The Journal of Wildlife Management 83(4):790–800; 2019; DOI: 10.1002/jwmg.21658

Featured Article

Maternal Behavior Indicates Survival and Cause-Specific Mortality of Moose Calves

TYLER R. OBERMOLLER,[1,2] *Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, 2003 Upper Buford Circle, Suite 135, Saint Paul, MN 55108, USA*

GLENN D. DELGIUDICE, *Forest Wildlife Populations and Research Group, Minnesota Department of Natural Resources, 5463 West Broadway Avenue, Forest Lake, MN 55025, USA*

WILLIAM J. SEVERUD, *Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, 2003 Upper Buford Circle, Suite 135, Saint Paul, MN 55108, USA*

ABSTRACT Continuing research on cause-specific mortality and annual survival of moose (*Alces alces*) calves in northeastern Minnesota, USA, is important to understanding the long-term trajectory of the population. In 2013 and 2014, we observed global positioning system (GPS)-collared, female moose exhibit a specific behavior (i.e., mortality movement) associated with the death of their GPS-collared neonate. The females made a rapid, long-distance movement (flee), followed by a return to the calf mortality site. We used characteristics of this movement in 2013–2014 ($n = 46$) to develop models for assessing calf survival, and then evaluated these models using female movement rates ($n = 49$) in 2015–2016. Using this behavior as an indicator of calf mortality in 2016, we conducted field investigations, leading to evidence of 15 mortalities at a mean age of 30.6 ± 15.5 (SE) days (range = 3–243 days). We launched 21 investigations in response to a mortality movement and they resulted in confirmation of 11 of the 15 calf mortalities. Specific causes of mortality included 9 wolf (*Canis lupus*)-kills, 3 black bear (*Ursus americanus*)-kills, 1 unknown predator-kill, and 2 deaths following vehicle collisions. The mean distance females fled after a mortality was 1,873 ± 412 m (range = 126–5,805 m, $n = 14$). Females that made return visits returned a mean 2.8 ± 0.5 times (range = 1–5, $n = 8$) to within a mean 106 ± 22 m (range = 34–230 m, $n = 8$) of the mortality site. Calf survival to 30 days of age was 67 ± 8% (95% CI = 53–84%, $n = 36$) but declined to 53 ± 8% (95% CI = 39–72%, $n = 36$) by 3 months of age. We developed 2 population-level movement models to improve the efficacy of using the mortality movement to identify and locate calf mortalities in real time via field investigations. The first approach, a temporal-based model, used a 3-day average movement velocity threshold (118 m/hr) for all females to indicate calf mortality and accurately predicted survival status in 51% ($n = 105$) of the cases. The second approach, an age-specific model using different thresholds (28–135 m/hr) for females relative to calf age, was 80% ($n = 231$) accurate. Using movement behavior of females to assess calf mortality yielded important insights into mechanisms influencing the population decline that will inform future management decisions. © 2019 The Wildlife Society.

KEY WORDS *Alces alces*, animal movement, behavior, calf, moose, mortality, neonates.

The near disappearance of moose (*Alces alces*) in northwestern Minnesota, USA, since the mid-1980s and a decline of the state's northeastern population since 2006 (Murray et al. 2006; Lenarz et al. 2009, 2010; DelGiudice 2016) prompted the Minnesota Department of Natural Resources (MNDNR) to launch companion studies of survival and cause-specific mortality of adults and calves using global positioning system (GPS)-collar technology (Carstensen et al. 2015, Severud et al. 2015*a*). Earlier work (2002–2008) in northeastern Minnesota, relying on very high frequency (VHF) telemetry, concentrated on adult moose survival, whereas GPS collars used in the more recent studies facilitated more expeditious investigations of causes of adult and calf mortalities (Butler et al. 2013; Carstensen et al. 2014, 2015; Severud et al. 2015*a*).

Ungulate calves are particularly vulnerable to predation during their first few months of life because of their limited mobility (Franzmann et al. 1980, Barber-Meyer et al. 2008, Carstensen et al. 2009, Keech et al. 2011, Patterson et al. 2013). Little had been known about survival and cause-specific mortality of moose calves in northeastern Minnesota, but Severud et al. (2015*b*) recently reported that 50% ($n = 17$) of GPS-collared neonates died within 50 days of birth. Most of these calves were killed by wolves (*Canis lupus*) and black bears (*Ursus americanus*). Other studies elsewhere in North America have reported similar findings

Received: 5 January 2018; Accepted: 8 January 2019

---

[1] *E-mail: Tyler.Obermoller@state.mn.us*

[2] *Present Address: Farmland Wildlife Populations and Research Group, Minnesota Department of Natural Resources, 35365 800th Avenue, Madelia, MN 56062, USA.*

(Ballard et al. 1981, Osborne et al. 1991, Keech et al. 2011, Patterson et al. 2013). Wolves may prey on calves throughout the entire year, whereas bears have their greatest effect closer to parturition when the calves are less mobile (Mech 1966, Peterson 1977, DelGiudice et al. 2009, Patterson et al. 2013, Basille et al. 2015).

A primary objective of the overall moose calf study initiated by the MNDNR in 2013 was to assess annual variation of cause-specific mortality over 4 years. However, capture-induced abandonment in 2013 and 2014 (DelGiudice et al. 2015, 2017) and capture-related mortality of adult moose in the companion study during winter 2014–2015 (Carstensen et al. 2017) resulted in a governor's executive order prohibiting additional capturing and collaring of moose. Consequently, since 2015, calf research continued without the benefit of neonates fitted with GPS collars (Severud et al. 2015*a,b*). In 2015, we monitored the remaining adult females with functioning GPS collars for calving activity (i.e., calving movement), and subsequently for a mortality movement (Severud et al. 2015*a,b*). A mortality movement is a maternal behavior described as a sudden long-distance movement (i.e., flee) from the mortality site of its calf, followed by ≥1 return to the origin of the flee (Fig. 1; Obermoller et al. 2017).

Many studies have examined ungulate movements to better understand forage selection (Johnson 2002), predation (Testa et al. 2000, Laundré 2010, Balogh 2012), and adult survival (Kunkel and Pletscher 2000, Johnsen 2013, Carstensen et al. 2015). But few studies have reported on maternal movement behavior relative to neonatal survival (Testa et al. 2000, DeMars et al. 2013). Ungulate females have exhibited foraging behaviors that may help them avoid detection by predators and prolong survival of their young (Bergman et al. 2006, Kittle et al. 2008, Basille et al. 2015), which increases their probability of being recruited into the population. Female moose in British Columbia, Canada, selected calving sites with reduced forage, but effective hiding cover, in an apparent effort to reduce the risk of predation (Poole et al. 2007). However, as females approach peak lactation at 21–31 days post-parturition, the importance of locating abundant quality forage to fulfill heightened energetic demands increases relative to predator avoidance (Reese and Robbins 1994, Bowyer et al. 1999, Schwartz and Renecker 2007). Females and their neonates remain at their calving sites for ≤14 days and the risk of predation increases markedly once they depart from those sites in search of more plentiful forage (Gustine et al. 2006, Bubenik 2007, Pinard et al. 2012, McGraw et al. 2014, Severud 2017).

Moose calves exhibit a hider strategy while at the calving site but increasingly become followers after departing the calving site (Altmann 1956, Geist 1966, Espmark 1969, Geist and Walther 1974). Severud (2017) reported a median monthly female-calf proximity of 67 m during the first year of life, but it varied by season. These females increased their movements with calf age, corroborating moose calves adopting follower tendencies. In contrast, caribou (*Rangifer tarandus*) neonates immediately exhibit a following strategy, which fosters greater confidence in using female movements to assess calf survival shortly after birth (Geist and Walther 1974).

Female moose with young calves-at-heel notably reduce their movements, which helps to identify individuals with and without calves (Testa et al. 2000, McLaren et al. 2017). Preliminary evidence suggests that changes in velocity of

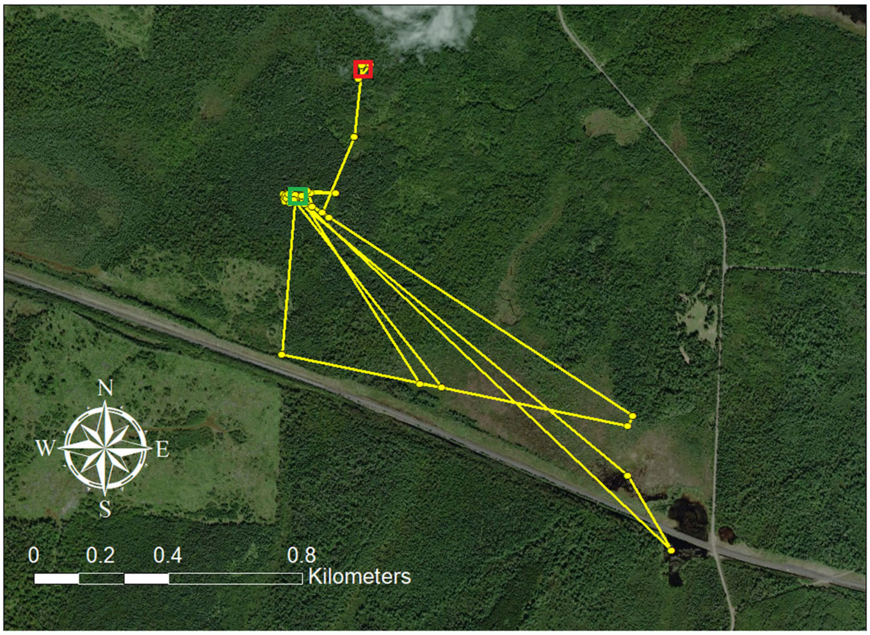

Figure 1. Movements of female moose number 13778 in northeastern Minnesota, USA, 5–11 May 2016. The green and red squares represent the beginning and end of the temporal interval, respectively. The female's movements show flees and return visits to the green square; a calf mortality occurred on 5 May 2016. This female made 3 return visits before leaving the area. At the mortality site, we found 3 wolf scats, which contained calf hair, teeth, vertebrae, and other bone fragments. The estimated age at mortality was 2.7 days.

ungulate females can lead to important inferences about neonate survival (Testa et al. 2000, DeMars et al. 2013, Nobert et al. 2016). Upon losing a calf, a female's movements may increase by up to 12% (Testa et al. 2000). In studying caribou neonate mortality, DeMars et al. (2013) applied a movement velocity threshold (using a 3-day average) to all females. When a female's velocity exceeded 186.5 m/hour, they presumed her calf was dead; normal movements resumed afterward. These authors correctly determined the survival status of 73% of the calves up to 4 weeks old. They also applied the mortality threshold to each female using an individual-based model (IBM) and correctly identified survival status for 87% of the calves up to 4 weeks old. Moose neonates localize at their calving sites after birth; consequently, an IBM would not be suitable because the female's movements may vary markedly but not directly related to their neonate(s) while they are bedded. This may lead to false positives, reducing the ability to determine survival and cause-specific mortality. We predicted a mortality threshold based on our 2013–2014 cohort movement data (rather than an IBM) was best to accomplish our objectives.

Our goal was to improve our understanding of maternal movement patterns relative to survival and cause-specific mortality of moose calves. Our objectives were to quantify the temporal and spatial aspects of 2013–2014 and 2014–2015 movement data of GPS-collared females relative to known mortalities of their GPS-collared calves; develop models to identify the occurrence of calf mortalities in real time during 2016–2017; and test these models by identifying, locating, and assigning cause of death by field investigation. We predicted that cause-specific mortality of calves could be determined via velocity changes of females and adjusting baseline velocities by calf age would increase our ability to determine calf mortality status. Twin status may influence the ability of our models to determine calf mortality, but low sample size did not allow us to evaluate this covariate.

STUDY AREA

We conducted this study during May 2016–April 2017; the 6,068-km^2 study area was located between 47°06′N and 47°58′N latitude and 90°04′W and 92°17′W longitude in the Northern Superior Upland (NSU) section of northeastern Minnesota (MNDNR 2015; Fig. 2). The study area is comprised largely of the Superior National Forest intermixed with state, county, and private lands. Upland forests consisted largely of trembling aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), and conifers that included balsam fir (*Abies balsamea*), jack pine (*Pinus banksiana*), and red pine (*P. resinosa*). Sugar maple (*Acer saccharum*), white pine (*P. strobus*), and yellow birch (*B. alleghaniensis*) occurred on the highlands near Lake Superior. Peatlands, including black spruce (*Picea mariana*), northern white cedar (*Thuja occidentalis*), and tamarack (*Larix laricina*), were widespread across this region. The NSU was formed by glacially weathered terrain, creating till and outwash plains, and abundant lakes. Rugged topography of cliffs and bedrock outcrops are common, but elevation is limited between 200 m and 650 m above sea level. Wolves and black bears were the primary predators of moose calves (Franzmann et al. 1980, Keech et al. 2011, Patterson et al. 2013, Severud et al. 2015*a*). Average wolf and bear densities were 3–4/100 km^2 and 23/100 km^2, respectively, across northern Minnesota and the study area (Garshelis and Noyce 2011, Erb and Sampson 2013, Mech

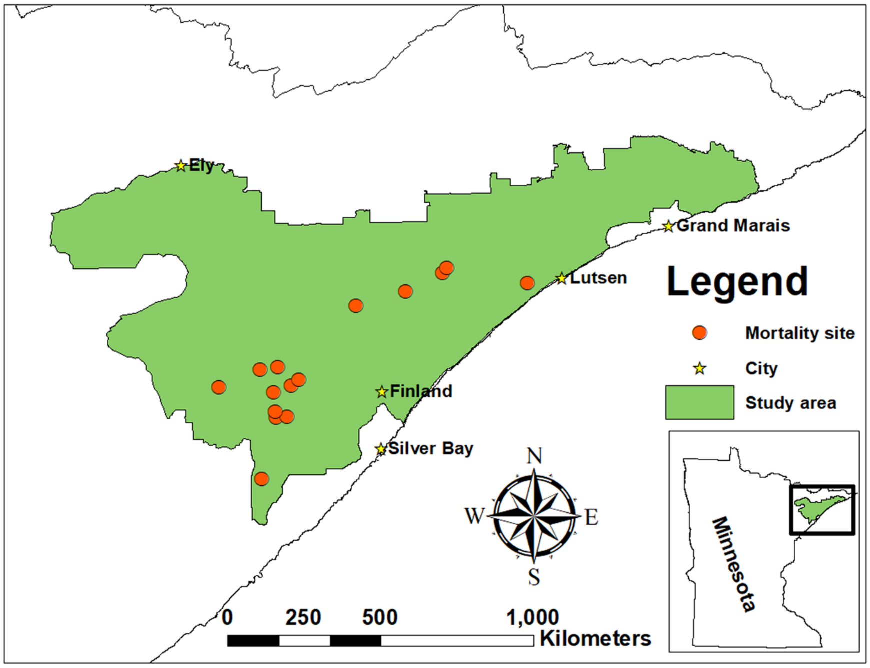

Figure 2. Moose calf study area (6,068 km^2) for examining survival and cause-specific mortality in northeastern Minnesota, USA. Solid orange circles depict mortality sites ($n = 15$) of calves during May 2016–January 2017.

et al. 2018). White-tailed deer (*Odocoileus virginianus*) were managed at pre-fawning densities of ≤4/km^2, and were the main prey of wolves (Nelson and Mech 1981, DelGiudice et al. 2002, MNDNR 2011). Mean daily maximum and minimum temperatures ranged from 0.6°C to 37.2°C and −5.6°C to 23.3°C, respectively, during May to August 2000–2015 at Ely, Minnesota, and from 2.2°C to 35.2°C and −5.6°C to 20.6°C at Grand Marias, Minnesota (Midwestern Regional Climate Center 2015).

METHODS

Monitoring GPS-Collared Females and Calves

Crews captured adult moose (129 females and 51 males) and fitted them with GPS collars (Vectronic Aerospace GmbH, Berlin, Germany) in winters 2013–2015 as part of a companion study examining survival and cause-specific mortality in northeastern Minnesota (Butler et al. 2013; Carstensen et al. 2014, 2015). The mean linear error of adult GPS collars was 3.7 ± 0.3 (SE) m (range = 0–17 m) and 7.0 ± 0.3 m (range = 1–36 m) under open and dense (>80%) canopy closure, respectively (Severud et al. 2015*a*, 2017). These collars were programmed to record a GPS location (fix) every hour from May to June, then resumed a schedule of 1 fix every 4 hours. We monitored these females for evidence of a calving movement during 2013−2016 (McGraw et al. 2014, Severud et al. 2015*a*).

In 2013 and 2014, we captured and fitted 74 neonates from 50 GPS-collared adult females with GPS collars (GPS Plus Vertex Survey-1 Globalstatr with mortality accelerometers; Vectronic Aerospace GmbH) to monitor survival and cause-specific mortality (Severud et al. 2015*a,b*). The collars logged hourly locations and transmitted every third successful fix. Collars entered mortality mode following 6 hours of limited motion. A notification was then transmitted to our base station, followed by a short message service (SMS) text and e-mail notification to field staff. After censoring calves because of collar slippage and capture-induced abandonment or mortality during 2013 and 2014, 49 calves were available to monitor cause-specific mortality (DelGiudice et al. 2015, 2017; Severud et al. 2015*a,b*). Beginning in 2015, calves were no longer fitted with GPS collars (Severud et al. 2015*a,b*), but we monitored 60 GPS-collared adult females for calving activity; 50 made movements indicative of calving. We monitored those 50 for movements indicative of calf mortality (Severud et al. 2015*a*, Severud 2017). Because of natural mortalities, malfunctioning GPS collars, and battery expiration, 35 females with functioning GPS collars were available for computer monitoring during the 2016 calving season. Twenty-three female collars were programmed to record a location every 4 hours and transmit them to our base station after 6 successful fixes. The remaining 12 collars were locked in mortality mode, programmed to take locations every hour and transmit them after 11 successful fixes. The mean fix success rate of GPS collars recording a fix every 1 hour was 95 ± 3% (range = 62–99%, *n* = 11) and 97 ± 1% (range = 78–100%, *n* = 19) for those recording a fix every 4 hours. The fix rate (i.e., 1 hr or 4 hr per location) did not appear to influence detection of survival status; 7 of 11 and 13 of 18 were correctly identified for 1 hour and 4 hours per location, respectively. In 2016, we remotely monitored the females to detect mortality events and then dispatched a team to conduct field investigations for confirmation. We used GPS-collared females of non-surviving (*n* = 26) and surviving calves (*n* = 23) from 2013 and 2014 to develop models because fate dates and causes of mortality were known (Severud 2015*a,b*; Severud 2017). We used movements of females of non-surviving (*n* = 24) and surviving calves (*n* = 32) of 2015 and 2016 to evaluate the reliability of our models to accurately determine survival status.

In early May of each year, we began monitoring all adult females for a calving movement, which is a long distance movement followed by a localization (~5–10-m diameter; McGraw et al. 2014, Severud et al. 2015*a*, Obermoller et al. 2017). Automated reports highlighting calving movements were generated twice daily based on 1- and 4-hour fix-rates for each adult female (Severud et al. 2015*a*, Obermoller et al. 2017). In spring 2016, we verified calving by examining the calving site for calf presence (e.g., tracks, pellets, hair) or evidence of birth (e.g., scrape in the earth, afterbirth) after the female left the area to minimize any risk of disturbance. In a few cases, calf presence was confirmed by a public-reported observation (often with photographs), follow-up camera traps, or by searching a subsequent localization. Following verification of a calf by 1 of these methods, we monitored each female's locations daily for a mortality movement (Fig. 1).

We first observed uncharacterized movements of females associated with mortalities of GPS-collared calves during 2013 and 2014, but we did not examine these movements for their utility as an indicator of calf mortality until 2015 (Severud et al. 2015*b*). Their reliability for this purpose appeared to be greatly diminished after calves were 3 weeks old. Subsequently, we began to examine these movements to ascertain whether discernible patterns indicative of calf mortality could be used to develop a more reliable monitoring approach for the 2016 field season. We calculated the distance the female fled following a calf mortality, the number of times she returned to the mortality site (return visits), her distance from the mortality site once returned, and the time between the initial flee and return to the mortality site. We also used distance of the fleeing female to water as supporting evidence of a calf mortality (based on observations from 2013 and 2014); if the flee ended near water, the probability of a mortality was lower. Beginning with the 2016 calving season (Apr–Jun), we conducted daily close computer monitoring of each female for movement patterns indicative of mortality. We did not conduct field investigations immediately following the initial flee and return so as not to risk influencing female movements. We considered the female's current location to decide when best to investigate.

At the presumed mortality site, determined by the mortality movement, a 3–4-person team searched the immediate area for sign of a calf mortality. If no evidence was readily apparent, we expanded our search to more efficiently and thoroughly cover the surrounding vicinity. One person carried a handheld GPS unit and hiked in each cardinal direction; the other team members spaced themselves in 10-m intervals to the right of the first person. We hiked for about 200 m, returned to the origin, and repeated the process in the remaining cardinal directions. Because of various factors (e.g., calf age, land cover type, topographical limitations, lack of female or calf sign), we adjusted our search area as needed. We looked for carcass remains, sign of a specific predator (e.g., tracks, scat, hair, feeding patterns), and other site evidence (e.g., broken vegetation, blood sprays) to aid in assigning the cause of death. Evidence indicative of a bear-kill included cached body parts, peeled or inverted hide, selective feeding on viscera or sensory organs, and claw marks across the body, whereas a wolf-kill was indicated by long bones chewed on the ends, presence of rumen and its contents, scattered remains over a large area, and puncture wounds on the head, neck, or hindquarters when present (Ballard et al. 1979, Franzmann et al. 1980). If we could not assign the cause of mortality to a specific predator, we sent scat and swab samples for hair or DNA analysis (T. D. Gable, Voyageurs National Park; K. L. Pilgrim, National Genomics Center for Wildlife and Fish Conservation).

We used the aforementioned information to assign a specific cause of death. Because litter size at birth was unknown, following a mortality or apparent mortality movement we performed survival investigations to determine whether the female lost 1 or 2 calves or retained a surviving twin. We executed these investigations by heading to areas where the female had localized following the presumed or confirmed calf mortality. We opportunistically placed camera traps in areas the female frequently used to attempt to capture evidence of an accompanying calf.

We conducted survey flights on 17–18 January 2017 and 19 April 2017 from a Bell Jet Ranger helicopter (OH-58; Bell Helicopter, Fort Worth, TX, USA) to locate all adult females with functioning GPS collars to determine 8-month and near-annual (recruitment) calf survival, respectively. This also allowed us to evaluate the success of our mortality and survival investigations during the previous summer. We determined success relative to our predetermined expectation of whether each adult female had a surviving calf or not, based on their movements post-calving. In cases where the female was not located, we searched for 15 minutes before moving on to the next animal. Ultimately, we monitored and assessed calf status of adult females via calf survival investigations, mortality investigations, and movement rates.

Movement Models and Analysis

Temporal-based model.—We analyzed temporal and spatial aspects of movement patterns of GPS-collared females with GPS-collared calves that died of known causes (e.g., wolf or bear predation) in 2013 and 2014 to determine characteristics indicative of calf mortality and aid in identifying mortalities in 2015 and 2016. Following DeMars et al. (2013), we applied a calf-loss movement threshold to the females; if the threshold was exceeded, we presumed the calf was dead. We assessed calf mortalities up to 3 months of age. Beyond that age, sample size of known mortalities were too small to evaluate the movement models. Nearly all calf mortalities occurred during the first 3 months of age (Ballard et al. 1981, Keech et al. 2011, Patterson et al. 2013, Severud et al. 2015*a*). The initial *post hoc* approach was the temporal-based model (TBM; DeMars et al. 2013); we examined different temporal (e.g., 4 hr, 24 hr, 72 hr) velocity (m/hr) thresholds to determine which had the highest success in determining calf loss.

We excluded the top 1% of velocities before calculating the moving average to increase overall sensitivity; we considered these movements to be atypical, perhaps caused by human or predator disturbance (DeMars et al. 2013). We developed a moving average function to calculate mean velocity over a specified window (i.e., 24 hr); data from females with varying fix rates (e.g., 1 hr or 4 hr) were not affected, because the specified window was based on duration, not the number of locations. We also found no difference in survival status relative to fix rates.

The calf loss movement threshold incorporated the movements of all individual females with a surviving calf or calves into an empirical distribution. To characterize movements of females with live calves, we used movement rates between estimated calf birth dates and 7 days before estimated calf mortality date to ensure velocities were not affected by factors immediately leading up to the mortality event. We also included movement rates of females with surviving calves between birth date and 7 days before collar removal or slippage. We converted the empirical distribution into a kernel density estimate and then into a cumulative distribution function (Fig. 3), the proportion of velocities above or below a given rate (DeMars et al. 2013). Unlike DeMars et al. (2013), we used the 100% quantile of the cumulative distribution function to obtain the maximum velocity and avoid a false negative (i.e., assigning a calf mortality status as alive when true status is dead). Rates above this threshold were indicative of calf mortality.

Age-specific model (ASM).—We developed different thresholds for the ASM to account for increasing calf mobility relative to age and season. We subsampled the 2013–2014 training set into 5 calf age groups: 1) 0–2 weeks, 2) >2–4 weeks, 3) >1–3 months, 4) >3–6 months, and 5) >6–12 months. We again examined the different temporal (e.g., 4 hr, 24 hr, 72 hr) velocity (m/hr) thresholds to determine which had the highest success in determining calf loss; we found the 72-hour moving window correctly identified the status of the most calves. We obtained a movement threshold by the same means as the TBM model but for each age group (e.g., 2–4 weeks). Because of lack of mortality events at older ages, we were unable to evaluate mortality beyond 3 months; however, we identify the older thresholds because some calves survived well beyond that age.

We assessed model success for TBM and ASM models by calculating true positives (proportion of calves correctly identified as having died within 7 days of the estimated mortality date), true negatives (proportion of calves correctly

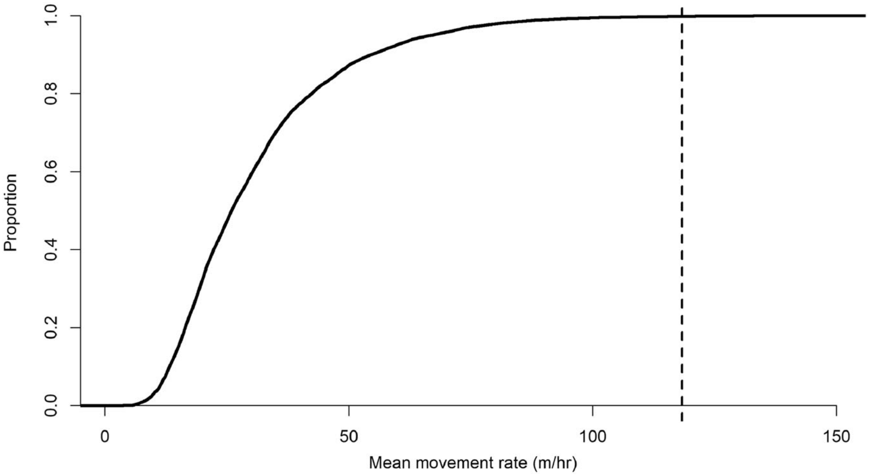

Figure 3. Cumulative distribution function of movement velocities of moose females ($n = 45$) with surviving calves, developed to determine the velocity threshold indicative of calf survival for the temporal-based model, northeastern Minnesota, USA, May 2016–January 2017. Vertical dashed line represents the 72-hour calf loss movement threshold at the maximum value (100% quantile).

identified as survived), and accuracy (overall proportion of calf status correctly identified). We used a 1-way analysis of variance to test whether velocities differed based on the survival status of a calf. We calculated Kaplan–Meier survival using the package KMsurv (Klein and Moeschberger 2005). We conducted all analyses with R version 3.2.5 (R Core Team 2017). Tests were significant at $\alpha \leq 0.05$.

RESULTS

Monitoring Mortality Movements

In 2016, we launched 21 field investigations and confirmed 11 of 15 calf mortalities associated with a female mortality movement. We also documented 4 additional calf mortalities investigated without an observable mortality movement; we investigated 3, because the females made a long-distance flee, but with no return to the presumed mortality site while the calf was very young and sedentary (i.e., female movements should be reduced if the neonatal calf was still at heel). The fourth was a vehicle collision reported by the public. Mean distance from the calving to mortality site was 932 ± 357 m (range = 0–3,500 m, $n = 13$). Four of 13 calves were killed at or near (<50 m) the calving site. Mean response time (time between the initial mortality movement and field investigation) following a mortality was 6.1 ± 1.4 days (range = 1–19 days, $n = 13$). Mean distance females fled from a mortality was 1,873 ± 412 m (range = 126–5,805 m, $n = 14$). The time between when females made the initial flee and return to the mortality site was an average 25.9 ± 6.2 hours (range = 4–72 hr, $n = 10$); all subsequent flee and return-trip times were similar. Females that made return visits to the mortality site returned a mean 2.8 ± 0.5 times (range = 1–5, $n = 8$). Once returned, females were within a mean 107 ± 22 m (34–230 m, $n = 7$) from the mortality site. Only 1 of 4 females made return visits to the mortality site when there was a surviving twin (confirmed via survival investigations and helicopter flights). Based on a preponderance of evidence at each mortality site, we recorded 9 wolf-kills, 3 bear-kills, 1 unknown predator-kill, and 2 deaths following a possible vehicle collision. We also observed 5 cases where females made an apparent mortality movement, but we did not observe evidence of calf mortality; winter survey flights confirmed these calves had been lost. The females' behaviors (increased movements) following the mortality movement indicated a calf or calves had been lost, but either we did not locate evidence during the investigation or the mortality occurred beyond the searched area. The 30-day calf Kaplan–Meier survival rate was 67 ± 8% (95% CI = 53–84%, $n = 36$). At the end of summer, 3-month survival was 53 ± 8% (95% CI = 39–72%, $n = 36$).

We observed a change in the mean velocity of females 72 hours before and after the calf mortality date ($F_{1,24} = 16.63$, $P \leq 0.001$). Velocities before and after calf mortality were 30.1 ± 9.5 m/hour (range = 2–125 m/hr, $n = 13$) and 142.0 ± 25.7 m/hour (range = 8–315 m/hr, $n = 13$), respectively. Winter survey flights confirmed these calves were no longer with their females and presumed dead. Furthermore, during the flights we noted 4 calves had been lost, but we had not previously observed a mortality movement.

Temporal-Based Model

We calculated 3 different velocity thresholds of females to indicate mortality. The 4-, 24-, and 72-hour thresholds were 342 m/hour, 164 m/hour, and 118 m/hour, respectively (Table 1). The 72-hour threshold identified 23 of 49 (47%), 15 of 30 (50%), and 16 of 26 (62%) calf mortalities in 2013–2014, 2015, and 2016, respectively (Table 1). The ability of the model to predict survival status during all years (2013–2016) was highest for the 72-hour threshold (Table 1). We detected 3 of 4 mortality events in 2013–2014 when females of twins retained a surviving calf but detected only 1 of those 4 within 7 days of the mortality event. Similarly, in 2016, we detected only 1 of 3 of these events within 7 days when a twin survived; we did not observe any confirmed twins associated with mortality events in 2015. The 4-hour moving window resulted in the

Table 1. Temporal-based model performance test of true positives (proportion of calf mortalities correctly identified), true negatives (proportion of calf survivors correctly identified), and accuracy (overall proportion of calves with survival status correctly identified) to determine moose calf mortality in northeastern Minnesota, USA, 2013–2016. Average moving windows used were 4 hours, 24 hours, and 72 hours. Velocities above these thresholds were indicative of calf mortality.

Performance test	Year	*n*	4-hr (342 m/hr)	24-hr (164 m/hr)	72-hr (118 m/hr)
True positives	2013–2014	49	0.58	0.42	0.23
	2015	30	0.82	0.55	0.45
	2016	26	0.62	0.62	0.54
True negatives	2013–2014	49	0.43	0.57	0.74
	2015	30	0.00	0.21	0.53
	2016	26	0.31	0.46	0.69
Accuracy	2013–2014	49	0.51	0.49	0.47
	2015	30	0.30	0.33	0.50
	2016	26	0.46	0.54	0.62

highest proportion of true positives but performed poorly in identifying true negatives (Table 1).

ASM

The mean velocity before rarefying the data (i.e., excluding top 1% of velocities) for all years (2013–2016) by age group was as follows: 42 ± 11 m/hour (range = 3–960 m/hr, *n* = 87) for 0–2 weeks, 52 ± 10 m/hour (range = 7–633 m/hr, *n* = 62) for 2–4 weeks, 106 ± 31 m/hour (range = 5–1,417 m/hr, *n* = 52) for 1–3 months, 46 ± 2 m/hour (range = 27–88 m/hr, *n* = 37) for 3–6 months, and 56 ± 31 m/hour (range = 9–1,062 m/hr, *n* = 34) for 6–12 months.

The female velocity threshold using the 72-hour window, 0–2-week-age threshold was 28 m/hour (*n* = 45), and then increased to 66 m/hour (*n* = 28) during 2–4 weeks. The 1–3-month subset increased to 135 m/hour (*n* = 19). The 3–6-month threshold was 109 m/hour (*n* = 10) and the >6–12-month threshold was 30 m/hour (*n* = 9), but we were unable to evaluate these thresholds because of low sample size. The model most accurately predicted survival status for 2–4 weeks (Table 2). The model performed similarly well for 0–2-week age group with an overall accuracy for survival status of 73–93% in 2013–2016 (Table 2). The model did not perform as well for the 1–3-month age group (Table 2). Accuracy for all age groups combined was 79%, 84%, and 73% in 2013–2014, 2015, and 2016, respectively (Table 2). The overall accuracy with 2013–2016 data pooled was 80% (*n* = 48). The success rate of detecting calf mortalities with a surviving twin was similar to the TBM.

Table 2. Age-specific model performance test of true positives (proportion of calf mortalities correctly identified), true negatives (proportion of calf survivors correctly identified), and accuracy (overall proportion of calves with survival status correctly identified) to determine moose calf mortality in northeastern Minnesota, USA, 2013–2016. The average moving window was 72 hours with the following age groups: 0–2 weeks, >2–4 weeks, and >1–3 months. Velocities above these thresholds were indicative of calf mortality.

Performance test	Year	*n*	0–2 weeks (107 m/hr)	>2–4 weeks (117 m/hr)	>1–3 months (196 m/hr)	Overall
True positives	2013–2014	24	0.67	0.63	0.57	0.63
	2015	11	1.00	1.00	0.50	0.91
	2016	13	0.67		0.75	0.69
True negatives	2013–2014	24	0.78	0.89	0.94	0.84
	2015	11	0.92	0.86	0.68	0.83
	2016	13	0.77	0.77	0.67	0.74
Accuracy	2013–2014	24	0.76	0.83	0.83	0.79
	2015	11	0.93	0.88	0.67	0.84
	2016	13	0.73	0.77	0.69	0.73

DISCUSSION

The approach we developed for monitoring the survival status of moose calves without GPS (or VHF) collars improves upon an earlier approach using female movements reported by Severud et al. (2015*b*). Those authors reported a 36% confirmation rate of detecting mortalities of neonates up to about 3 weeks old. Identifying mortalities beyond this age became increasingly difficult because of increased velocities of female-calf pairs. In 2016, we increased our success of locating calf deaths to 53% up to 3 months of age using the mortality movement. This was likely attributable to more thorough searches (systematic vs. haphazard) for evidence of calf mortalities, closer computer monitoring, and analysis of female movement characteristics associated with previous known mortalities of GPS-collared calves (e.g., flee distance, return distance). We also launched mortality investigations within the first few weeks of neonate life when their mobility was typically limited, but females made long (>500–1,000 m) movements away from the presumed mortality site. Young calves were unlikely to make those long-distance movements (Testa et al. 2000), leading us to suspect a calf mortality. Our mean investigative response time was somewhat inflated, particularly when a mortality movement was more immediately evident (<24 hr), because we did not want to disturb the female's behavior and movements by initiating a field investigation too rapidly.

Initially, we conjectured that the mortality movement was a behavioral response to predators chasing the female, but we documented 2 vehicle-kills in 2016 associated with similar female movements. One of these females made the most return visits (5) to the mortality site and stayed with the dead calf the longest (9.2 days) before leaving permanently compared to natural calf mortalities. Others have reported females defending calf carcasses (LeResche 1968, Mech 1998). Most notable, a female defended 2 dead, 9-month old calves for 7–8 days (Mech 1998). Multiple examples suggest females have a maternal instinct that motivates them to return and defend their young even post-mortem.

Along with mortality investigations, fall and winter calf survival flights allowed us to assess the accuracy of mortality determinations based on movement analyses, and provided supplemental data for estimating calf production and recruitment. By way of survival investigations and flights, we recorded 5 cases where a calf mortality-related movement of the female occurred in 2016, with no evidence of a mortality found, but subsequently no calf was present with the female during our flights. We also noted cases where a female with a surviving twin did not make a mortality movement. Locating evidence of a calf mortality during field investigations was frequently difficult; typically, we found only scant calf remains to determine specific causes of mortality.

Generally, our TBM for moose followed the approach of DeMars et al. (2013) to characterize movement behavior of caribou females relative to calf mortality. Our 4-hour moving-average velocity captured a higher proportion of true positives, but a smaller proportion of true negatives (Table 1), because smaller averaged temporal windows were more susceptible to detecting random non-mortality flee events. Longer averaged windows (e.g., 72 hr) smoothed out these non-mortality flees above the mortality movement threshold. More sustained increases in velocity (no longer hindered by limited calf mobility) were required to detect the loss of a calf. This led to a lower proportion of true positives being detected. The DeMars et al. (2013) population-based model performed 22% better for detecting true positives (up to 4 weeks of age) of caribou calves than our similar TBM model (up to 3 months of age), highlighting the importance of evaluating a model relative to species, population, and age before applying it blindly in the field. Overall, our TBM model did not identify moose calf mortalities well for any of the different temporal windows (e.g., 4 hr, 24 hr, 72 hr), because we observed large differences in calf mobility relative to age.

We used the 72-hour temporal window for our ASM because it performed best for both true positives and true negatives. Our ASM performed 29% better than our TBM at predicting moose calf survival during 2013–2016. Changing movement thresholds by age allowed us to adjust for calf mobility, whereas the TBM used all female locations regardless of calf age. Moose neonate mobility up to 2 weeks of age was low. Calves presumably used a hider strategy, remaining localized at the calving site for roughly their first 7 days, then adopted the follower strategy, increasing their movements, and consequently, velocity (Altmann 1956, Geist 1966, Espmark 1969, Geist and Walther 1974). The hider–follower strategies may have in part led to the ASM outperforming the TBM. We observed the highest velocity at 1–3 months of age, which coincided with peak forage availability (Schwartz and Renecker 2007). Moose calf velocity also varied more at that age, which likely contributed to our lower success than at younger ages in predicting calf survival status. Adjusting the mortality movement threshold of the 1–3-month age subset may allow substantially greater success.

Our ASM for moose was similar to the IBM developed for caribou by DeMars et al. (2013), but the ASM model changed the velocity threshold indicative of calf mortality by discrete age groups (e.g., 0–2-week intervals), whereas the IBM changed the same threshold for each female in a continuous fashion as calf age increased. The IBM performed 5% better during the same time period (i.e., 0–4 weeks), and only 7% better overall (i.e., 0–3 months) than our ASM. The IBM for caribou may have performed better than our ASM for moose because of the different survival strategies (e.g., follower vs. hider) of calves of the 2 species. Caribou females with increased movement rates following birth are highly predictive of calf mortality, whereas moose females may flee and leave their calves hidden in thick cover. Also, our study area was heavily forested, which likely made confirming mortalities more difficult.

Calf mortalities were difficult to detect when the female retained a surviving twin. None of the 3 approaches, monitoring for mortality movements, the TBM, nor the ASM, performed well under these circumstances. Females with a surviving twin rarely exhibited the mortality movement but instead took their surviving calf and localized elsewhere, not increasing her velocity above the mortality threshold. Twinning rates of moose vary greatly (15–58%) across North America (Osborne et al. 1991, Keech et al. 2011, Patterson et al. 2013, Severud et al. 2015*a*). Ungulate studies with high twinning rates may find these methods of limited value, although small sample sizes precluded us from thoroughly evaluating this question.

This approach to assessing survival and cause-specific mortality of unmarked calves has limitations and challenges compared to fitting neonates with GPS collars. Without capturing and handling live neonates, we could not determine sex, record morphological measurements, collect blood samples, or assess general health status, which may reveal factors predisposing calves to specific causes of subsequent mortality (Ballard et al. 1979, Carstensen Powell and DelGiudice 2005). Furthermore, upon detecting a mortality movement, follow-up field investigations can be time intensive, partly because it was often difficult to find scant evidence in the field that confirmed a calf mortality. Often, we were unable to obtain location data on these uncollared calves because it was unknown until the fall helicopter survey whether a surviving calf was present.

Generally, GPS-collaring ungulate neonates may be most desirable for collecting survival and cause-specific mortality data, but this approach has not yet been widely used because of collar design and capture-induced abandonment challenges (Ballard et al. 1979, Livezey 1990, DelGiudice et al. 2017, Severud 2017). However, timely identification of calf mortalities via movements of GPS-collared females allowed us to continue, with limitations, our assessments of reproductive and recruitment impacts on the performance of a declining moose population. We obtained valuable cause-specific mortality data from this monitoring that included non-predation mortality events. There were significant expenses associated with GPS-collaring calves, including $1,600 per calf capture and $1,000 per calf collar (G. D. DelGiudice, MNDNR, unpublished data). However, the present method was non-invasive and eliminates the risk of capture-induced abandonment of ungulate neonates (DelGiudice et al. 2015, 2017).

Changes in female movement velocities indicative of calf mortality were observed in caribou, and now in moose; with GPS-collared females, this method could be adapted to other ungulate species as well (DeMars et al. 2013, Obermoller et al. 2017). We increased the monitoring period from DeMars et al. (2013) to determine survival of calves from the first 4 weeks to 3 months of life. We also expanded on this method by determining cause-specific mortality in real time. With an increased sample size of older calves, we believe this technique could monitor calves to recruitment. During analyses, we examined velocities at the population level because a primary objective was to use previous data to detect mortality in real time. The IBM would have hampered fulfillment of our objectives but could prove useful when determining mortality *post hoc* (DeMars et al. 2013, Nobert et al. 2016). An improvement upon these models may include covariates that address distance to water and roads, slope, and canopy closure, most of which were associated with calf survival in this study (Severud et al. 2019).

MANAGEMENT IMPLICATIONS

The decline in Minnesota's moose population has initiated aggressive adult and neonate moose survival studies. Using the mortality movement to detect calf mortalities, we determined 87% of the calf mortalities were related to predators, with wolves accounting for 70% of these mortalities. Predator management may be an effective tool to increase calf survival. However, currently, wolves in Minnesota are federally listed as a threatened species, limiting options for managing wolves in the state. The mortality movement approach we tested for monitoring survival during the most vulnerable period (0–3 months of age) of a moose's life will provide information important to understanding population performance and dynamics and contribute to more informed management decisions.

ACKNOWLEDGMENTS

We thank B. D. Smith, J. L. Goethlich, and R. A. Willaert for their technical contributions to the fieldwork. We appreciate the Wildlife Health Program's (M. Carstensen, M. H. Dexter, E. C. Hildebrand, C. S. Jennelle, and D. M. Plattner) cooperation during the calving season, and J. D. Forester's preparation of the automated calving reports using 4-hour fix rates. We also thank J. H. Giudice and V. St-Louis for their data analysis expertise and M. A. Larson, L. J. Cornicelli, T. W. Arnold, and L. D. Mech for their guidance during this project. We are grateful to R. G. Wright for assistance with the buffered search areas using ArcMap, and L. J. Schmidt for providing microscopes for identifying hair samples. We also thank T. D. Gable and K. L. Pilgrim for hair and DNA analyses. We recognize all the observers who emailed us photos and information on calf sightings, including K. Crowley, J. Greenlee, and J. Hicks. This study was funded in part by the Minnesota Environmental and Natural Resources Trust Fund (ENRTF), the Wildlife Restoration (Pittman-Robertson) Program, and MNDNR Section of Wildlife's Wildlife Populations and Research Unit.

LITERATURE CITED

Altmann, M. 1956. Patterns of social behavior in big game. Transactions of the North American Wildlife Conference 21:538–545.

Ballard, W. B., A. W. Franzmann, K. P. Taylor, T. H. Spraker, C. C. Schwartz, and R. O. Peterson. 1979. Comparison of techniques utilized to determine moose calf mortality in Alaska. Alces 15:362–387.

Ballard, W. B., T. H. Spraker, and K. P. Taylor. 1981. Causes of neonatal moose calf mortality in south central Alaska. Journal of Wildlife Management 45:335–342.

Balogh, G. 2012. Mobility and space use of moose in relation to spatial and temporal exposure to wolves. Thesis, Swedish University of Agricultural Sciences, Uppsala, Sweden.

Barber-Meyer, S. M., L. D. Mech, and P. J. White. 2008. Elk calf survival and mortality following wolf restoration to Yellowstone National Park. Wildlife Monographs 169:1–30.

Basille, M., D. Fortin, C. Dussault, G. Bastille-Rousseau, J.-P. Ouellet, and R. Courtois. 2015. Plastic response of fearful prey to the spatiotemporal dynamics of predator distribution. Ecology 96:2622–2631.

Bergman, E. J., R. A. Garrott, S. Creel, J. J. Borkowski, R. Jaffe, and F. G. R. Watson. 2006. Assessment of prey vulnerability through analysis of wolf movements and kill sites. Ecological Applications 16:273–284.

Bowyer, R. T., V. Van Ballenberghe, J. G. Kie, and J. A. K. Maier. 1999. Birth-site selection by Alaskan moose: maternal strategies for coping with a risky environment. Journal of Mammalogy 80:1070–1083.

Bubenik, A. B. 2007. Behavior. Pages 173–222 *in* A. W. Franzmann, and C. C. Schwartz, editors. Ecology and management of the North American moose. Second edition. University Press of Colorado, Boulder, USA.

Butler, E., M. Carstensen, E. Hildebrand, and D. Pauly. 2013. Determining causes of death in Minnesota's declining moose population: a progress report. Pages 97–105 *in* L. Cornicelli, M. Carstensen, M. D. Grund, M. A. Larson, and J. S. Lawrence, editors. Summaries of wildlife research findings 2012. Minnesota Department of Natural Resources, St. Paul, USA.

Carstensen, M., G. D. DelGiudice, B. A. Sampson, and D. W. Kuehn. 2009. Survival, birth characteristics, and cause-specific mortality of white-tailed deer neonates. Journal of Wildlife Management 73:175–183.

Carstensen, M., E. Hildebrand, D. Pauly, R. G. Wright, and M. Dexter. 2014. Determining cause-specific mortality in Minnesota's northeast moose population. Pages 133–143 *in* L. Cornicelli, M. Carstensen, M. D. Grund, M. A. Larson, and J. S. Lawrence, editors. Summaries of wildlife research findings 2013. Minnesota Department of Natural Resources, St. Paul, USA.

Carstensen, M., E. C. Hildebrand, D. Plattner, M. Dexter, C. Janelle, and R. G. Wright. 2015. Determining cause-specific mortality of adult moose in northeast Minnesota. Pages 161–171 *in* L. Cornicelli, M. Carstensen, M. D. Grund, and M. A. Larson, editors. Summaries of wildlife research findings 2014. Minnesota Department of Natural Resources, St. Paul, USA.

Carstensen, M., E. C. Hildebrand, D. Plattner, M. Dexter, C. Jennelle, and R. G. Wright. 2017. Determining cause-specific mortality of adult moose in northeast Minnesota, February 2013–July 2016. Pages 188–197 *in* L. Cornicelli, M. Carstensen, G. D'Angelo, M. A. Larson, and J. S. Lawrence, editors. Summaries of wildlife research findings 2015. Minnesota Department of Natural Resources, St. Paul, USA.

Carstensen Powell, M. C., and G. D. DelGiudice. 2005. Birth, morphologic, and blood characteristics of free-ranging white-tailed deer neonates. Journal of Wildlife Diseases 41:171–183.

DelGiudice, G. D. 2016. 2016 Aerial moose survey. Minnesota Department of Natural Resources, St. Paul, USA.

DelGiudice, G. D., K. R. McCaffery, D. E. Beyer, and M. E. Nelson. 2009. Prey of wolves in the Great Lakes Region. Pages 155–173 *in* A. P. Wydeven, T. R. Deelen, and E. J. Heske, editors. Recovery of gray wolves in the Great Lakes Region of the United States. Springer, New York, New York, USA.

DelGiudice, G. D., M. R. Riggs, P. Joly, and W. Pan. 2002. Winter severity, survival, and cause-specific mortality of female white-tailed deer in north-central Minnesota. Journal of Wildlife Management 66:698–717.

DelGiudice, G. D., W. J. Severud, T. R. Obermoller, and V. St-Louis. 2017. Gaining a deeper understanding of capture-induced abandonment of moose neonates. Journal of Wildlife Management 82:287–298.

DelGiudice, G. D., W. J. Severud, T. R. Obermoller, R. G. Wright, T. A. Enright, and V. St-Louis. 2015. Monitoring movement behavior enhances recognition and understanding of capture-induced abandonment of moose neonates. Journal of Mammalogy 96:1005–1016.

DeMars, C. A., M. Auger-Méthé, U. E. Schlägel, and S. Boutin. 2013. Inferring parturition and neonate survival from movement patterns of female ungulates: a case study using woodland caribou. Ecology and Evolution 3:4149–4160.

Erb, J., and B. A. Sampson. 2013. Distribution and abundance of wolves in Minnesota, 2012–2013. Minnesota Department of Natural Resources, St. Paul, USA.

Espmark, Y. 1969. Mother-young relations and development of behaviour in reindeer. Viltrey 6:461–540.

Franzmann, A. W., C. C. Schwartz, and R. O. Peterson. 1980. Moose calf mortality in summer on the Kenai Peninsula, Alaska. Journal of Wildlife Management 44:764–768.

Garshelis, D., and K. Noyce. 2011. Status of Minnesota black bears, 2010. Final Report to Bear Committee. Minnesota Department of Natural Resources, St. Paul, USA.

Geist, V. 1966. Some ethological observations on North American cervids. Zoologische Beiträge 12:219–251.

Geist, V., and F. Walther. 1974. Behaviour of ungulates and its relation to management. Volume 2 *in* Symposium on the behavior of ungulates and its relation to management. International Union for Conservation of Nature and Natural Resources, Calgary, Alberta, Canada.

Gustine, D. D., K. L. Parker, R. J. Lay, M. P. Gillingham, and D. C. Heard. 2006. Calf survival of woodland caribou in a multi-predator ecosystem. Wildlife Monographs 165:1–32.

Johnsen, S. 2013. To run or stay: anti-hunter behaviour of female moose. Thesis, Hedmark University College, Elverum, Norway.

Johnson, C. J., K. L. Parker, D. C. Heard, and M. P. Gillingham. 2002. A multiscale behavioral approach to understanding the movements of woodland caribou. Ecological Applications 12:1840–1860.

Keech, M. A., M. S. Lindberg, R. D. Boertje, P. Valkenburg, B. D. Taras, T. A. Boudreau, and K. B. Beckmen. 2011. Effects of predator treatments, individual traits, and environment on moose survival in Alaska. Journal of Wildlife Management 75:1361–1380.

Kittle, A. M., J. M. Fryxell, G. E. Desy, and J. Hamr. 2008. The scale-dependent impact of wolf predation risk on resource selection by three sympatric ungulates. Oecologia 157:163–175.

Klein, J. P., and M. L. Moeschberger. 2005. Survival analysis: techniques for censored and truncated data. Springer Science & Business Media, New York, New York, USA.

Kunkel, K. E., and D. H. Pletscher. 2000. Habitat factors affecting vulnerability of moose to predation by wolves in southeastern British Columbia. Canadian Journal of Zoology 78:150–157.

Laundré, J. W., L. Hernández, and W. J. Ripple. 2010. The landscape of fear: ecological implications of being afraid. Open Ecology Journal 3:1–7.

Lenarz, M. S., J. Fieberg, M. W. Schrage, and A. J. Edwards. 2010. Living on the edge: viability of moose in northeastern Minnesota. Journal of Wildlife Management 74:1013–1023.

Lenarz, M. S., M. E. Nelson, M. W. Schrage, and A. J. Edwards. 2009. Temperature mediated moose survival in northeastern Minnesota. Journal of Wildlife Management 73:503–510.

LeResche, R. E. 1968. Spring-fall calf mortality in an Alaskan moose population. Journal of Wildlife Management 32:953–956.

Livezey, K. B. 1990. Toward the reduction of marking-induced abandonment of newborn ungulates. Wildlife Society Bulletin 18:193–203.

McGraw, A. M., J. Terry, and R. Moen. 2014. Pre-parturition movement patterns and birth site characteristics of moose in northeast Minnesota. Alces 50:93–103.

McLaren, A. A. D., J. F. Benson, and B. R. Patterson. 2017. Multiscale habitat selection by cow moose (*Alces alces*) at calving sites in central Ontario. Canadian Journal of Zoology 95:891–899.

Mech, L. D. 1966. The wolves of Isle Royale. U.S. National Park Service Fauna Series, No. 7. U.S. Government Printing Office, Washington, D.C., USA.

Mech, L. D. 1998. The wolves of Denali. University of Minnesota Press, Minneapolis, USA.

Mech, L. D., J. R. Fieberg, and S. M. Barber-Meyer. 2018. An historical overview and update of wolf-moose interactions in northeastern Minnesota. Wildlife Society Bulletin 42:40–47.

Midwestern Regional Climate Center. 2015. cli-MATE, MRCC application tools environment. http://mrcc.isws.illinois.edu/CLIMATE/. Accessed 30 Jan 2019.

Minnesota Department of Natural Resources [MNDNR]. 2011. Minnesota moose research and management plan. Final Plan Division of Fish and Wildlife. Minnesota Department of Natural Resources, St. Paul, USA. http://files.dnr.state.mn.us/fish_wildlife/wildlife/moose/management/mooseplan-final.pdf.

Minnesota Department of Natural Resources [MNDNR]. 2015. Ecological classification system. Minnesota Department of Natural Resources, St. Paul, USA. http://www.dnr.state.mn.us/ecs/index.html.

Murray, D. L., E. W. Cox, W. B. Ballard, H. A. Whitlaw, M. S. Lenarz, T. W. Custer, T. Barnett, and T. K. Fuller. 2006. Pathogens, nutritional deficiency, and climate influences on a declining moose population. Wildlife Monographs 166:1–30.

Nelson, M. E., and L. D. Mech. 1981. Deer social organization and wolf predation in northeastern Minnesota. Wildlife Monographs 77:3–53.

Nobert, B. R., S. Milligan, G. B. Stenhouse, and L. Finnegan. 2016. Seeking sanctuary: the neonatal calving period among central mountain woodland caribou (*Rangifer tarandus caribou*). Canadian Journal of Zoology 94:837–851.

Obermoller, T. R., G. D. DelGiudice, W. J. Severud, B. D. Smith, J. L. Goethlich, and R. A. Willaert. 2017. Using movement behavior of female moose to estimate survival and cause-specific mortality of calves in northeastern Minnesota. Pages 98–109 *in* L. Cornicelli, M. Carstensen, G. D'Angelo, M. A. Larson, and J. S. Lawrence, editors. Summaries of wildlife research findings 2015. Minnesota Department of Natural Resources, St. Paul, USA.

Osborne, T. O., T. F. Paragi, J. L. Bodkin, A. J. Loranger, and W. N. Johnson. 1991. Extent, cause, and timing of moose calf mortality in western interior Alaska. Alces 27:24–30.

Patterson, B. R., J. F. Benson, K. R. Middel, K. J. Mills, A. Silver, and M. E. Obbard. 2013. Moose calf mortality in central Ontario, Canada. Journal of Wildlife Management 77:832–841.

Peterson, R. O. 1977. Wolf ecology and prey relationships on Isle Royale. U.S. National Park Service Scientific Monograph Series, No. 11, Washington, D.C., USA.

Pinard, V., C. Dussault, J.-P. Ouellet, D. Fortin, and R. Courtois. 2012. Calving rate, calf survival rate, and habitat selection of forest-dwelling caribou in a highly managed landscape. Journal of Wildlife Management 76:189–199.

Poole, K. G., R. Serrouya, and K. Stuart-Smith. 2007. Moose calving strategies in interior montane ecosystems. Journal of Mammalogy 88:139–150.

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reese, E. O., and C. T. Robbins. 1994. Characteristics of moose lactation and neonatal growth. Canadian Journal of Zoology 72:953–957.

Schwartz, C. C., and L. A. Renecker. 2007. Nutrition and energetics. Pages 141–171 *in* A. W. Franzmann, and C. C. Schwartz, editors. Ecology and management of the North American moose. University Press of Colorado, Boulder, USA.

Severud, W. J. 2017. Assessing calf survival and the quantitative impact of reproductive success on the declining moose (*Alces alces*) population in northeastern Minnesota. Dissertation, University of Minnesota, Saint Paul, USA.

Severud, W. J., G. D. DelGiudice, and T. R. Obermoller. 2017. Survival, cause-specific mortality, and space use of moose calves in a declining population. Pages 110–123 *in* L. Cornicelli, M. Carstensen, G. D'Angelo, M. A. Larson, and J. S. Lawrence, editors. Summaries of wildlife research findings 2015. Minnesota Department of Natural Resources, St. Paul, USA.

Severud, W. J., G. D. DelGiudice, and T. R. Obermoller. 2019. Association of moose parturition and post-parturition habitat with calf survival. Journal of Wildlife Management 83:175–183.

Severud, W. J., G. D. DelGiudice, T. R. Obermoller, T. A. Enright, R. G. Wright, and J. D. Forester. 2015*a*. Using GPS collars to determine parturition and cause-specific mortality of moose calves. Wildlife Society Bulletin 39:616–625.

Severud, W. J., G. D. DelGiudice, T. R. Obermoller, R. J. Ryan, and B. D. Smith. 2015*b*. An alternate method to determine moose calving and cause-specific mortality of calves in northeastern Minnesota. Pages 93–108 *in* L. Cornicelli, M. Carstensen, M. D. Grund, M. A. Larson, and J. S. Lawrence, editors. Summaries of wildlife research findings 2014. Minnesota Department of Natural Resources, St. Paul, USA.

Testa, J. W., E. F. Becker, and G. R. Lee. 2000. Movement of female moose in relation to birth and death of calves. Alces 36:155–162.

Associate Editor: Barbara Zimmermann.