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Research Article

Survival and Cause-Specific Mortality of Moose Calves in Northeastern Minnesota

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ABSTRACT Ungulate reproductive success (calf production and survival) influences population performance. The moose (*Alces alces*) population in northeastern Minnesota, USA, has declined 65% from 2006 to 2018 but has begun to stabilize. Because causes of this decline were largely unknown, we investigated production, survival, and cause-specific mortality of calves of the global positioning system (GPS)-collared females in this population. In 2013 and 2014, we GPS-collared 74 neonates and monitored them for survival. In 2015 and 2016, we monitored 50 and 35 calving females for signs of neonatal mortality using changes in adult female velocities and assessed seasonal calf survival by aerial surveys. In 2013 and 2014 (pooled), survival to 9 months was 0.34 (95% CI = 0.23–0.52) for collared calves, and in 2015 and 2016 (pooled) survival was 0.35 (95% CI = 0.26–0.48) for uncollared calves. Mortality in all 4 years was high during the first 50 days of life. In 2013 and 2014 (pooled), calving sites were relatively safe for collared neonates; predator-kills occurred a median 17.0 days after departure and a median 1,142 m from calving sites. Predation was the leading cause of death of collared calves (84% of mortalities), with wolves (*Canis lupus*) accounting for 77% of these. Other forms of mortality for collared and uncollared calves included drowning, infection, vehicle collision, and natural abandonment. We documented higher wolf predation than other recent studies with similar predator communities. 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 ecologically sound management responses. © 2019 The Wildlife Society.

KEY WORDS *Alces alces*, calves, *Canis lupus*, cause-specific mortality, GPS collars, moose, neonates, predation, survival.

Population declines of large herbivores can be caused by low and variable juvenile survival (Raithel et al. 2007, Pinard et al. 2012, Forrester and Wittmer 2013), especially when adult survival is relatively stable (Gaillard et al. 1998, 2000; Lenarz et al. 2010). The moose (*Alces alces*) population in northeastern Minnesota, USA, declined an estimated 65% from 2006 to 2018 but has recently shown signs of stabilization (ArchMiller et al. 2018, DelGiudice 2018). Survival and cause-specific mortality of calves were largely unknown in this area, but using survey flights, average first-year survival from 2002 to 2008 was estimated at 0.40 (range = 0.24–0.56; Lenarz et al. 2010).

Neonatal ungulate survival can be affected by many factors, but in systems with extant predators, predation is often the primary cause of mortality (Linnell et al. 1995, Carstensen et al. 2009, Severud et al. 2015*a*). Twinning status, calf sex, birth size, and maternal age have all been associated with calf mortality (Testa et al. 2000*a*, Keech et al. 2011, Patterson et al. 2013). It is not always clear 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 mortality from predation on moose calves in Alaska, USA (Keech et al. 2011). Predator manipulations in Alaska have consistently suggested that predation is an additive source of mortality (Boertje et al. 2010), but moose were often the primary prey in systems that include wolves (*Canis lupus*), black bears (*Ursus americanus*), and grizzly bears (*U. arctos*). These Alaskan study areas were also devoid of white-tailed deer (*Odocoileus virginianus*) and the diseases and parasites

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they transmit to moose. Results from Alaska may not be transferable to Minnesota or elsewhere.

Recent advances in global positioning system (GPS) collars and movement analyses have made it possible to identify birthing and neonatal mortality events (DeMars et al. 2013). Pregnant moose often move long distances before localizing (calving movement) for up to 15 days to give birth (Testa et al. 2000*b*, McGraw et al. 2014, Severud et al. 2015*a*). Females with GPS collars also have been observed making repeated movements away from and return-trips to focal areas where their calves have been preyed upon (e.g., a mortality movement; Severud et al. 2015*b*, Obermoller et al. 2019). Until recently, expandable GPS collars had not been fitted to moose neonates. They had only been used on neonates of white-tailed deer (Long et al. 2010) and fallow deer (*Dama dama*; Kjellander et al. 2012). Observable fine-scale movement patterns, made possible by GPS collars, facilitated rapid investigation of mortality events to more confidently assign proximate causes and gather evidence of contributing factors. Having both females and their calves GPS-collared also allowed us to examine the importance of proximity of mother and offspring to juvenile survival.

Our goal was to better understand the influence of calf production and survival on the population trajectory of northeastern Minnesota's moose population. Facilitated by the first large-scale deployment of GPS collars on free-ranging neonates, our specific objectives were to estimate survival and cause-specific mortality of GPS-collared moose calves. Based on previous modeling (Lenarz et al. 2010) and empirical studies on calf mortality (Ballard et al. 1981, Gasaway et al. 1992, Boertje et al. 2010, Keech et al. 2011, Patterson et al. 2013), we predicted that calf survival would be low (50% and 30% by Jan and May) and predation would be the leading cause of mortality. We further predicted American black bears would have their greatest effect on the youngest calves, whereas wolf predation would occur throughout the year. We also predicted that survival would be influenced by a variety of covariates, including maternal age, litter size, calf mass, calf hind foot length (HFL), and the distance between calf and mother.

STUDY AREA

We conducted this study on 6,068 km^2 between 47°06′N and 47°58′N latitude and 90°04′W and 92°17′W longitude in northeastern Minnesota (Fig. 1) during spring 2013–winter 2017. This region has been characterized as the Northern Superior Upland within the Laurentian mixed forest province (Minnesota Department of Natural Resources [MNDNR] 2015). Topography is undulant, with rugged cliffs and exposed bedrock outcrops common. Elevation ranges from 200 m to 650 m above sea level. The region received much of its annual precipitation as snow and experienced prolonged snow cover

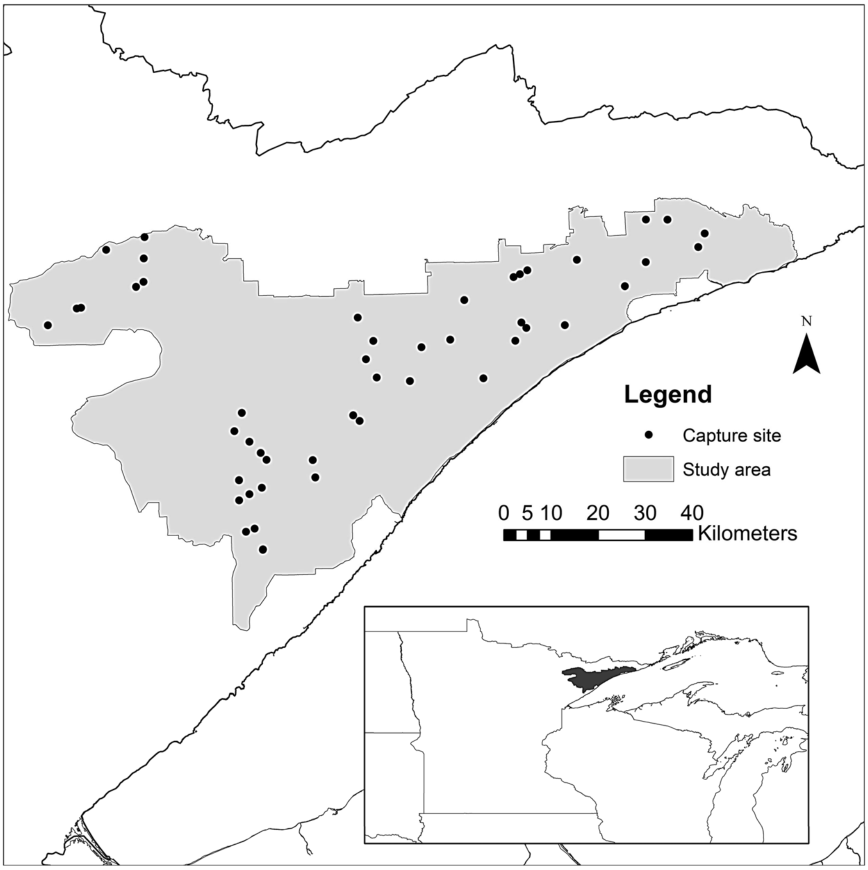

Figure 1. Calving sites of moose neonates ($n = 175$; 6,068 km^2 study area) during May–June 2013–2016, northeastern Minnesota, USA.

and a shorter growing season compared to the rest of the state (Minnesota Department of Natural Resources 2015). Mean monthly temperatures in Isabella, Minnesota (centrally located within the study area) ranged between 8.2°C and 14.8°C during May–June 2013–2016; mean maximum and minimum temperatures ranged from 14.2°C to 21.1°C and from 2.1°C to 9.0°C, respectively. During July–April 2013–2016, mean monthly temperatures ranged between −20.4°C and 18.3°C; mean maximum and minimum temperatures ranged from −13.9°C to 24.3°C and from −26.9°C to 12.2°C, respectively (www.dnr.state.mn.us/climate/historical/acis_stn_meta.html, accessed 11 Mar 2019).

The Northern Superior Upland is a mosaic 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*), intermixed with quaking aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*). Timber harvest declined in the area from 2001 to 2013 (Wilson and Ek 2013).

Harvest and predation pressure in the study area were relatively low for adult moose (Carstensen et al. 2018). 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 are the most common predators of moose in the area and can have a pronounced effect on calf survival (Patterson et al. 2013; Severud et al. 2015*a*,*b*); their densities were estimated at 4.4/100 km^2 and 23/100 km^2, respectively (Garshelis and Noyce 2011, Mech et al. 2018). White-tailed deer, managed at prefawning densities no higher than 4 deer/km^2, 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 before 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. 2015*a*). Annual bear harvest during 2011–2016 in the bear management unit 31 (which largely overlaps our study area) ranged from 197 to 363 bears (5-yr $\bar{x} = 289$; Garshelis and Tri 2017).

METHODS

Moose Capture and Handling

In January and February 2013–2015, crews captured, handled, and fitted 129 adult female moose with GPS collars as part of an MNDNR study of cause-specific mortality (Butler et al. 2013; Carstensen et al. 2014, 2015). Handling included extracting a last incisor (I4) to estimate age and collecting a blood sample to assess pregnancy status via serum progesterone concentrations (Sergeant and Pimlott 1959, Murray et al. 2006). Additional details of the capture and handling protocols may be viewed elsewhere (Butler et al. 2013; Carstensen et al. 2014, 2015). Capture and handling protocols met American Society of Mammalogists guidelines (Sikes and the Animal Care and Use Committee of the American Society of Mammalogists 2016). Adult collars collected hourly locations during May and June (calving season) and then every 4 hours during July–April.

We monitored collared adult females for a calving movement and subsequently located calves by approaching clusters of location-fixes (Severud et al. 2015*a*). In 2013, a capture crew (Quicksilver Air, Fairbanks, AK) located eligible neonates (>24 hr old) via helicopter and then landed to allow 1–2 handlers to disembark. Typically, crews easily approached and captured neonates within 10 m of where they were initially observed (DelGiudice et al. 2015). In 2014, in response to a high incidence of capture-induced abandonment during 2013 (DelGiudice et al. 2015), crews conducted all captures without the assistance of a helicopter. We never administered immobilizing drugs to adult females or neonates during neonate captures (Ballard et al. 1979). During 2013 and the first phase of 2014 capture operations (8−15 May), we weighed (±0.5 kg) by spring-scale, ear-tagged, and blood-sampled ($n = 16$ in 2013; 2 in 2014) neonates, took morphological measurements (HFL, upper and lower neck circumference, chest girth, total body length [±1 cm]) and a rectal temperature (±0.05°C), and fitted a GPS collar to each neonate. During the second phase of captures in 2014 (21 May−19 Jun), we limited handling to sexing and fitting the GPS collar (Ballard et al. 1979, Severud et al. 2016). We estimated age of all neonates at capture based on localization of the female (birth was assumed to occur ≤12 hr after initial localization). We handled, collared, and released twins together to minimize the risk of capture-related abandonment (Keech et al. 2011, DelGiudice et al. 2015). We placed collars in bags with vegetation and other ground debris for ≥24 hours before captures to minimize human and collar scent. In 2014, we also placed clothing and other capture-related gear in similar bags. All neonate captures and handling protocols followed requirements of the Institutional Animal Care and Use Committee for the University of Minnesota (protocol number 1302-30328A) and were consistent with guidelines recommended by the American Society of Mammalogists (Sikes and the Animal Care and Use Committee of the American Society of Mammalogists 2016).

In response to capture-induced abandonment of neonates and capture-related mortality of adults (Carstensen et al. 2015; DelGiudice et al. 2015, 2018) 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. For the 2015 and 2016 calving seasons, we monitored remaining adult females with GPS collars for a calving movement, and subsequently for indications of a mortality movement (see below).

Calf Collars and Location Error Measurement

In 2013, we fitted calves with a GPS PLUS VERTEX Survey-1 GLOBALSTAR collar with an expandable belt (420 g, box dimensions 85 × 59 × 75 mm, belt 3 cm wide, initial circumference 35 cm, fully expanded circumference 65 cm; Vectronic Aerospace GmbH, Berlin, Germany). We slightly modified collar bands in 2014 to avoid neck abrasions. For additional details on collars, see Severud et al. (2015*a*) and Obermoller et al. (2018). All collars were below 5–10% of body mass as recommended by the American Society of Mammalogists (Sikes and the Animal Care and Use Committee of the American Society of Mammalogists 2016), and with early rapid growth (Schwartz 2007), collar weights were <1% of body mass within about 40 days (Severud et al. 2015*a*).

We placed adult and calf collars at known locations (under open and closed [>80%] canopy) and collected locations for 24 hours (Obermoller et al. 2018). Linear error was defined as the distance (m) between the known locations and the recorded fixes. We then created an empirical cumulative distribution function for each collar and canopy class and evaluated goodness of fit of various distributions using the fitdist and gofstat functions in the fitdistrplus R package (Delignette-Muller and Dutang 2015). We then used the parameters for the best-fitting distribution for each collar-cover combination (gamma for adult collars in open canopy and lognormal for all other combinations) to simulate 10,000 linear errors. We assumed the angle of error was random. We converted polar coordinates of error and angle to Cartesian coordinates and then calculated distance between the simulated points. Summer field tests demonstrated that mean linear error (±SE, range) of calf collar locations was 24.9 ± 2.7 m (1–274 m) in the open and 40.3 ± 1.3 m (0–368 m) under dense forest canopies (≥80% closure; Obermoller et al. 2018).

We removed adult female and calf location data thought to be erroneous (locations that resulted in velocities >30 km/hr; V. St-Louis, MNDNR, unpublished data). We then calculated proximity of mothers and their calves. To understand the effects of adult and calf GPS-collar error on proximity calculations, we simulated 10,000 paired locations using observed linear error measurements from collar testing and measured Euclidean distance between these locations.

Mother-Calf Monitoring

Collared calves.—In 2013 and 2014, we monitored collared mother-calf groups by computer several times daily as updated locations were received by the base station. We examined proximity (distance between) and synchrony of female and calf GPS locations until fate was known (mortality, slipped collar, and failed collar). When we received a mortality alert text message or suspected (via monitoring) a mortality had occurred, a response team initiated a field investigation to determine cause of death (Severud et al. 2015*a*). In response to a high rate of slipped collars in 2014, we assessed apparent survival of affected calves via helicopter in March 2015 by locating their GPS-collared mothers.

Uncollared calves.—In 2015 and 2016, we used calving movements to identify calving activity, and then mortality movements to initiate mortality investigations. We estimated time of death using the time at which the female initially fled. We conducted flights via helicopter to assess apparent seasonal survival rates in 2015 during late November–early December (~190 days old) and late March 2016 (~320 days old). If a calf was not observed with a female during a flight, we assumed it had died and estimated its date of death as the midpoint between last known date alive and the flight (Johnson 1979, Berger 2012). We attempted to observe all adult females during each flight, including females that did not have a calf nearby during early winter flights.

Survival Analysis

Data imputation.—Because of missing values in calf handling data (maternal age [$n = 8$], HFL [$n = 12$], mass [$n = 16$]), we used the function aregImpute in the R package Hmisc to generate 20 imputed data sets (Harrell and Dupont 2018). We then ran a correlation matrix on the numerical covariates and eliminated one from a pair of correlated variables ($|r| > 0.35$). We used contingency tables to test for independence of categorical variables (e.g., litter size and sex). Mass was correlated with HFL and birth date. Because HFL is a better indicator of fetal development than mass (Schwartz and Hundertmark 1993), we excluded mass from further analyses. Maternal age was correlated with HFL and excluded. We retained birth date, HFL, litter size, sex, and proximity. We ran models with each imputed data set and then calculated extracted coefficient means and standard errors that account for imputation uncertainty (Harrell and Dupont 2018).

Collared calves.—We calculated Kaplan–Meier survival estimates using the R package KMsurv (R Core Team 2017). Because calf births were tightly synchronized (Severud et al. 2015*b*), we modeled survival as a function of calf age, with day zero being birth (Fieberg and DelGiudice 2009). We calculated cause-specific mortality rates with a cumulative incidence function using the R package wild1 (Sargeant 2011). We used a log-rank test, implemented using the survdiff function in the survival package (Harrington and Fleming 1982, Therneau 2015) to determine if calf survival was affected by the abandonment of a calf's twin. We also used a cluster-level bootstrap in which we resampled all calves from the same mother with replacement to relax the assumption that twins have independent fates. We estimated time of death using the mortality mode of collars and calf and mother locations relative to the mortality site.

We created a daily survival history of each calf using the splitLexis function in the R package Epi (Plummer and Carstensen 2011, Carstensen et al. 2017). We then modeled daily survival as a smooth function of age using generalized linear models with a complementary log-log link. We used regression splines to model the effect of age. We used the ns function in the splines package to create the basis vectors for age and chose the degree of smoothing (df = 1–5) using Akaike's Information Criterion (AIC; Fieberg and DelGiudice 2009). We interacted HFL and birth date with age because we thought those covariates would likely affect survival differently as calves mature. This framework allowed us to relax the proportional hazards assumption. We created a simplified set of models based on biological realism and previous research (Testa et al. 2000*a*, Keech et al. 2011, Patterson et al. 2013). We evaluated model support using AIC corrected for small sample size (AIC_c); we considered models within 2 AIC_c units of the best approximating model to be competitive alternatives but deemed models within 2 AIC units with 1 additional parameter to be uninformative (Arnold 2010). We also calculated an average AIC_c (over all imputations) for models that included HFL.

Uncollared calves.—In 2015 and 2016, we assumed that the time of death of uncollared calves was marked by an initial flee of an adult female from a focal point where we located calf remains, or the midpoint between last known sighting and first known absence. We used Kaplan–Meier survival estimators to report up to 30-day and 338-day survival estimates for these data.

RESULTS

Collared Calves (2013, 2014)

We collared 49 neonates from 31 females in 2013 and 25 neonates from 19 females in 2014 (58% and 32% twinning rates of collared calves, respectively; however, these rates were not representative of the population and were focused at the onset of calving when twins are more likely to occur [Boertje et al. 2019]). Overall, the sex ratio (females:males) was 18:19. Seven females abandoned 9 calves in 2013 and 6 females abandoned 9 calves in 2014 (DelGiudice et al. 2015, 2018). Two additional calves died during or shortly after capture from trampling by the female and not nursing because of unknown causes (DelGiudice and Severud 2016). These 20 calf fates were assumed to be associated with capture and therefore not included in survival analyses; however, we calculated survival rates with them included to examine the effect their exclusion had on survival estimates (i.e., assuming their premature deaths were compensatory to other causes of mortality). Of the remaining 54 calves, 4 and 10 slipped their collars in 2013 and 2014, respectively. Median calving dates for 2013, 2014, 2015, and 2016 were 14, 19, 10, and 11 May, respectively. We did not detect a difference in survival between calves of females that abandoned 1 calf from a set of twins and calves of nonabandoning females (log-rank test, $\chi^2_1 = 0.10$, $P = 0.72$); therefore, we pooled all collared calves in subsequent analyses. Confidence intervals using the cluster-level bootstrap were similar to those estimated assuming independence (Fig. S1, available online in Supporting Information). Therefore, we also assumed the fates of twins were independent when comparing survival models using AIC. Measurement error associated with distances between mothers and calves was similar for all canopy classes and averaged 25.6 m (95% CI = 25.0–26.2 m).

Blood profiles of calves sampled in 2013 were reported elsewhere (DelGiudice and Severud 2016). Mean rectal temperature was 38.7 ± 0.07°C (range = 37.7–39.7°C, $n = 43$), mean body mass was 15.8 ± 0.3 kg (range = 12–20.5 kg, $n = 38$) and mean HFL was 45.9 ± 0.3 cm (range = 42–49 cm, $n = 42$). Body mass and HFL were correlated ($r = 0.64$, $P < 0.001$). There were no statistically significant differences in mass or HFL by sex or between twins and singletons. Mean maternal age of all collared calves was 6.4 ± 0.5 years old (range = 1–14 yr, $n = 43$). Median monthly proximity of mothers and calves was 67.4 ± 10.3 m (range = 34.4–1,593.5 m, $n = 161$), with a trend of calves and mothers moving farther apart as summer progressed and then coming together through winter (Fig. 2). We excluded 1 calf from proximity calculations because it separated from its mother and twin in November by >28 km. It survived alone from November until February when we removed its collar.

Modeling daily survival using age with 1 degree of freedom (i.e., a linear effect on the complementary log-log scale) yielded the lowest AIC value (335.75) and resulted in survival estimates that agreed well with the Kaplan–Meier survival estimator (Fig. 3A). Using 2 degrees of freedom to model the effect of age resulted in a model within 2 AIC_c units of the top model (336.85) but did not appreciably alter the shape of the survival curve (Fig. S2, available online in Supporting Information). Including other covariates, except proximity, always led to models with larger AICs than the age-only model (Table 1). The proximity model did yield a lower AIC, but the effect size was minimal (Table 1). The conditional daily mortality was high for the first 50 days of age, then began to approach zero (Fig. 3B). This resulted in a survival curve that dropped quickly with age (until about 50 days old; Fig. 3A). By 100 days of age, predicted survival remained constant.

For pooled 2013 and 2014 collared calves, 30-day survival was 0.58 (95% CI = 0.46–0.74; Fig. 3A) and declined to 0.34 (95% CI = 0.23–0.52) by 206 days of age (6–10 Feb 2014), when we removed all remaining collars (Fig. 3A). Follow-up flights (25 Feb 2014 and 3 Mar 2015) assessed survival of calves that slipped their collars, which adjusted survival to 0.29 (95% CI = 0.18–0.46) by 206 days of age. Rather than removing abandoned calves from the analysis, if we assumed these individuals would have died from other causes within the first 30 days of life, 30-day survival would be 0.42 (95% CI = 0.32–0.56) and 206-day survival would be 0.21 (95% CI = 0.12–0.35), a decrease in survival at 30 and 206 days of 28% and 38%, respectively.

Mortalities from predation ($n = 26$) occurred a mean 31.6 ± 6.5 days (median = 17.0 days, range = 0–120.5) after departing from the calving site and 1,553 ± 289 m (median = 1,142 m, range 107–5,788) from the calving site. Mean response time from estimated time of death to site investigation was 24.9 ± 2.3 hours (range = 9.5–52.5 hr, $n = 23$) when collars were working properly.

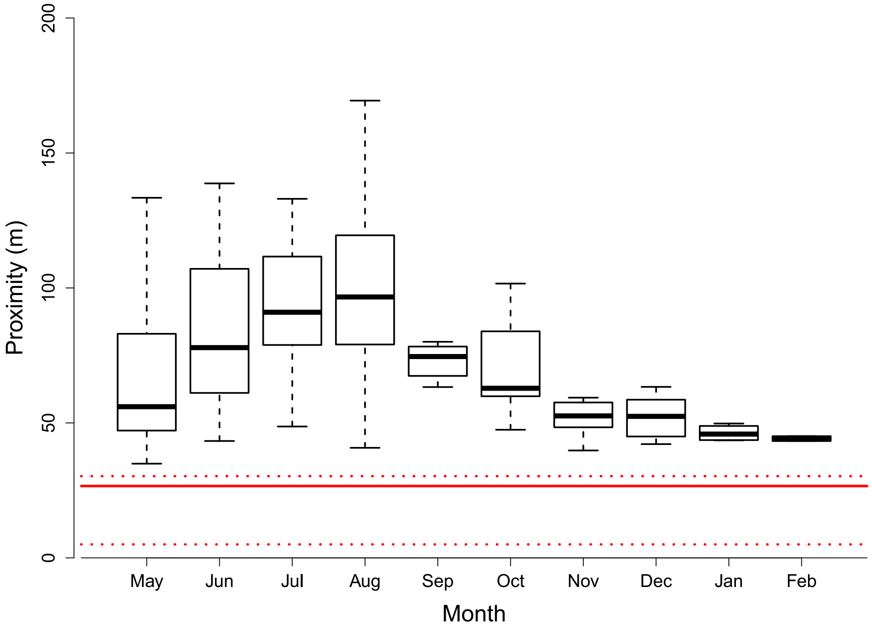

Figure 2. Monthly proximity (m) of moose mothers and calves (*n* = 161 mother-calf months) during May 2013 and 2014 to February 2014 and 2015 (pooled), northeastern Minnesota, USA. Boxes depict interquartile range, dark lines are median values, and whiskers are 1.5× interquartile range. Horizontal red line depicts simulated mean linear error associated with calf and adult global positioning system collars; dashed lines are the interquartile range.

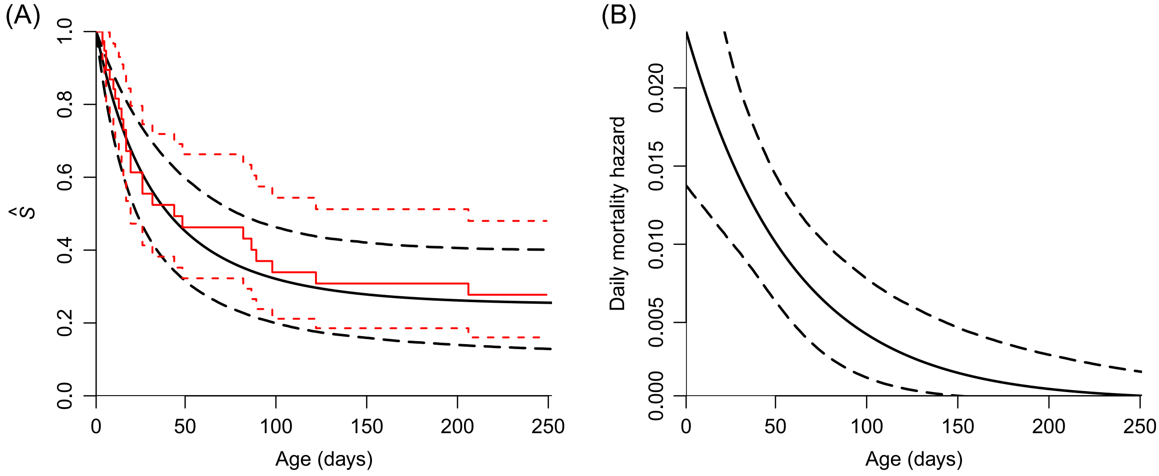

Figure 3. Cumulative daily survival ($\hat{S}$; A) from a generalized linear model using age as a predictor (black) and Kaplan–Meier survival estimates (red), and predicted daily mortality hazard (B) of moose calves during 2013 and 2014, northeastern Minnesota, USA. Dashed black lines represent bootstrapped 95% confidence intervals for the generalized linear model, dashed red lines represent a 95% confidence interval for the Kaplan–Meier survival curve.

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 septicemia resulting from wolf-inflicted wounds. Cumulative incidence functions of mortality rose rapidly from birth to 50 days of age (Fig. 4). Over the first 9 months of age, the cumulative probability of being preyed upon by wolves or bears was 50.2% (90% CI = 37.1–63.5) and 11.7% (90% CI = 3.5–19.9), respectively, and the cumulative probability of succumbing to other causes was 9.6% (90% CI = 2.9–16.3). Predation accounted for 84% of all natural mortalities, with wolves having the greatest impact overall (77% of predation events).

Uncollared Calves (2015, 2016)

In 2015 and 2016, we observed calving movements or localizations alone (i.e., no prior long-distance movement) of 50 and 35 GPS-collared females and monitored them for mortality movements. Assuming a 30% twinning rate (M. W. Schrage, Fond du Lac Natural Resource Management Division, unpublished data), this yielded an estimated 65 uncollared calves for monitoring during 2015. In 2016, we used evidence of a surviving twin (e.g., calf tracks and pellets), rather than assuming a 30% twinning rate, to estimate 36 calves under observation (pooled *n* for 2015–2016 = 101 calves).

Pooling 2015–2016, 30-day survival for uncollared calves was 0.65 (95% CI = 0.58–0.74) and 338-day survival was

Table 1. Coefficients (β) and 95% confidence interval (CI) of covariates used to model daily survival of moose calves during May 2013 and 2014 to February 2014 and 2015 (pooled), northeastern Minnesota.

Model[a]	AIC_c	ΔAIC_c	Covariate	β	95% CI	P
Age + prox + age × prox	229.7	0.0	Age	−9.291	−15.026, −3.556	0.002
			Prox	1.376	0.312, 2.440	0.011
			Age × prox	0.034	−0.017, 0.086	0.188
Age	335.7	106.0	Age	−5.370	−8.174, −2.565	<0.001
Age + sex + age × sex	337.1	107.4	Age	−3.775	−6.992, −0.559	0.021
			Sex (male)	−0.182	−1.158, 0.794	0.716
			Age × sex (female)	−0.014	−0.036, − 0.007	0.196
Age + sort + age × sort	337.6	107.9	Age	−4.030	−6.834, −1.225	0.005
			Sort (twin)	−0.826	−1.942, 0.290	0.147
			Age × sort (single)	−0.045	−0.099, 0.009	0.106
Age + BD + age × BD	337.9	108.2	Age	−3.162	−9.682, 3.358	0.342
			BD	0.048	−0.018, 0.114	0.151
			Age × BD	−0.001	−0.003, 0.002	0.584
Age + HFL + age × HFL	339.2	109.5	Age	7.763	−77.066, 92.592	0.774
			HFL	0.013	−0.247, 0.274	0.623
			Age × HFL	−0.001	−0.007, −0.005	0.733

[a] Age = age of calf in days; prox = distance between mother and calf (km); HFL = hind foot length at capture (cm); sort = twin or singleton; and BD = birth date (defined as number of days after 1 May).

0.35 (95% CI = 0.26–0.48). According to aerial observations in early winter (30 Nov–3 Dec 2015) and late winter (28–29 Mar 2016), 2015 survival estimates were 0.43 (95% CI = 0.33–0.57) and 0.40 (95% CI = 0.30–0.54), respectively. Similarly, 17–18 January and 19 April 2017 observations indicated 2016 survival declined to 0.34 (95% CI = 0.21–0.54) at almost 1 year of age. We documented 26 natural mortalities (pooled 2015–2016), 18 wolf-kills, 4 bear-kills, 2 unknown predator-kills, and 2 deaths following vehicle collisions.

DISCUSSION

As predicted, we observed low annual survival for calves. Survival dropped to 50% much earlier than predicted (by Jul rather than Jan). We were unable to monitor survival to 1 year of age (i.e., recruitment) because of collar removal and slippage (Obermoller et al. 2017), but 9-month survival estimates aligned closely with our annual survival prediction (30% vs. observed 34–35%). Mortalities decreased and stabilized after 100 days of age, similar to other studies of moose calf survival where large predators included wolves and bears (Ballard et al. 1981, Hauge and Keith 1981, Larsen et al. 1989, Boertje et al. 2010, Patterson et al. 2013). These findings are in stark contrast to recent study results from wolf-free New England, USA, where 60-day calf survival was estimated at 77–94% (compared to our 47%) and mortalities were attributed to winter tick (*Dermacentor albipictus*) infestation, lungworm (*Dictyocaulus viviparus*) parasitism, and poor body condition (Musante et al. 2010), and were concentrated in late winter-early spring (Jones et al. 2017). Our results support that predation is having an additive effect on calf survival.

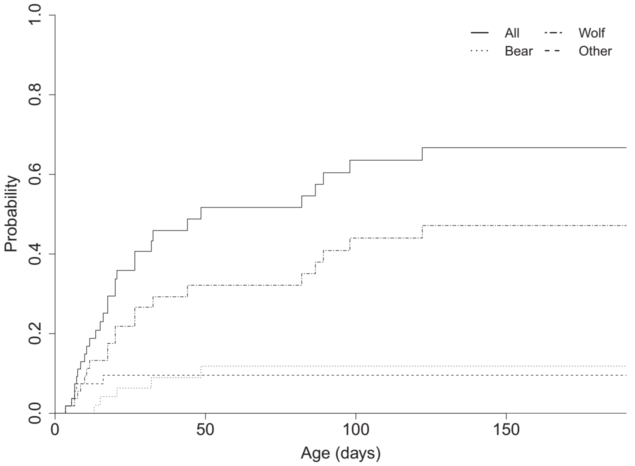

Figure 4. Cumulative incidence function for cause-specific mortality of global positioning system-collared moose calves ($n = 40$ calves) during May 2013 and 2014 to February 2014 and 2015 (pooled), northeastern Minnesota, USA. Causes of mortality were wolf predation ($n = 20$), black bear predation ($n = 5$), and other (natural abandonment [$n = 2$], drowning [$n = 1$], abandonment of unknown cause [$n = 1$], unknown predator [$n = 1$], and infection resulting from wolf attack [$n = 1$]).

Estimated annual survival in all 4 years using collared and uncollared calves were similar (within 95% CIs) and closely match rates estimated by Lenarz et al. (2010) in the same study area during 2002–2008, before the declining population trend was indicated by the MNDNR's annual survey (Giudice et al. 2012, ArchMiller et al. 2018, DelGiudice 2018). Our observed rates approach those reported in northern New Hampshire, northeastern Alberta, and western Interior Alaska (0.29–0.45; Hauge and Keith 1981, Musante et al. 2010, Keech et al. 2011) but were 46% lower than rates observed in Ontario (0.64; Patterson et al. 2013). Low juvenile survival can be an early indication of reduced resources, followed by increased age at first reproduction, reduction in reproductive rates, and ultimately an increase in the adult mortality rate (Eberhardt 2002). Moose in northeastern Minnesota have been exhibiting low adult survival and a subsequent reduction in reproductive output (Lenarz et al. 2010, Carstensen et al. 2018).

As we predicted, predation was the primary cause of neonate mortality, consistent with findings of other studies of moose calf mortality conducted in areas with extant predators (Ballard et al. 1981, Hauge and Keith 1981, Keech et al. 2011, Patterson et al. 2013). Contrary to our prediction, bear predation was relatively low, but affected younger calves (aged 10–48 days), as we predicted. Franzmann et al. (1980) also reported that bear predation occurred primarily when moose calves were small, then nearly ceased as they became more mobile at 1–2 months old. A study in Ontario, Canada with a similar predator guild also found equal bear and wolf predation, but bear densities were higher than ours (31–45 vs. 23 bears/100 km^2; Garshelis and Noyce 2011, Patterson et al. 2013). The authors postulated that bear sex and age structure may have influenced predation rates more than simple abundance.

Wolf predation on calves decreased at about 100 days of age, whereas we predicted wolf-kills would occur year-round. Historically, wolves and moose have been sympatric in this system, yet wolves have recently been implicated in the moose population decline (Mech and Fieberg 2014, Severud et al. 2014, Carstensen et al. 2018, Mech et al. 2018). In a portion of moose range in northeastern Minnesota that partially overlaps our study area, an increasing wolf population was subsidized by deer while also preying upon moose calves, which contributed to the moose decline (Barber-Meyer and Mech 2016). Also, unhealthy moose were more vulnerable to wolf predation throughout northeastern Minnesota (Mech and Nelson 2013, Carstensen et al. 2018). Wolf population estimates for Minnesota remained stable (within survey 90% CIs) between 2,211 and 2,423 wolves during 2012–2016 (Erb et al. 2017). A concurrent study of wolf diet in northeastern Minnesota also documented a high occurrence of moose calves in spring diets (11 May–30 Jun; Chenaux-Ibrahim 2015). Moose populations have been limited by wolf effects on calf survival (Gasaway et al. 1992, Testa et al. 2000*a*, Bertram and Vivion 2002, Boertje et al. 2010).

Wolf predation accounted for 30% of mortalities of adult moose in this study area during 2013–2018, but ≥40% of these individuals exhibited symptoms of health issues, possibly predisposing them to predation (e.g., winter tick infestation, encephalitis, pneumonia; Carstensen et al. 2018). Health issues were the proximate cause of mortality for 62% of cases, whereas the remaining 8% consisted of accidents and hunter harvest. The overall poor health of the northeastern Minnesota moose population could potentially explain the high number of capture-induced abandonments observed (DelGiudice et al. 2015, 2018) and the high rates of predation on calves. Mothers defended their calves less vigorously following harsh winters or when in poor nutritional condition in Alaska and Ontario (Keech et al. 2011, Patterson et al. 2013). In 2013, calf and adult survival rates were lowest during the MNDNR's studies (2013–2018; Severud et al. 2015*a*, Carstensen et al. 2018), and several adult mortalities resulted from winter tick infestation (Carstensen et al. 2018). Coupled with 2013's serious winter tick infestation, we also physiologically documented the most severe nutritional restriction of moose population-wide (DelGiudice and Severud 2017). All these factors may have contributed to suppressing the moose population, but it is still unclear what initiated the downward trajectory.

We predicted intrinsic factors may predispose calves to various sources of mortality, yet we failed to detect any measurable effects of birth date, twinning status, sex, or HFL on survival (Table 1). Proximity of mother and calf may be important to survival but not adequately assessed using current technology (e.g., collar linear error, location schedules dictated by battery life), or with our limited sample size of individuals. Additionally, we observed a calf that survived November to at least February independent of its mother. Previous studies have observed mixed findings regarding how calf sex, litter size, maternal age, or birth date influenced survival (Franzmann and Schwartz 1986, Larsen et al. 1989, Ballard et al. 1991, Schwartz and Franzmann 1991, Ballard 1992). There is some evidence that litter size effects may disappear at high levels of mortality (Testa et al. 2000*b*, Bertram and Vivion 2002), but Keech et al. (2011) reported higher singleton than individual twin survival across wide ranges of overall calf survival and predation pressure and concluded that mortality was largely independent of calf condition during high levels of predation pressure because predators had few alternatives and wolves and bears are efficient predators. Patterson et al. (2013) reported slightly higher survival for calves that were heavier at capture but only for calves that died of non-predation causes. In cases where intrinsic factors were not shown to affect survival, habitat characteristics can have a more pronounced effect via facilitation of predator search efficiency or deficient nutrition for lactating mothers (Jacques et al. 2015).

Calving habitat may be an important determinant of neonatal survival (Bowyer et al. 1999, Poole et al. 2007, Jacques et al. 2015). Generally, we observed mortalities to occur once females and their calves departed calving sites, consistent with other studies that reported calves were rarely killed at calving sites (Bubenik 2007). Previous studies have documented considerable variability in land cover types used by females for calving and during post-parturition (Leptich and Gilbert 1986, Addison et al. 1990, McGraw et al. 2012) but have generally agreed that females tradeoff forage for predator avoidance (Bowyer et al. 1999, Testa et al. 2000*b*, Severud et al. 2019). However, there is risk to either movement or remaining cryptic (Lima and Dill 1990). Peak energetic demands for females due to lactation occur 21–31 days postpartum (Schwartz and Renecker 2007), which coincides with the highest hazard calves experienced. This suggests females seeking high quality or quantities of forage to meet this demand may be traveling in areas that expose their young calves to greater risk of predation, or that the movement itself increases that risk (Lima and Dill 1990, Frair et al. 2007). Once the female and calf begin moving from the calving site, the likelihood of calves being preyed upon increases because the foraging female frequently leaves the calf bedded (Bubenik 2007). Our proximity data corroborate this; calves spent more time away from mothers as summer progressed, coincident with weaning and calves incorporating more forage into their diets.

Calves slipped their collars at a high rate in 2014 and to a lesser degree in 2013. In all 4 years of the study, we were able to assess calf survival over winter using helicopter survey flights. Proximity data showed close association of mothers and calves throughout winter (indicating we were likely to see calves during surveys); however, 1 calf did survive after being separated from its mother and twin. Although surveys yielded coarse survival estimates, the exact timing of mortality, cause, and initial litter size were unknown in many cases. We treated lone adult females that made a calving movement the previous spring as losing a single calf, resulting in 2015 survival estimates that are likely biased.

In 2013 and 2014, we conservatively removed 20 neonates from the survival analyses because of capture-related mortality or abandonment. In some cases (e.g., calf not nursing), the neonate was unlikely to survive in the absence of collaring activities. In other cases, capture and handling more likely caused (e.g., mother trampling calf) or contributed to mortality (e.g., abandonment). Capture-induced abandonment is poorly understood, but there is evidence that more viable calves (i.e., those that moved farther from capture-sites post-handling) were less likely to be abandoned (DelGiudice et al. 2015, 2018). Removing these 20 individuals likely biased our survival rates high. Including these calves as individuals likely to succumb to other sources of mortality (compensatory mortality) yielded slightly lower survival estimates. Another potential bias arises because our 2013 cohort was largely captured and handled early in the calving season and may not be representative of all calves.

Calving movements were a reliable method for identifying calving in all 4 years of the study. Use of this behavior, coupled with specific locations of females and their calves from GPS collars, allowed us to efficiently locate neonates for capture, estimate timing of births, investigate calving sites, and monitor in near real-time calf survival, movements, proximity to females, and post-parturition habitat use. Furthermore, mortality movements by females have shown much promise in determining the timing and cause of death of uncollared calves (Obermoller et al. 2019). These indirect methods can be used to answer questions relative to management but still leave others unanswered (e.g., twinning rates, more certain cause-specific mortality information throughout the year). Additionally, these non-invasive methods (relative to calves) still required GPS-collaring of adult females. Using GPS collars on calves to estimate survival and cause-specific mortality was far superior to using movement to infer neonatal status. Examining capture-induced abandonment, non-predation mortalities, and fine-scale habitat use were all greatly facilitated using GPS calf collars.

Neonatal ungulate survival can dramatically influence population dynamics (Gaillard et al. 1998, 2000; Unsworth et al. 1999; Raithel et al. 2007). Calf survival to 30 days has been consistently low in northeastern Minnesota. In 2015 and 2016, without GPS collars on calves, survival of twins may have been overestimated because females rarely made the mortality movement with a surviving calf present. Yet, our annual survival estimates were similar for all years (2013–2016), ranging between 29% and 40% (with some bias and imprecision, see above), perhaps more stable than reported for juveniles in other ungulate studies but low (Gaillard et al. 1998, 2000; Raithel et al. 2007; Keech et al. 2011; Patterson et al. 2013). Annual adult survival, 81−88% during the same interval, was moderately depressed and less variable (Carstensen et al. 2018). These demographic rates likely account for the poor performance, but recent stability, of this depressed population (ArchMiller et al. 2018, DelGiudice 2018).

Lastly, we note that although the Kaplan–Meier estimator is by far the most popular method for estimating survival in wildlife studies, an advantage of our daily survival modeling approach is that it provides more realistic, smooth hazard and survival curves (Fieberg and DelGiudice 2009). Our Kaplan–Meier plot shows constant survival from 50 to 100 days of age, but this result is likely due to sample size limitations. Similarly, the Kaplan–Meier estimator is overly sensitive to a few deaths when sample sizes decrease (DelGiudice et al. 2006), as occurred at the end of our time scale. In addition to providing more informative summaries of changes in calf survival as individuals age, smoothing, as allowed for in our survival models, tends to increase precision when faced with small sample sizes (Fieberg and DelGiudice 2011).

As of publication, the executive order that barred collaring moose in Minnesota continues to be in effect. Northeastern Minnesota's moose population, although recently showing signs of stabilization, is still markedly diminished compared to 2006 (ArchMiller et al. 2018, DelGiudice 2018). Northwestern Minnesota's population exhibited similar intermittent short-term intervals of apparent stability before ultimately becoming functionally extirpated (Murray et al. 2006, Lenarz 2007). We made strides in gleaning information about calves indirectly from GPS-collared adults. Placement of collars on free-ranging animals is still a critical tool in the wildlife biologist's armamentarium. Without the advantages afforded by GPS-collaring neonates and their mothers, our understanding of the specific mechanisms most responsible for population changes will be limited.

MANAGEMENT IMPLICATIONS

Predator control has often been invoked as a management strategy to increase ungulate populations. In this case, we observed high rates of predation on calves, yet underlying health issues for adults at the population level are still evident, so it is unclear if predator reduction would result in overall population growth. Wolves are currently state- and federally protected in Minnesota. The other major predator of calves that could possibly be managed at lower densities is the black bear, yet the effect of bears on calf survival was minimal compared to wolves.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.