sites, habitat use, survival, and cause-specific mortality of neonates. Identifying the association of specific landscape characteristics with neonate survival should yield insight into mechanisms contributing to the declining moose population and serve as a basis for an ecologically sound management response. We compared habitat characteristics of pre-calving, calving, peak-lactation, and mortality sites at a fine and broad scale. We also compared calving sites of females that successfully reared a calf to winter to those that did not. In general, females tended to move to areas of more conifer cover to calve. During peak-lactation, females and their calves used steeper areas with abundant forage and high concealment but less conifer cover. Mortalities occurred at sites that were more level than other site types. Females that successfully reared a calf to 1 February typically calved in areas with more deciduous forest and less forested wetland cover than females whose calves died before 9 months of age. Habitat improvement projects for moose should consider forage requirements and placement on the landscape in relation to cover and slope. © 2018 The Wildlife Society.

**KEY WORDS** *Alces alces*, calf, calving site, habitat use, lactation, Minnesota, moose, survival.

Understanding the intricate relationship between the survival and reproduction of ungulates and habitat use and availability is fundamentally important to sound population management. This is particularly important during the calving or fawning season when females must balance their enhanced requirements for nutrition and predator-avoidance strategies, often trading off between cover types to meet these needs (Bowyer et al. 1999, Poole et al. 2007, Pinard et al. 2012, Pitman et al. 2014). Forage availability influences the recovery of females following the nutritional restriction of winter and must support energetically costly lactation, but quality food patches in proximity to their neonates are often located in areas frequented by predators (Edwards 1983, Creel et al. 2005). Moose (*Alces alces*) calves are most vulnerable to mortality by predation during their first 30 days of life (Keech

et al. 2011, Patterson et al. 2013, Severud et al. 2015a). High calf mortality, particularly during this young stage, can lead to low annual recruitment, which can have a profound effect on population performance (Gaillard et al. 1998, 2000; Raithel et al. 2007). Vegetative hiding cover, landscape heterogeneity, and linear features affect detection of neonates by predators, and consequently, vulnerability to predation (Stephens and Peterson 1984, Griffith and Youtie 1988, Jacques et al. 2015, Karsch et al. 2016, Gulsby et al. 2017).

Adult female moose use a variety of cover types for calving, often in proportion to their availability (Addison et al. 1990, Bowyer et al. 1999, Poole et al. 2007, McLaren et al. 2017), yet some studies have reported selection for specific cover types used in post-parturition areas, such as lowland conifer, shrublands, and regenerating forest (McGraw et al. 2012, McLaren et al. 2017). Recently (2013–2015) in northeastern Minnesota, USA, few calf mortalities were observed at calving sites (Severud et al. 2017), similar to observations elsewhere (Bubenik 2007). Moose and elk (*Cervus canadensis*) may use anthropogenic features as shields against predators, calving near roads or campsites that predators often avoid (Edwards 1983, Lehman et al. 2016). Moose calving sites have been

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associated with increased elevation, steeper slopes, and lower tree density, characteristics that may allow earlier detection of predators (Addison et al. 1990, Wilton and Garner 1991, Bowyer et al. 1999, Poole et al. 2007).

As nutritional demands from lactation increase, and rapidly growing calves begin to browse, forage may become more important than predator avoidance for both females and calves. Additionally, calf mobility increases, allowing juveniles to better keep up with their mothers and evade predators (Altmann 1958). Lactation is a high energy-demanding phase of reproduction for mammalian mothers, requiring 2–3 times more energy than gestation (Robbins 1993). Habitat selection by females during this time is influenced primarily by the need for abundant forage (Belovsky 1978, Thompson and Stewart 2007); however, females with calves-at-heel have selected habitats that provided protection from predation rather than higher amounts of forage during spring and summer (Dussault et al. 2005).

Grey wolves (*Canis lupus*) prey on adult moose and calves where the 2 species are sympatric (Peterson 1999, DelGiudice et al. 2009, Keech et al. 2011, Severud et al. 2015a). Adults are formidable, often standing their ground rather than fleeing when approached by wolves (Mech et al. 2015); however, calves are more vulnerable, especially during their first summer (Patterson et al. 2013, Severud et al. 2015a). Hunting behavior of wolves often involves coursing, but they may use thick vegetation during all seasons to stalk and ambush prey (Kunkel and Pletscher 2001, Mech et al. 2015, Gable et al. 2016).

Northeastern Minnesota's moose population declined an estimated 65% from 2006 to 2018 (DelGiudice 2018), during which time estimated annual calf survival was 0.28–0.40 (Lenarz et al. 2010, Severud et al. 2017). Patterns of calving and post-parturition habitat use and their association with neonatal survival are largely unknown. Our descriptive study investigated female habitat use before, during, and after calving at 2 scales of spatial resolution. Our objectives were to assess differences in habitat characteristics at pre-calving, calving, peak-lactation, and mortality sites. We further assessed differences in calving sites of females that successfully reared a calf to winter versus those that did not. We expected female moose would trade off forage availability for predator avoidance during calving, but energetic demands of lactation would outweigh predator avoidance post-parturition. Specifically, we predicted females would use calving sites with lower amounts of forage and more concealment cover for calves but greater visibility for females to detect predators. We further predicted calf survival would be higher at calving sites that afforded more forage availability and concealment cover. Third, we predicted females would use areas with more forage during peak lactation, and finally, mortality sites would have low concealment for calves and visibility for females.

## STUDY AREA

We conducted this study during May–July 2013–2015 in northeastern Minnesota along the edge of moose range in North America (Lenarz et al. 2010, Timmermann and

Rodgers 2017). A mosaic of the Superior National Forest and various state, county, and private lands, the area comprised 6,068 km<sup>2</sup> between 47°06'N and 47°58'N latitude and 90°04'W and 92°17'W longitude and has been characterized as the Northern Superior Upland (NSU), within the Laurentian mixed forest province (Minnesota Department of Natural Resources [MNDNR] 2015). Topography was undulant, with rugged cliffs and exposed bedrock outcrops not uncommon. Elevation ranged from 200 m to 650 m above sea level. The NSU received much of its annual precipitation as snow and experienced prolonged snow cover and a shorter growing season compared to the rest of the state (MNDNR 2015). Mean monthly temperatures during the study in Isabella, Minnesota (centrally located within study area) ranged between 8.2°C and 18.2°C; mean maximum temperatures ranged from 14.4°C to 24.3°C and mean minimum temperatures from 2.1°C to 12.2°C ([www.dnr.state.mn.us/climate/historical/acis\\_stn\\_meta.html](http://www.dnr.state.mn.us/climate/historical/acis_stn_meta.html), accessed 10 Jul 2018).

Vegetation was a mixture of wetlands, lowland stands of northern white cedar (*Thuja occidentalis*), black spruce (*Picea mariana*), and tamarack (*Larix laricina*), and upland stands of balsam fir (*Abies balsamea*), jack pine (*Pinus banksiana*), eastern white pine (*P. strobus*), and red pine (*P. resinosa*). The upland conifer stands included quaking aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*). Timber harvest and forest disturbance (e.g., wind, weather, fire, flood, humans, and unknown causes) throughout northeastern Minnesota moose range declined from 9% to 6% during 2001–2011, and was estimated at 3% during 2008–2009 (Wilson and Ek 2013).

State and tribal moose harvests were suspended in 2013 because of the steady population decline, but a limited tribal harvest resumed in 2016 (DelGiudice 2012, Edwards 2018, Schrage 2018). Grey wolves and American black bears (*Ursus americanus*) preyed on moose calves (Lenarz et al. 2009; Patterson et al. 2013; Severud et al. 2015a, b); their densities were estimated at 4.4/100 km<sup>2</sup> and 23/100 km<sup>2</sup>, respectively (Garshelis and Noyce 2011, Mech et al. 2018). White-tailed deer (*Odocoileus virginianus*), managed at pre-fawning densities of <4/km<sup>2</sup>, were primary prey of wolves in the area (Nelson and Mech 1981, DelGiudice et al. 2002, MNDNR 2012). Alternate wolf prey included American beavers (*Castor canadensis*), snowshoe hares (*Lepus americanus*), black bears, and various small mammals (Stenlund 1955, Frenzel 1974, Van Ballenberghe et al. 1975, Chenaux-Ibrahim 2015). Wolves were harvested in this region during 2012–2014 (Stark and Erb 2014; D. Stark, MNDNR, personal communication), immediately prior to and during this study, but were federally relisted in December 2014. Upon den emergence, bears consumed succulent roots of aquatic grasses, flowers and catkins from a variety of tree and shrub species, and supplemented their diet with ungulate neonates and ants (family Formicidae) during May and June (Kunkel and Mech 1994, Garshelis and Noyce 2008, Severud et al. 2015a). Bear harvest during 2011–2016 in bear management unit 31 ranged from 197 to 363 bears (5-yr mean = 289; Garshelis and Tri 2017).

## METHODS

### Moose Captures and Monitoring

Adult moose and calves received global positioning system (GPS) collars as part of the MNDNR's survival and cause-specific mortality studies (Severud et al. 2015a, Carstensen et al. 2017). Their collars collected hourly locations during May and June (calving season). Median age of calves at capture was 2 days (range = 1–5 days). We monitored 155 females (50 in 2013, 56 in 2014, and 49 in 2015) and 139 calves (49 collared in 2013 and 25 collared in 2014, approximately 65 uncollared calves were remotely monitored in 2015 via their mother's movements; Severud et al. 2017). Details of moose capture and collar specifics were described elsewhere (Butler et al. 2013; Carstensen et al. 2015, 2017; Severud et al. 2015a; Obermoller et al. 2017). All captures and handling met American Society of Mammalogists guidelines (Sikes and the Animal Care and Use Committee of the American Society of Mammalogists 2016). Additionally, neonate captures and handling protocols followed requirements of the Institutional Animal Care and Use Committee for the University of Minnesota (protocol number 1302-30328A). We monitored survival of calves and investigated mortalities within 1 day of death; we assigned cause of death by the preponderance of evidence at the mortality site (Severud et al. 2015a, Severud 2017). Pregnant moose often moved long distances and subsequently localized to give birth (i.e., calving movement); we used this movement to locate neonates for collaring and to identify calving sites (Severud et al. 2015a). Females fitted with GPS collars also have been observed making repeated movements away from and return-trips to focal areas where calves have been preyed upon (mortality movement); we used this movement to target mortality investigations of uncollared calves of collared females (Severud et al. 2015b, Obermoller et al. 2017).

### Fine-Scale Habitat Assessment

In 2015, we recorded site characteristics at pre-calving and calving sites (averaged GPS coordinates over 40–48 hours immediately following the calving movement, adjusted on site as confirmed by calving evidence; Fig. 1) of females that calved in May–June 2015. We used starting and ending points of calving movements to identify pre-calving and calving sites, respectively (Severud et al. 2015a). In 2015, we similarly surveyed locations where calf mortalities were confirmed by site evidence (e.g., bone fragments, hooves, hair, predator sign) following a mortality movement of the female, because neonates were not collared (Severud et al. 2015b, Obermoller et al. 2017). We recorded mortalities occurring at the birth-site as both calving and mortality sites. When mortalities occurred outside of the birth-site, we collected new habitat data.

Milk production peaks 21–31 days post-parturition for female moose (Schwartz and Renecker 2007). In 2015, when evidence indicated a calf survived  $\geq 26$  days (pellets and tracks, continued reduction in female movement), we recorded site characteristics at the corresponding female's peak-lactation location (assumed to be 26 days post-

parturition). If the location was in the middle of a long movement, we used the center of the nearest grouping of  $\geq 3$  locations (typically 1 hr apart). We conducted all habitat surveys so that phenological conditions (i.e., leaf-off vs. leaf-on) were consistent with those of the initial location of the moose (e.g., we surveyed sites used by females pre-leaf-on in spring the following autumn post-leaf-off).

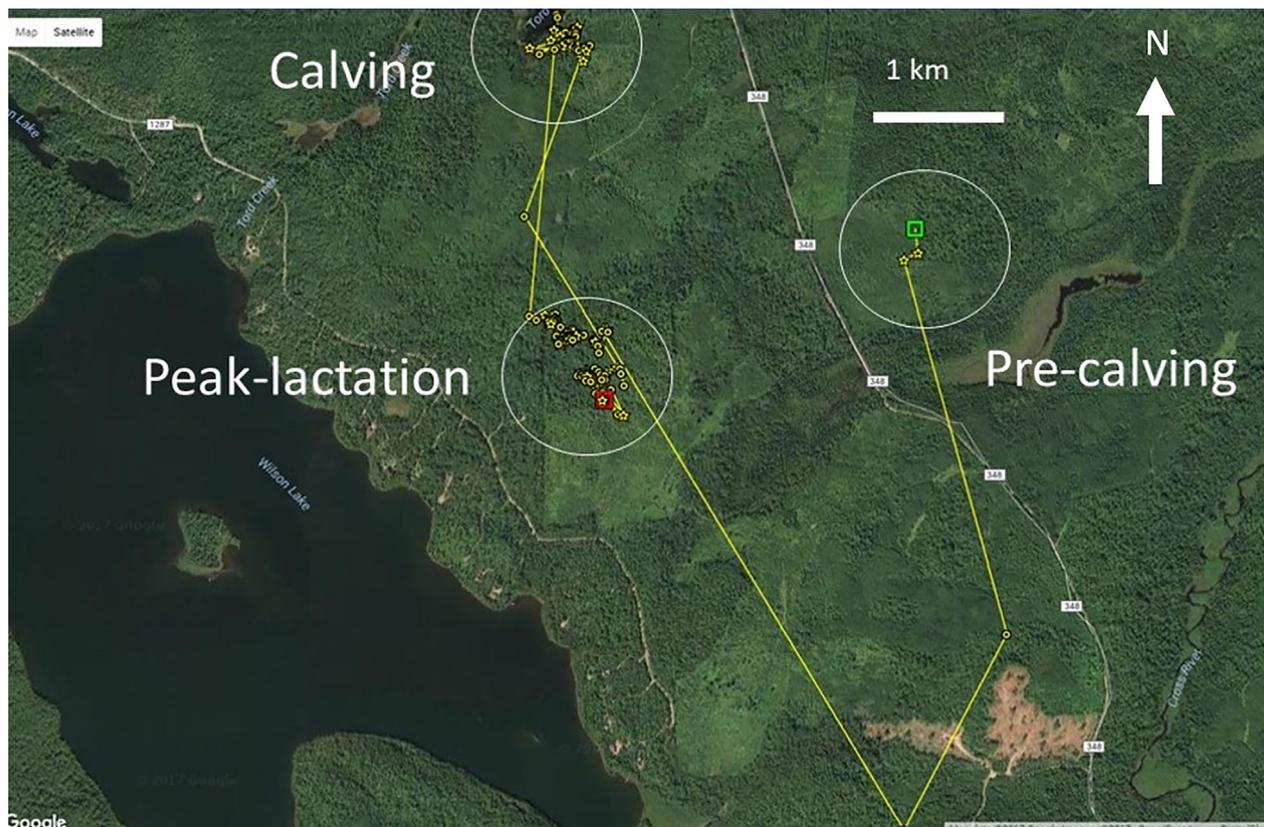
We centered habitat plots at each female's GPS location closest to the time of interest, unless that location was refuted by visual evidence. This typically occurred at calving and mortality sites when calving beds or kill-sites were readily observed; we established plot centers in the middle of the female's calving bed or at the primary location of calf remains or sign of a struggle. We recorded an average waypoint in the center of each plot using a handheld GPS unit, determined 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 ( $^{\circ}$ ) using a clinometer and compass.

We recorded canopy density (in addition to being measured at plot center) and horizontal visibility 15 m from 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, 100%) of each of 19 bands (Poole et al. 2007). We calculated mean and standard deviation of canopy density and visibility at each habitat plot. To estimate calf visibility, we held a life-size cardboard cut-out of a standing moose calf silhouette at the center of the plot; an observer recorded the percentage of the cut-out ( $\pm 5\%$ ) that could be seen from 15 m at a 1-m height in each cardinal direction (lower values reflected higher concealment). We trained observers and conducted double-counts with multiple observers to ensure consistency. The observer then moved towards the cut-out, maintaining a 1-m height, and recorded the distance from the calf when visibility reached 25, 50, 75, and 100%. We then calculated mean calf visibility and standard deviation at 15 m for each plot and distance to calf for each visibility class (25, 50, 75, 100% visible).

We recorded trees, saplings, and shrubs within an 11-m radius from the central point. We defined trees as any upright ( $< 45^{\circ}$  lean) woody plant with a diameter at breast height (DBH)  $\geq 10$  cm. We defined saplings and shrubs as DBH  $< 10$  cm. We determined the species and DBH of each tree, alive or dead, and counted number of stems of saplings and shrubs by species. We further classified living trees  $< 18$  cm DBH and shrubs as forage or non-forage species (Peek et al. 1976, Portinga and Moen 2015).

### Broad-Scale Habitat Assessment

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 expand plots to about 100 ha, which approximated the area used by females with calves during post-parturition (Poole et al. 2007, McGraw et al. 2012). We overlaid these circular plots on a land-cover-classification layer (Minnesota Land Cover Classification and Impervious Surface Area by Landsat and Lidar) and calculated the



**Figure 1.** Example of moose pre-calving, calving, and peak-lactation sites during May–July 2013–2015 in northeastern Minnesota, USA. We defined pre-calving sites as the origin of the calving movement; peak-lactation sites were locations of females 26 days post-parturition (milk production peaks 21–31 days postpartum).

proportion of each cover-class. We also calculated the amount of edge within the buffers, distance to edge and road, and road density. We used road, trail, and snowmobile trail layers (manmade linear features, i.e., roads), then summed road length (km) and divided by area (km<sup>2</sup>) to calculate road density. Traffic patterns in the study area were largely dictated by logging activity and we did not actively monitor changes in traffic levels. We delineated edge using Geospatial Modelling Environment (Beyer 2015); we conducted all other analyses in ArcGIS version 10.3.1 (Environmental Systems Research Institute, Redlands, CA, USA).

### Statistical Analyses

We used a cluster bootstrapped analysis of variance (ANOVA) to compare habitat characteristics by site types (pre-calving, calving, peak-lactation, and mortality). To account for non-independence of observations obtained from the same moose and unbalanced design (i.e., individual moose had observations ranging from 1 to all 4 site types), we created 10,000 bootstrapped samples of the data in which we sampled clustered observations associated with individual moose with replacement. We used these bootstrapped samples to estimate the distribution of an *F* statistic under a null model that all means were equal for each site type. For each habitat characteristic, we shifted each observation by subtracting the sample mean of its site type and then added the overall sample mean such that the means of each site type

were all equal to the overall sample mean. We computed a bootstrapped *P*-value for the *F* statistic associated with the original data by calculating the proportion of bootstrapped *F* values that were larger than the observed *F* statistic. We concluded site types differed for that specific variable if *P* < 0.05. To investigate which site types differed, we also created bootstrapped distributions of differences in site means for all pairwise comparisons. If the bootstrapped ANOVA showed a significant effect of site type, we conducted pairwise comparisons by constructing 95% confidence intervals for the pairwise mean differences. If the confidence intervals did not include zero, we concluded the site means differed. We compared calving sites of surviving and non-surviving calves using linear models, and similarly calculated confidence intervals for effect sizes using bootstrapping as above.

## RESULTS

Only 3% (*n* = 5) of 155 monitored parturient females did not make a calving movement, but we confirmed calving via direct observation of a calf or site evidence. Calves were confirmed alive during peak-lactation for 73 females, and we surveyed sites of 36 natural mortalities of calves. Causes of mortality included wolf predation (*n* = 24), bear predation (*n* = 6), unknown predator-kill (*n* = 3), and 1 of each of the following: drowning, infection resulting from wolf-inflicted

injury, and natural abandonment. Further details on survival and cause-specific mortality of calves were published elsewhere (Severud et al. 2015a, Severud 2017).

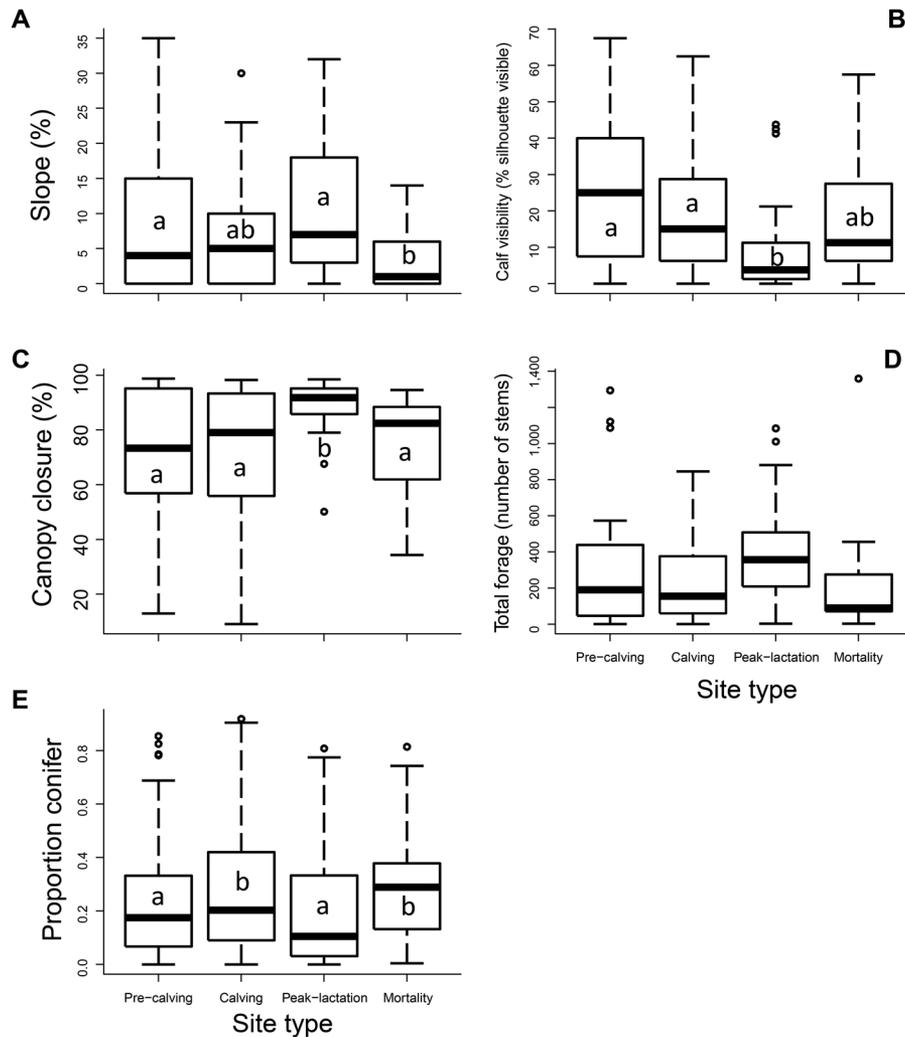
### Fine-Scale Habitat Assessments

Of the 49 females that calved in 2015, we measured fine-scale habitat characteristics at 34 pre-calving, 37 calving, 25 peak-lactation, and 10 mortality sites. We did not survey all 49 pre-calving and calving sites because of personnel limitations, and only surveyed peak-lactation sites if a calf was still at-heel. Models indicated significant variation by site type for slope (Fig. 2A,  $P=0.03$ ), mean calf visibility at 15 m (Fig. 2B,  $P=0.02$ ), and mean canopy closure (Fig. 2C,  $P=0.04$ ). *Post hoc* comparisons for slope indicated mortality sites were 4.8 (95% CI = 0.4–9.2) and 6.7% (95% CI = 2.3–11.1) flatter than pre-calving and peak-lactation sites, respectively (Fig. 2A). Slope should be interpreted cautiously because of the small differences ( $\bar{x}_{\text{peak-lactation}} = 10.1\%$  vs.

$\bar{x}_{\text{mortality}} = 3.5\%$ ; Fig. 2A). Calf visibility at 15 m at peak-lactation sites was 10.3% (95% CI = 2.3–18.0) lower than at calving sites and 16.0% (95% CI = 6.6–25.1) lower compared to pre-calving sites but was not different from mortality sites (Fig. 2B). Peak-lactation sites had 12.8–17.0% denser canopy closure than all other site types (Fig. 2C). Although peak-lactation sites contained nearly twice as much forage compared to all other site types (Fig. 2D), this was not statistically significant ( $P=0.16$ ). Fine-scale habitat variables were similar between calving sites of females of surviving versus non-surviving calves.

### Broad-Scale Habitat Assessment

We analyzed 150 pre-calving, 155 calving, 73 peak-lactation, and 36 mortality sites from 2013 to 2015. At a broad scale these sites did not differ by any landcover or heterogeneity measures (i.e., edge and road metrics), except for coniferous forest (Fig. 2E,  $P=0.006$ ). Calving and mortality sites



**Figure 2.** Prevailing slope (%; A), calf visibility (from 15 m; B), mean canopy closure (%; C), forage (number of forage species stems <18 cm diameter at breast height; D) at pre-calving, calving, peak-lactation, and mortality sites ( $n=34, 37, 25,$  and  $10,$  respectively) of moose calves during May–July 2015; and proportion of 100-ha buffers of conifer forest cover type (E) at pre-calving, calving, peak-lactation, and mortality sites ( $n=150, 155, 73,$  and  $36,$  respectively) of moose calves during May–July 2013–2015 in northeastern Minnesota, USA. We identified forage species according to Peek et al. (1976) and Portinga and Moen (2015). Boxes depict interquartile range, dark lines are median values, circles are outliers, and whiskers are  $1.5\times$  interquartile range. Different letters depict significantly different groups based on bootstrapped 95% confidence interval differences that do not include 0.

contained 4–10% (95% CI = 1–18) more conifer cover than pre-calving and peak-lactation sites (Fig. 2E).

We again compared calving sites of females that successfully reared  $\geq 1$  calf to 1 February ( $n = 10$ ) to calving sites of females that lost calves to mortality ( $n = 30$ ). Calving sites of females of surviving calves contained 25% (95% CI = 9–39) more deciduous forest ( $F_{1,38} = 10.33$ ,  $P = 0.003$ ) but 17% (95% CI = 10–25) less forested wetlands than females of non-surviving calves ( $F_{1,38} = 7.80$ ,  $P = 0.008$ ). Calving sites for survivors contained  $0.39 \pm 0.06$  ( $\bar{x} \pm SE$ ) deciduous forest and  $0.06 \pm 0.01$  forested wetland, whereas calving sites for non-survivors contained  $0.14 \pm 0.04$  deciduous forest and  $0.23 \pm 0.03$  forested wetland.

## DISCUSSION

Ungulates typically tradeoff forage availability for avoidance from predators during vulnerable life stages, such as calving. As we predicted, results suggested calving sites contained higher amounts of non-forage cover type (conifer forest) yet more calf visibility as compared to peak-lactation sites. This is consistent with previous reports of female moose using areas with less forage during calving (Bowyer et al. 1999, Poole et al. 2007). Localization at calving sites can be so extreme, and the amount of forage so sparse, that we occasionally observed bark-stripping, a sign of severe nutritional deprivation (Miquelle and van Ballenberghe 1989).

As we predicted, females moved into areas with more available forage when lactation demands peaked. Although this difference was not statistically significant, lactation sites had nearly twice as much forage as calving sites. This increase in forage was revealed at both a fine (more forage stems, greater concealment cover, and higher canopy closure) and a broad scale (less conifer cover). Lactating females require 65–125% more energy than non-lactating females (Robbins 1993); nursing twins increases this cost an additional 67% (Schwartz and Renecker 2007). Lactation increases daily protein requirements for moose 10–14% (Schwartz and Renecker 2007). Peak-lactation usually coincides with peak vegetation abundance (Robbins and Robbins 1979). These pronounced increases in nutritional requirements underscore the importance of ample quality forage during lactation. Moose and red deer (*Cervus elaphus*) have been observed seeking out high quality forage during lactation (Clutton-Brock et al. 1982, Melin et al. 2015). However, other ungulates typically continue to avoid predation at the expense of access to forage while juveniles are at-heel (Pitman et al. 2014, Smith et al. 2015, Karsch et al. 2016). Restricted access to forage during lactation in white-tailed deer has resulted in fawns gaining less mass, nursing more, and spending more time with their mothers foraging, and in survival decreasing 35% (Therrien et al. 2007, 2008). Segments of northeastern Minnesota's moose population may be nutritionally stressed in winter to the extent that many females and their calves must then contend with greater predation risk to access high-quality forage to offset those seasonal nutritional deficiencies and meet increased nutritional requirements of lactation (DelGiudice and Severud 2017).

We predicted females that calved in areas with abundant forage and high concealment to hide calves from predators

would exhibit higher calf survival. Calf visibility did not differ among pre-calving, calving, or mortality sites but was lower at peak-lactation sites. Wolves and bears may depend more on olfaction or chance encounter rather than vision to locate prey (Bastille-Rousseau et al. 2011, Mech et al. 2015). In our study, females that calved in areas with more deciduous forest, indicative of good foraging habitat (Mabille et al. 2012), were more likely to rear a calf to winter. Conversely, calving sites in areas with higher amounts of forested wetlands, which generally contain less palatable forage (Mabille et al. 2012), were associated with lower calf survival. Because concealment cover was often vegetative (i.e., small diameter conifers, large diameter trees), locations on the landscape that offer abundant forage and concealment pre-leaf-out may be rare. Females that calve in deciduous forest may have sufficient quality forage available without requiring increased movement and associated predation risk, and can therefore recover nutritionally while localized with their calf. If forage availability is associated with less movement (Saïd and Servanty 2005), detection by predators may be reduced. This increase in nutrition may have facilitated a higher quantity and quality of milk and an increased ability of the female to protect its calf from predators because moose that are nutritionally stressed defend calves less vigorously (Oftedal 1985, Keech et al. 2011, Patterson et al. 2013). A possible alternate explanation is that predators differentially use land cover types during this time of year and were less likely to use deciduous forest (Hebblewhite et al. 2005, Bastille-Rousseau et al. 2011, DeCesare 2012).

Peak-lactation sites offered more forage and greater concealment cover. However, these factors may limit visibility for the female, potentially hindering her ability to detect approaching predators. Movement can increase detection by predators (Lima and Dill 1990, Frair et al. 2007), thus making females and calves more vulnerable to predation (Stephens and Peterson 1984). Movement through thick forested cover may be even more dangerous. Wolves may use vegetation to ambush prey in a variety of landscapes and seasons (Kunkel and Pletscher 2001, Gable et al. 2016). Wolf movement rate explained more variation in kill rates of moose in winter (Vander Vennen et al. 2016), yet protective cover can aid prey in avoiding detection (Kunkel and Pletscher 2000).

We predicted that mortality sites would have low calf concealment cover and obstructed female views (horizontal visibility). Fine-scale analyses of mortality sites showed that calves died at flatter sites (more limited female visibility). Hypothetically, moose moved to steeper slopes for calving to be able to detect approaching predators (Wilton and Garner 1991, Poole et al. 2007). Greater detection distances increase the female's ability to move off before being encountered and avoid being ambushed.

## MANAGEMENT IMPLICATIONS

The decline of northeastern Minnesota's moose population has prompted many habitat restoration projects aimed at ensuring moose persistence in the region. Our results can serve as a guide

for planting species that may increase calf survival, such as deciduous and mixed forest species most palatable to moose. These foraging areas should be close to areas of dense concealment cover in which females and calves can hide during calving. Because calving generally occurs pre-leaf-on, dense concealment cannot be achieved with deciduous shrubs and saplings, but rather requires small-diameter conifers associated with sloping topography. Managing foraging areas on slopes >4% might allow females to more easily detect approaching predators and better defend their calves. Assuring that pregnant females exiting winter in compromised body condition have access to calving areas and peak-lactation sites with plentiful forage and concealment cover could contribute to increased calf recruitment.

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