

USING MOVEMENT BEHAVIOR OF ADULT FEMALE MOOSE  
TO ESTIMATE SURVIVAL AND CAUSE-SPECIFIC MORTALITY  
OF CALVES IN A DECLINING POPULATION

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## **Dedication**

This thesis is dedicated to my wife, Sarah, who has supported and encouraged me during my field work and long nights working on my thesis. I am thankful for having you in my life.

## Abstract

Low calf production and survival can contribute to ungulate population declines and sustained low numbers. Continuing research on cause-specific mortality and annual survival of moose (*Alces alces*) calves in northeastern Minnesota is critical to understanding the long-term trajectory of the population. Beginning in late April 2016, 35 global positioning system (GPS)-collared adult females were computer-monitored for calving movements, a long distance movement followed by an intense localization. I observed 28 of 33 (85%) females make a calving movement, and with additional field observations of calves, determined 31 of the 35 (89%) females were pregnant. Mean birth-date was 12 May 2016 (median = 11 May 2016, range = 24 Apr–10 June. In 2013–2014, I observed an unusual behavior by dams, a “mortality movement,” associated with the death of their neonate. The dam made a rapid, long-distance movement (“flee”), followed by a return to the calf mortality site. In 2016, using this behavior as a calf mortality indicator, I documented evidence of 15 mortalities at a mean age of 30.6 days ( $\pm 15.5$  [SE], range = 3–243 days). Based on observations of mortality movements, 21 investigations were launched and 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. Predation accounted for 87% of all mortalities. The cumulative probability of calves being killed by wolves and bears was 33% and 11%, respectively. The mean distance dams fled after a mortality was 1,873 m ( $\pm 412$ , range = 126–5,805 m,  $n = 14$ ). Dams that made return visits returned a mean 2.8 times ( $\pm 0.5$ , range = 1–5,  $n = 8$ ) to the

mortality site. Dams returned to within a mean 106 m ( $\pm 22$ , range = 34–230 m,  $n = 8$ ) from the mortality site. Calf survival to 30 days of age was 67% ( $\pm 8$ , 95% CI = 53–84%,  $n = 36$ ). Survival declined to 33% ( $\pm 8$ , CI = 20–53%,  $n = 36$ ) at almost 1 year of age, associated with an estimated calf:cow ratio of 0.35. I developed 2 population-level movement models to improve efficacy of the mortality movement for identifying calf mortalities during the first summer of life. The first approach, a temporal-based model, used a single, estimated movement velocity threshold (164 m/hr) for the dam to indicate calf mortality and accurately predicted survival status 51% of the time. My second approach, an age-specific model, using different thresholds (28–135 m/hr) for the dam relative to calf age, was 80% accurate. Using movement behavior of dams to assess calf mortality can yield important insights into mechanisms related to the decline of the population in northeastern Minnesota and aid in future management decisions.

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**CHAPTER 1**

**USING MOVEMENT BEHAVIOR OF ADULT FEMALE MOOSE TO  
ESTIMATE SURVIVAL AND CAUSE-SPECIFIC MORTALITY OF CALVES IN  
NORTHEASTERN MINNESOTA**

## INTRODUCTION

The near disappearance of moose (*Alces alces*) in northwestern Minnesota since the mid-1980s and a dramatic decline of northeastern Minnesota's population since 2006 (Murray et al. 2006; Lenarz et al. 2009, 2010; DelGiudice 2016) prompted the Minnesota Department of Natural Resources (MNDNR) to launch aggressive companion studies of survival and cause-specific mortality of adults and calves in northeastern Minnesota (Fig. 1) using cutting-edge global positioning system (GPS)-collar technology (Carstensen et al. 2015, Severud et al. 2015a). 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. 2015a).

Ungulate calves are particularly vulnerable to predation within their first few months of life due to 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. (2015b) recently reported that 50% 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 have reported similar findings (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

impact 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 parent moose calf study initiated by the MNDNR in 2013 was to assess annual variation of cause-specific mortality over a 4-year period. However, capture-induced abandonment in 2013 and 2014 (DelGiudice et al. 2015, in press) 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, remaining adult females with functioning GPS collars were monitored for calving activity (i.e., calving movement), and subsequently for a mortality movement. A mortality movement is a behavior described as a dam (mother) making a sudden long distance movement (“flee”), followed by  $\geq 1$  return to the origin of the flee (Fig. 2; Obermoller et al. 2017).

Many studies have examined ungulate movements to better understand forage selection (Johnson et al. 2002), predation (Testa et al. 2000, Laundré et al. 2010, Balogh 2012), and adult survival (Kunkel and Pletscher 2000, Johnsen 2013, Carstensen et al. 2015). But few studies have reported on dam movement behavior relative to neonatal survival (Testa et al. 2000, DeMars et al. 2013). Preliminary evidence suggests that changes in velocity of ungulate dams can lead to important inferences about neonate 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). Ungulate neonates are most vulnerable during the first few weeks of life (Franzmann et al. 1980, Ballard et al. 1981). Young (and dams) able to avoid predators at this early age are most likely to survive and be recruited into the population. Female moose in British Columbia selected calving sites with reduced forage, but effective hiding cover in an apparent effort to reduce risk of predation (Poole et al. 2007). However, as dams approach peak lactation at 21–31 days post-parturition, the importance of locating more 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). Dams and their neonates remain at their calving sites for up to 14 days; the risk of predation increases markedly once they depart from those sites in search of more plentiful forage (Bubenik 2007, McGraw et al. 2014, Severud et al. 2015a, Severud 2017).

Dams with young calves-at-heel exhibit a marked reduction in movements (Testa et al. 2000), which helps to identify cows with and without calves. Upon losing a calf or calves of the same age, a dam's movements may increase by up to 12% (Testa et al. 2000). In studying caribou (*Rangifer tarandus*) neonate mortality, DeMars et al. (2013) applied a movement velocity threshold (using a 3-day average) to dams. When a dam's velocity exceeded 186.5 m/hour, her calf was assumed to be dead, and "normal movements" resumed. These authors correctly determined the survival status of 73% of the calves up to 4 weeks old.

I attempted to improve our understanding of maternal movement patterns relative to moose calf mortalities. My research objectives were to quantify the temporal and spatial aspects of 2013–2014 and 2014–2015 movement data of GPS-collared dams relative to known mortalities of their GPS-collared calves; develop models to identify calf mortalities in real-time during 2016–2017; and to test these models by identifying, locating, and assigning cause of death of calves by field investigation and confirmation.

### **STUDY AREA**

The 6,068-km<sup>2</sup> 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. 1). 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 were not uncommon, but elevational changes across the study area are limited. The most common predators of moose calves were gray wolves and black bears. Average wolf and bear densities for moose range in northeastern Minnesota were 3/100 km<sup>2</sup> and 23/100 km<sup>2</sup> across northern Minnesota and my study area, respectively (Garshelis and Noyce 2011, Erb and Sampson 2013). White-tailed

deer (*Odocoileus virginianus*) were managed at pre-fawning densities of  $\leq 4/\text{km}^2$ , and were the main prey of wolves (Nelson and Mech 1981, DelGiudice et al. 2002, MNDNR 2011).

## **METHODS**

### **Monitoring GPS-collared Adult Females and Calves**

Adult moose (129 females, 51 males) were captured and fitted 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 (Carstensen et al. 2014, 2015, 2017). The mean linear error of adult GPS collars was 3.7 m ( $\pm 0.3$  [SE], range = 0–17 m) and 7.0 m ( $\pm 0.3$ , range = 1–36 m) under open and dense (>80%) canopy closure (Severud et al. 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.

In 2013 and 2014, we captured and fitted 74 neonates from 50 GPS-collared adult females with GPS PLUS VERTEX Survey-1 GLOBALSTATR collars (with mortality accelerometers; Vectronic Aerospace GmbH, Berlin, Germany) to monitor survival and cause-specific mortality (Severud et al. 2015*a, b*). The collars logged hourly locations and transmitted every third successful fix (Severud et al. 2015*a*). Collars entered mortality mode following 6 hour of limited motion. A notification was then sent to the base station, followed by a SMS text message and e-mail notification to field staff. After censoring calves due to collar slippage and capture-induced abandonment or mortality during 2013 and 2014, 49 calves were available to monitor cause-specific mortality

(DelGiudice et al. 2013; Severud et al. 2014, 2015*b*). In 2015, we monitored 60 adult females for calving; 50 made movements indicative of calving. We monitored those 50 for movements indicative of calf mortality (Severud et al. 2015*a*, Severud 2017). Due to natural mortalities, malfunctioning GPS collars, and battery expiration, 35 adult females with functioning GPS collars were available for intense computer-monitoring during the 2016 calving season. Twenty-three female collars were programmed to record a location every 4 hours and transmit these locations 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 these locations after 11 successful fixes. In 2016, I remotely monitored the collared adult females to detect mortality events and then dispatched a team to conduct field investigations for confirmation. I used GPS-collared non-surviving ( $n = 26$ ) and surviving calves ( $n = 23$ ) from 2013 and 2014 to develop models (see below), because fate dates and causes of mortality were known (Severud et al. 2015*a, b*; Severud 2017). Non-surviving ( $n = 24$ ) and surviving calves ( $n = 32$ ) of 2015 and 2016 were used to evaluate the ability of the models to accurately determine survival status.

In early May of each year, all cows were monitored for a calving movement, which is a long distance movement followed by an intense localization (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 cow (Severud et al. 2015*a*; Obermoller et al. 2017; J. D. Forester, University of Minnesota, unpublished data). In spring 2016, I 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 dam 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, I monitored each cow's locations daily for a mortality movement (Fig. 2).

Uncharacterized movements of dams associated with mortalities of GPS-collared calves were first observed during 2013 and 2014, but were not used for their potential as an indicator of calf mortality until 2015 (Severud et al. 2015*b*). During that spring-summer field season mortalities could not be reliably identified and located after the calves were 3 weeks old. Subsequently, I began to closely examine these dam movements to ascertain whether there were common patterns indicative of calf death that I could use in developing a more elaborate approach for monitoring calf mortality during the 2016 field season. I calculated the distance the dam fled following a mortality, the number of times the cow returned to the mortality site (return visits), and the distance the dam returned (i.e., how close she came to the mortality site). I also used distance of the fleeing dam 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–June), I conducted daily close computer-monitoring (<https://www.vectronic-wildlife.com/index.php>) of each cow for movement patterns indicative of mortality. I did not conduct field investigations immediately following the initial flee and return so as not to risk influencing dam

movements. I used a dam's current location to decide when best to perform the investigation.

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 immediately found, I 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. Due to various factors (e.g., calf age, habitat type, topographical limitations, and lack of cow or calf sign), I adjusted our search area as needed. Evidence sought included 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 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. 1981, Severud et al. 2015a).

The aforementioned information was used to assign specific causes of death. Since litter size at birth was unknown, following a mortality or apparent mortality movement, I performed survival investigations to determine whether the dam lost 1 or 2 calves or still had a calf alive. I executed these investigations by heading to areas where

the dam had localized following the presumed or confirmed calf mortality. I opportunistically placed camera traps in areas the dam frequently occupied to attempt to capture evidence of an accompanying calf.

I conducted flight surveys on 17–18 January 2017 and 19 April 2017 from a Bell Jet Ranger (OH-58) helicopter to locate all adult females with functioning GPS collars to determine 8-month and near-annual (recruitment) calf survival, respectively. This also allowed me to evaluate the success of our mortality and survival investigations during the previous summer. Success was determined relative to my predetermined expectation of whether each dam would have a calf or not based on their movements post-calving. In cases where the female was not located, I searched for a maximum 15 minutes before moving onto the next animal. Collectively, calf status of dams was monitored and assessed via calf survival investigations, mortality investigations, and movement rates.

### **Temporal-based Model**

I analyzed temporal and spatial aspects of movement patterns of GPS-collared dams of GPS-collared calves that died of known causes in 2013 and 2014 to determine characteristics indicative of calf mortality (e.g., wolf or bear predation) and aid in identifying mortalities in 2015 and 2016. Similar to DeMars et al. (2013), I applied a “calf-loss movement threshold” to the dams; if the threshold was exceeded, the calf was presumed dead. I assessed calf mortalities up to 3 months of age. Beyond that age, sample size of “known mortalities” was too small to evaluate the movement models. Importantly, nearly all calf mortalities occurred during the first 3 months of age (Severud et al. 2015a, Obermoller et al. 2017). The initial post-hoc approach was the temporal-

based model (TBM, DeMars et al. 2013); I examined different temporal (e.g., 4-, 24-, and 72-hr) velocity (m/hr) thresholds to determine which had the highest success in determining calf loss.

I excluded the top 1% of velocities prior to calculating the moving average to increase overall sensitivity; these movements were considered atypical, perhaps caused by human or predator disturbance (DeMars et al. 2013). I developed a moving average function to calculate mean velocity over a specified window (i.e., 24 hr); cows with varying fix rates (e.g., 1- or 4-hr) were not affected, because the specified window was based on duration, not number of locations.

The calf loss movement threshold was developed by incorporating the movements of all individual dams with a surviving calf or calves into an empirical distribution. All movement rates between estimated calf birth-dates and 7 days prior to estimated calf mortality-date were used to ensure velocities were not affected by factors immediately leading up to the mortality event. Movements of dams with surviving calves were also used to calculate the threshold until 7 days prior to collar removal or slippage. I converted the empirical distribution into a kernel density estimate and then into a cumulative distribution function (CDF; Fig. 3), the proportion of velocities above or below a given rate (DeMars et al. 2013). Unlike DeMars et al. (2013), I used the 100% quantile of the CDF, to obtain the maximum velocity and avoid censoring a potential mortality movement. Rates above this threshold were indicative of calf mortality.

## **Age-specific Model**

The age-specific model (ASM) developed different thresholds to account for changing velocities relative to calf age and season. I 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. I used the 72-hour moving window for these analyses, because it identified the status of a higher proportion of calves than the 4- and 24-hour windows. A movement threshold was obtained by the same means as for the TBM model, but for each age group (e.g., 2–4 weeks). Due to lack of mortality events at older ages, I was unable to evaluate age beyond 3 months; however, I determined thresholds, because calves survived well beyond that age.

## **Data Analysis**

I assessed model success 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 identified as survived), and accuracy (overall proportion where calf status was correctly identified). I used a 1-way analysis of variance (ANOVA) to test whether velocities differed based on survival status of a calf. All analyses were conducted with R version 3.2.5 (R Core Team 2017). Tests were significant at  $\alpha \leq 0.05$ .

## **RESULTS**

### **Monitoring Mortality Movements**

Overall, in 2016, I documented 15 calf mortalities from 28 investigations of presumed mortalities (54% confirmation rate). I confirmed mortalities during 11 of 21

investigations where a dam made a mortality movement in 2016. For the 4 mortalities investigated without an observable mortality movement, 3 were investigated because the dam made a long distance flee with no return to the presumed mortality site while the calf was very young and immobile. The fourth was a vehicle collision reported by the public. Mean distance from the calving to mortality site was 932 m ( $\pm 357$ , range = 0–3,500 m,  $n = 13$ ). Four of 13 calves were killed at or near ( $<50$  m) the calving site. Mean response time following a mortality was 6.1 days ( $\pm 1.4$ , range = 1–19 days,  $n = 13$ ). Mean distance dams fled from a mortality was 1,873 m ( $\pm 412$ , range = 126–5,805 m,  $n = 14$ ). Dams that made return visits to the mortality site returned a mean 2.8 times ( $\pm 0.5$ , range = 1–5,  $n = 8$ ). Once returned, dams came to within a mean 107 m ( $\pm 22$ , 34–230 m,  $n = 7$ ) from the mortality site. Only 1 of 4 dams 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, I recorded 9 wolf-kills, 3 bear-kills, 1 unknown predator-kill, and 2 deaths following a possible vehicle collision. I also observed 5 cases where a dam made an apparent mortality movement, but no evidence of calf mortality was observed. The dams' behaviors (increased movements) following the mortality movement indicated a calf or calves had been lost, suggesting evidence simply was not located during the investigation or the mortality occurred beyond the searched area. The 30-day calf survival rate was 67% ( $\pm 8$ , 95% CI = 53–84%,  $n = 36$ ). At the end of summer, 3-month survival was 53% ( $\pm 8$ , CI = 39–72%,  $n = 36$ ).

I observed a change in the mean velocity of dams 3 days before and after the calf mortality date ( $F_{1,24} = 16.63$ ,  $P \leq 0.001$ ). The velocities before and after the calf mortality were 30.1 m/hr ( $\pm 9.5$ , range = 2–125 m/hr,  $n = 13$ ) and 142.0 m/hr ( $\pm 25.7$ , range = 8–315 m/hr,  $n = 13$ ), respectively. Winter survey flights confirmed these calves were no longer with their dams and presumed dead. Furthermore, during the flights I noted 4 calves had been lost, but no mortality movement had been observed previously.

### **Temporal-based Model**

I calculated 3 different dam velocity thresholds to indicate mortality. The 4-, 24-, and 72-hour thresholds were 342, 164, 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%) in 2013–2014, 2015, and 2016, respectively (Table 1). The ability of the model to predict survival status during all years (2013–2016) pooled was highest for the 72-hour threshold (Table 1). I noted 3 of 4 mortality events in 2013–2014 were detected when the dam had a remaining calf survive, but only 1 of 4 was detected within 7 days of the mortality event. Similarly, 1 of 3 in 2016 was detected for both the surviving calf and within 7 days of the mortality event; 2015 did not have any confirmed twins associated with mortality events. The 4-hour moving window resulted in the highest proportion of true positives, but performed poorly in identifying true negatives (Table 1).

### **Age-specific Model**

The mean velocity prior to rarefying the data (i.e., excluding top 1% of velocities) for all years (2013–2016) by age group was as follows: 42 m/hour ( $\pm 11$ , range = 3–960 m/hr,  $n = 87$ ) for 0–2 weeks, 52 m/hour ( $\pm 10$ , range = 7–633 m/hr,  $n = 62$ ) for 2–4 weeks, 106

m/hour ( $\pm 31$ , range = 5–1,417 m/hr,  $n = 52$ ) for 1–3 months, 46 m/hour ( $\pm 2$ , range = 27–88 m/hr,  $n = 37$ ) for 3–6 months, and 56 m/hour ( $\pm 31$ , 9–1,062 m/hr,  $n = 34$ ) for 6–12 months.

The dam velocity threshold using the 72-hour-window, 0–2-week-age threshold was 28 m/hour, and then increased to 66 m/hour during 2–4 weeks. The 1–3-month subset increased to 135 m/hour. The 3–6-month and 6–12-month thresholds were 109 and 30 m/hour, respectively, but these thresholds were unable to be evaluated due to low sample size. The model most accurately predicted survival status for 2–4 weeks (Table 2). The model performed similarly well for the 0–2 week age group with an overall accuracy for survival status of 77–88% 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%. One of 4 and 1 of 3 calf mortalities were detected within 7 days of the mortality event when a cow had a remaining calf survive in 2013–2014 and 2016, respectively.

## **DISCUSSION**

The approach I developed for monitoring survival status of calves without GPS (or VHF) collars improves upon the earlier approach using dam movements in 2015 (Severud et al. 2015b). Those authors reported a 36% confirmation rate of detecting mortalities associated with this movement until moose neonates were approximately 3-weeks old. Identifying mortalities beyond this age became increasingly difficult, because of increased velocities of the dam-calf pair. I increased our success of locating calf deaths

using the mortality movement to 53% up to 3-months of age. This was likely attributable to more thorough searches (patterns versus casual searches) for mortality evidence, closer computer-monitoring, and analysis of previous mortality movement characteristics (e.g., flee distance, return distance). In the first few weeks of age when neonate mobility typically was limited, mortality investigations were also launched when dams 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.

Initially, I conjectured that the mortality movement was a behavioral response to predators chasing the dam, but I documented 2 vehicle-kills in 2016 associated with similar dam movements. One of these dams made the most return visits (5) to the mortality site and stayed with the dead calf the longest (9.2 days) before ultimately leaving the calf carcass. Others have reported cows defending calf carcasses (M.W.Schrage, Fond du Lac Resource Management Division, personal communication; LeResche 1968; Mech 1998). In the last case, a cow defended 2, 9-month old calves for 7–8 days. In the first year (2013) of our calf study, the capture crew returned to a collared calf carcass with the dam in close proximity (Severud et al. 2015*b*; M.A Keech, Quicksilver Air, Inc., personal communication). The many examples suggest that these dams have a maternal instinct that motivates them to protect or return to their calf. Difficult to prove, a theory associated with this behavior is that these dams were returning to their calves to “mourn,” a behavior similarly observed in elephants

(*Loxodonta* spp.) and great apes (*Hominidae* spp.) following the death of their young or other family members (Marrone 1998, Bradshaw 2004).

In conjunction with the mortality investigations, fall and winter calf survival flights allowed me to assess the accuracy of mortality determination based on movement analyses, and provided supplemental data for estimating calf production and recruitment. By way of survival investigations and flights, I recorded 5 cases where a calf mortality movement occurred in 2016, but no evidence of a mortality was found and no calf was present with its dam. I also noted cases where a dam with a surviving twin did not make a mortality movement. Locating evidence of a calf mortality during field investigations was frequently difficult; typically only small pieces of calf remains were found to determine specific causes of mortality.

Generally, my TBM followed the approach of DeMars et al. (2013) to characterize dam movement behavior relative to calf mortality. The 4-hour moving average 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 time was required to detect a sustained increase in velocity (no longer hindered by limited calf mobility) and 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) than my similar TBM model (up to 3 months of age), highlighting the importance of evaluating a model relative to a species,

population, and age before applying it in the field. Overall, my TBM model did not identify mortalities well for any of the different temporal windows (e.g., 4-, 24-, and 72-hr), because I observed large differences in calf mobility relative to age.

I used the 72-hour temporal window for the ASM, because it performed best for both true positives and true negatives. The ASM performed 29% better than the TBM at predicting calf survival during 2013–2016. Using the 4-hour window and increasing the number of field investigations might prove advantageous, because the model detects a higher proportion of true positives, even though it would also result in a higher proportion of false negatives. Changing movement thresholds by age allowed me to adjust for calf mobility, whereas the TBM used all cow locations regardless of calf age. Neonate mobility up to 2 weeks of age was very low; calves remained localized at the calving site for roughly their first 7 days, and then only slowly began to increase their velocity (Severud et al. 2015a, Obermoller et al. 2017). I observed the highest velocity at 1–3 months of age, which coincided with peak forage availability (Schwartz and Renecker 2007). Calf velocity also varied more at that age, which contributed to 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. Finally, calf mortalities were difficult to detect when the dam retained a surviving twin. None of the 3 approaches, monitoring for mortality movements, the TBM, nor the ASM performed well under these circumstances. But the TBM and ASM were more flexible, because dam-velocity thresholds could be adjusted. The mortality movement approach was largely based on the cow returning to the mortality site, and the

dams rarely exhibited this behavior with a surviving twin. Ungulate studies with high twinning rates may find these methods of limited value.

This approach to assessing survival and cause-specific mortality of unmarked calves has limitations and challenges. Without capturing and handling live neonates, I could not record morphological measurements, determine sex, collect blood samples, or assess general health status. 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 confirms a calf mortality. Also, dams did not typically make a mortality movement when only 1 calf of a set of twins died. The dam would flee with her surviving calf, and then localize elsewhere. Often, I was also unable to obtain location data on these uncollared calves, because it was unknown until the fall helicopter survey whether a surviving calf was present. All of these disadvantages could be alleviated by GPS-collaring neonates.

Global positioning system-collaring neonates is most desirable for collecting survival and cause-specific mortality data, but timely identification of calf mortalities via movements of GPS-collared dams, allowed me to continue, with limitations, assessments of reproductive and recruitment impacts on population performance. I obtained valuable cause-specific mortality data from this monitoring that included non-predation mortality events. This method can be used as an alternative to neonate collaring, and in conjunction with helicopter flights, although less precise, will allow estimates of calf production, recruitment, and twinning. There were significant expenses for GPS-collaring calves, including \$1,600/calf capture and \$1,000/calf collar (G. D. DelGiudice,

MNDNR, unpublished data). The present method was non-invasive, and would reduce the risk of capture-induced abandonment of ungulate neonates (DelGiudice et al. 2015, in press).

Changes in dam movement velocities indicative of calf mortality were observed in caribou, and now in moose; with GPS-collared ungulate dams, this method could be adapted to other ungulate species as well (DeMars et al. 2013, Obermoller et al. 2017). During analyses, I only examined velocities at the population level, because my objectives were to use previous data to detect mortality in real-time. An individual-level method would have hampered fulfillment of my objectives, but could prove useful when determining mortality post hoc (DeMars et al. 2013). An improvement upon these models may include covariates that contain distance to water, slope, canopy closure, and distance to roads, most of which were associated with calf survival in this study (Severud 2017). The new approach I tested for monitoring survival during the most vulnerable period (0–3 months of age) of a moose’s life, may provide information important to understanding population performance and dynamics.

Table 1. Temporal-based method (TBM) 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, 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	<i>n</i>	4-hour (342 m/hr)	24-hour (164 m/hr)	72-hour (119 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	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

Table 2. Age-specific Model (ASM) 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, 2013–2016. 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	<i>n</i>	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	NA	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

Figure 1. Moose calf study area (6,068 km<sup>2</sup>) for examining survival and cause-specific mortality in northeastern Minnesota. Solid orange circles depict mortality sites (*n* =15) of calves during May 2016–January 2017.

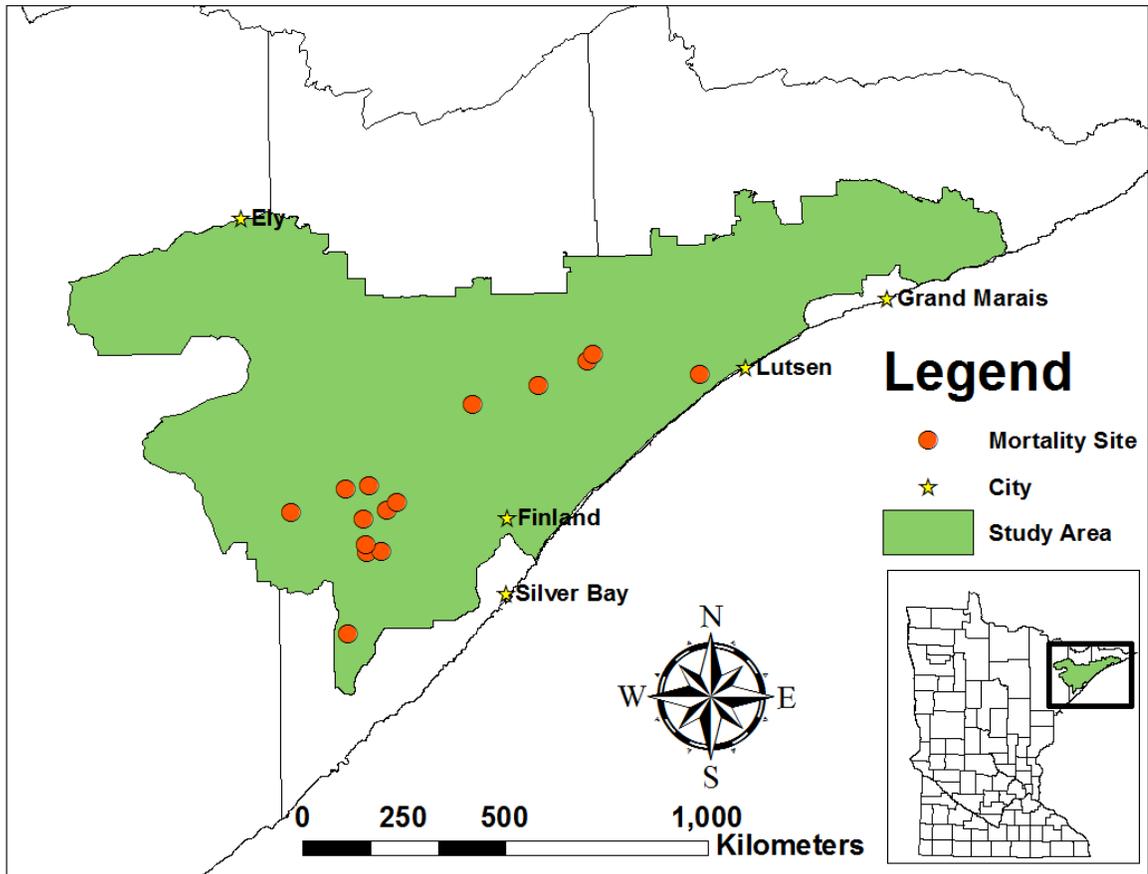


Figure 2. Vectronic Aerospace website (<https://www.vectronic-wildlife.com>) displaying the path of adult female moose number 13778 in northeastern Minnesota, 5–11 May 2016. The green and red squares represent the beginning and end of the temporal interval, respectively. The cow's movements show flees and return visits to the green square; a calf mortality occurred on 5 May 2016. This cow 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.

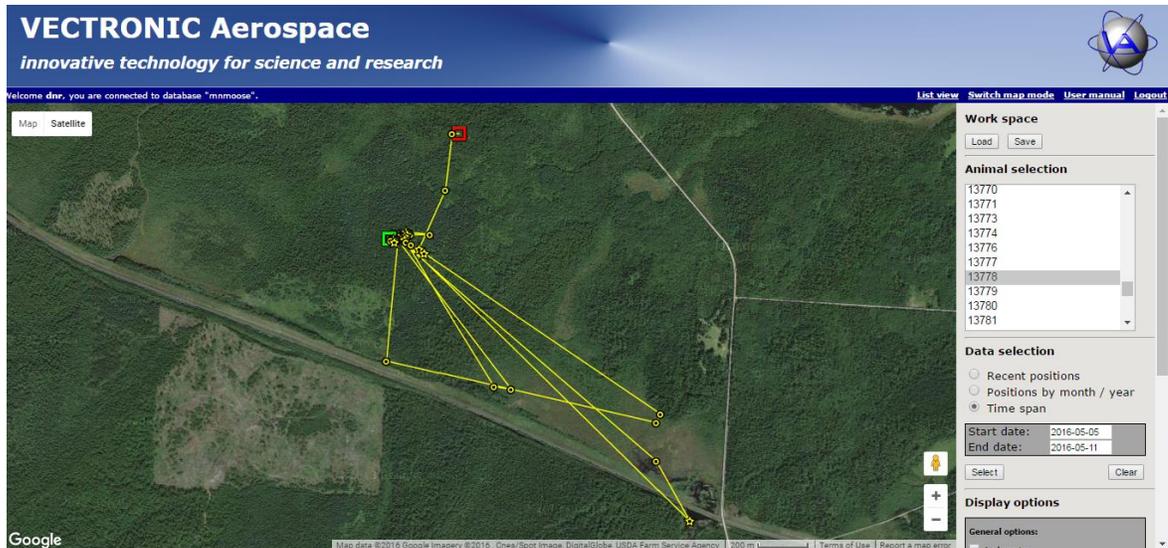
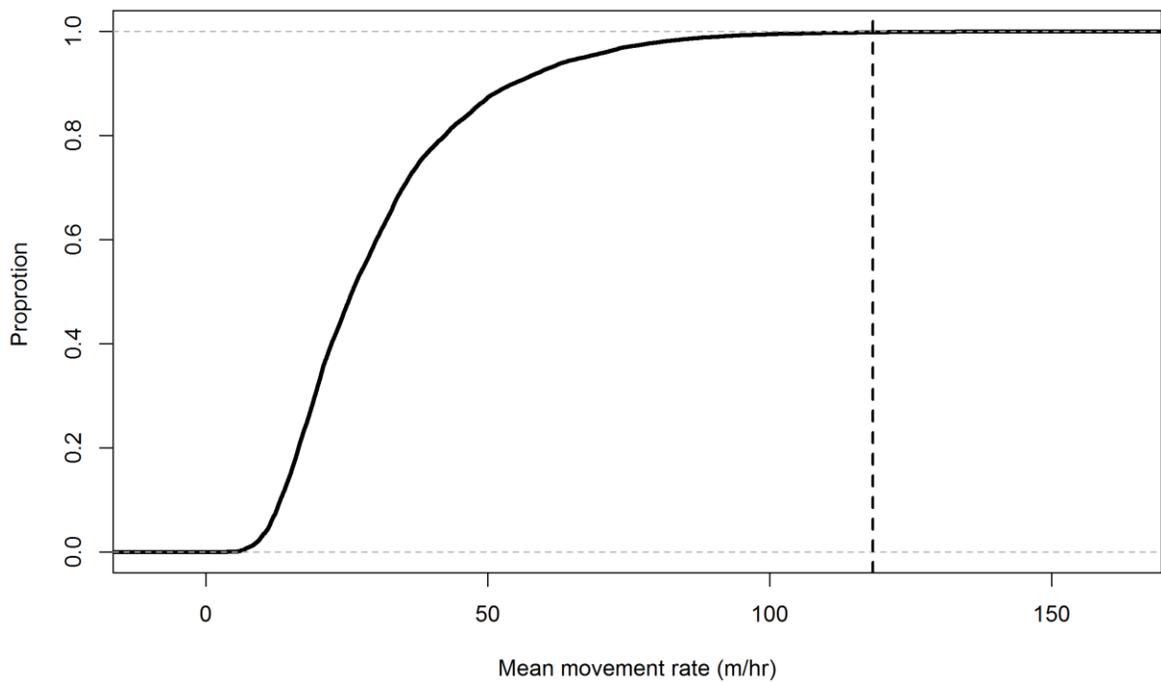


Figure 3. Cumulative distribution function (CDF) of movement velocities of dams ( $n = 45$ ) with surviving calves, developed to determine the velocity threshold indicative of calf survival for the temporal-based model, northeastern Minnesota, May 2016–January 2017. Vertical dotted line represents the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



## **CHAPTER 2**

### **Predation and calf survival in a depressed moose population in northeastern Minnesota**

## INTRODUCTION

Survival and reproduction are the primary drivers of ungulate population performance (Gaillard et al. 2000, Raithel et al. 2007). Generally, adult survival has a more pronounced effect than juvenile survival on population growth ( $\lambda$ ; Gaillard et al. 1998, 2000; Lenarz et al. 2010). However, low and highly variable juvenile survival can also contribute markedly to declines (Hatter and Janz 1994, Cooley et al. 2008, Forrester and Wittmer 2013). Elk (*Cervus elaphus*) calf survival rates in a declining population ranged between 0.32 and 1.00 from 1997–2004 (White et al. 2010). During 2013–2015, moose calf survival in northeastern Minnesota varied at a low level (0.29–0.40) and had a strong negative impact on  $\lambda$  of the population (Severud 2017). Large variation in juvenile survival highlights the value of relying on long-term data ( $\geq 6$  yr) to make inferences.

Aggressive studies of adult moose and calf survival and cause-specific mortality were initiated in northeastern Minnesota in response to a 52% population decline from 2006 to 2012. (Lenarz 2012, DelGiudice 2013). Global Positioning System (GPS) collars were fitted to neonates in spring 2013 and 2014 to closely monitor their survival and to expedite cause-specific mortality investigations. Although a great deal was learned, high levels of capture-induced abandonment and capture-related mortality of GPS-collared adults (Carstensen et al. 2015, DelGiudice et al. 2015) induced the Governor of Minnesota to issue Executive Order 15-10 (28 Apr 2015) discontinuing all collaring of moose. Additionally, in 2013 and 2014, 12% and 63% of the GPS collars fitted to neonates prematurely slipped from their necks precluding complete data collection (Obermoller et al., in press). A final challenge to data collection involved occasional

failure of mortality text notifications due to poor transmission (e.g., collars buried by predators, Severud et al. 2015a).

During 2013 and 2014, dams were observed making atypical movements in response to collared calf mortalities (Severud et al. 2015b). As described in Chapter 1, the cows made a “mortality movement,” a sudden long-distance movement (“flee”), followed by a return to the origin of the flee, often multiple times (Severud et al. 2015b, Obermoller et al. 2017). Using the mortality movement approach to estimating survival rates and assigning cause-specific mortality (Chapter 1) was of notable value to understanding population trajectories when GPS collars could no longer be deployed on calves.

Predation is often the leading cause of mortality for ungulate neonates during their first summer of life (Barber-Meyer et al. 2008, Keech et al. 2011, Patterson et al. 2013, Severud et al. 2015a). After removing predators (brown bears [*Ursus arctos*], black bears [*U. americanus*], gray wolves [*Canis lupus*]) from a study area in Alaska, researchers observed a 29% increase in moose calf survival during the following 4 years (Keech et al. 2011). Wolf predation had the greatest influence on calf survival in northeastern Minnesota (Severud et al. 2015a, b). Other sources of calf mortality (e.g., drowning, malnutrition, meningeal worm [*Parelaphostrongylus tenuis*]) have been reported, and may still have important implications for population dynamics (Lankester 2010, Keech et al. 2011, Patterson et al. 2013, Severud et al. 2015a).

My objectives were to estimate summer and annual survival rates of moose calves, determine specific causes of mortality, and determine which had the greatest

impact on survival. I predicted low survival rates during their first summer of life (~3 mos of age), primarily due to wolf and bear predation, with wolves continuing to have the greatest impact.

## **STUDY AREA**

As described in Chapter 1, my study area, 6,068 km<sup>2</sup>, is part of the Northern Superior Upland region. Gray wolves and black bears, primary predators of moose calves, were estimated at 3/100 km<sup>2</sup>, and 23/100 km<sup>2</sup> throughout northern Minnesota and my study area, respectively (Garshelis and Noyce 2011, Erb and Sampson 2013). Pre-fawning white-tailed deer (*Odocoileus virginianus*) were estimated at densities of  $\leq 4/\text{km}^2$ , and were the main prey of wolves (Nelson and Mech 1981, DelGiudice et al. 2002, MNDNR 2011).

## **METHODS**

As described in Chapter 1, 129 adult female moose were captured and fitted with Iridium GPS collars (Vectronic Aerospace GmbH, Berlin, Germany) in 2013–2015 (Carstensen et al. 2017). Problems with malfunctioning GPS collars, battery life, and natural mortalities reduced the cohort to 35 adult females with functioning GPS collars available for intense computer-monitoring during the 2016 calving season.

In late April 2016, I began monitoring females for a calving movement, a long-distance movement followed by an intense localization (McGraw et al. 2014, Severud et al. 2015a). See Chapter 1 for more information on calving and calf mortality monitoring. Cause of death was assigned by locating carcass remains, signs of a specific predator (e.g., tracks, scat, hair, feeding patterns), and other site evidence (e.g., broken vegetation,

blood sprays). Following a mortality investigation, we conducted survival investigations at areas previously occupied by the dam (see Chapter 1 for further details). Survival field investigations and helicopter flight surveys allowed me to roughly estimate a twinning rate by either identifying evidence of a dam's surviving calf following a calf mortality, or by visually observing a second calf during the survey.

Flight surveys were conducted on 17–18 January 2017 and 19 April 2017 using a Bell Jet Ranger (OH-58) helicopter to locate all females with functioning GPS collars and to determine 8-month and near-annual (recruitment) calf survival, respectively (Chapter 1). Ultimately, I monitored the status of the dam (i.e., with or without a calf) via survival and mortality investigations, and movement rates.

### **Survival Analysis**

Annual survival was estimated from the birth-date of each calf to spring flights (19 Apr 2017). I estimated birth-date as 12 hours after the dam's calving localization (Severud et al. 2015a). Survival was analyzed by calf age, with Time 0 being equal to birth-date. Death-date was estimated by the initial flee of the dam from where evidence of a calf mortality was documented. If a calf was not observed with its dam during survey flights, it was assumed to be dead; mortality date was assigned as the mid-point between the birth-date and survey-date. When a cow was not observed during the survey, it was censored from the analysis. I calculated Kaplan-Meier (KM) survival using the R package, *KMsurv*. Twins confirmed by survival investigations or flights were treated as individuals in the KM survival curve. Calves that survived to the spring flights were considered recruited. Age-specific hazard of calves was determined using the R package,

*muha*. I smoothed the curve using a k-nearest neighbor distance bandwidth. The cause-specific mortality rates were calculated using a cumulative incidence function with R package, *wildl* (Sargeant 2011). All analyses were conducted with R version 3.2.5 (R Core Team 2017).

## RESULTS

In spring 2016, I determined that 31 of the 35 (89%) cows were pregnant based on a calving movement and site confirmation or by visual observation of  $\geq 1$  calf. Of the 4 initially considered not pregnant, 1 resumed transmitting during the calving season, and a calf was confirmed via camera trap. Another cow was killed by wolves with a calf *in utero* (M. Carstensen, MNDNR, unpublished data). I was unable to confirm calving for the 2 remaining cows. I observed 85% (28 of the 33) of the females, or 97% (28 of 29) of the pregnant females, make a calving movement. Only 1 female was observed not making a calving movement, but was seen with a calf by the public. Mean duration of the calving movement was 24.5 hours ( $\pm 2.5$  [SE], range = 3–64 hr,  $n = 28$ ), and mean total path length over this period was 5.3 km ( $\pm 0.8$ , range = 0–18 km,  $n = 28$ ). Mean displacement from the start of the calving movement to the birth location was 2.3 km ( $\pm 0.6$ , range = 0–15 km,  $n = 28$ ).

I confirmed evidence of a calf for 27 of 31 cows via calf pellets, tracks, afterbirth, or visualization of the calf (e.g., camera trap or observed by public). In the 4 remaining cases, I was only able to confirm the presence of a calving bed, but subsequent evidence of reduced movements by the cow further increased our confidence a calf was at-heel.

Mean birth-date was 12 May 2016 (median = 11 May, range = 24 Apr–10 Jun); 75% of the localizations occurred during 4–14 May 2016.

I documented 14 calf mortalities from 13 cows during the spring-summer (7 May to 21 June 2016) field season (Fig. 1). On 12 January 2017, the last calf mortality was reported as a vehicle collision-kill at 243 days of age (Fig. 1). Following a mortality, I checked and confirmed evidence (e.g., tracks, pellets, hair) of a surviving twin for 5 cows. The remaining cows were checked and had no confirmed evidence of a surviving calf and exhibited increased movement rates. Primary evidence for predator-caused mortalities was scat containing calf bones or hair ( $n = 9$ ) and feeding patterns on calf remains ( $n = 4$ ) indicating a particular predator. Predation, primarily by wolves, accounted for 87% of all mortalities (Fig. 1). Including both calf mortalities and confirmation of calf presence (a survivor), 30-day calf survival was 67% ( $\pm 8$ , 95% CI = 53–84%,  $n = 36$ ; Fig. 2). Calves died at a mean 30.6 days ( $\pm 15.5$ , range = 3–243 days,  $n = 15$ ) of age. I also observed 5 cases where a dam made a mortality movement, but no evidence of a calf mortality was found. Either evidence of a mortality was not detected within the searched area or the mortality occurred beyond this area. Winter survey flights confirmed these calves were likely dead. Furthermore, during the flights I noted 4 calves were not observed with their dams, but no mortality movement was previously observed. The annual survival rate was 33% ( $\pm 8$ , CI = 20–53%,  $n = 36$ ; Fig. 2).

The hazard was greatest during the first 50 days of life, with a more gradual decline from 50 to 100 days of age (Fig. 3). The probability of death beyond 100 days of age was very low. The risk of mortality rose quickly for the first 30 days of life (Fig. 4).

The cumulative probability of calves being killed by wolves and bears was 33% (90% CI = 18–49%) and 11% (90% CI = 1–21%), respectively, whereas the probability for all other causes was 11% (90% CI = 0–22%; Fig 4).

During the 17–18 January 2017 survey flight, I observed 14 moose calves from 25 of the original 35 cows monitored at calving. There were 10 moose not located during the winter survey (3 mortalities, 7 with non-functioning GPS collars). During the subsequent spring survey (19 Apr 2017), I located 6 moose calves from 17 cows (0.35 calf:cow ratio); 8 additional moose were not located (3 cows were not found, 2 collars had been remotely removed, 3 collars were non-functioning). For the 2016 study cohort, the estimated twinning rate was 29% (7 of 24 cows with known calf production).

## **DISCUSSION**

Identifying parturition via the calving movement continued to be a reliable tool for estimating pregnancy rates. I observed only 1 case where a cow did not make the calving movement, but was subsequently observed with a calf. With this technique, recapturing GPS-collared cows to fit vaginal implant transmitters (VITs) each year to monitor calving activity would not be necessary, which reduces operational costs and stress to the animals. In 2016, total path length and displacement associated with calving movements were comparable to movements of 2012 to 2015 (McGraw et al. 2014; Severud et al. 2015a, b). I noted that 85% of monitored cows (97% of our pregnant cows) made a calving movement, similar to cows in 2014 and 2015 (Severud et al. 2014, 2015b). Lower pregnancy rates were observed in 2013, likely attributable in part to the higher winter tick (*Dermacentor albipictus*) infestation, severe nutritional restriction, and lower

survival rate of adult females (DelGiudice et al. 2013, Carstensen et al. 2014). Average birth-dates varied little during the past 4 years in this population. The median birth-date of 2016 (11 May) was closest to those reported for 2013 (14 May) and 2015 (10 May) in northeastern Minnesota, whereas it was later in 2014 (19 May), possibly attributable to a severe, prolonged winter (Severud et al. 2015*a, b*). The later average birth-date of 2014 may be indicative of poorer condition of adult females during the calving season or previous rut compared to 2013, 2015, and 2016 (Cameron et al. 1993; Testa and Adams 1998; Severud et al. 2014, 2015*a, b*).

Similar to 2013–2015, the proportion of predator-kills remained consistently high during 2016, increasing confidence that predators, especially wolves, are the leading cause of calf mortality in northeastern Minnesota (Severud et al. 2015*a, b*). Predation was the primary cause of natural mortalities in many ungulate neonate studies where predators are present (Ballard et al. 1981, Osborne et al. 1991, Kunkel and Pletscher 2001, Keech et al. 2011). However, contrary to findings elsewhere, wolves had a greater impact than bears on calf survival in my study. In central Ontario bears preyed on calves until early summer, whereas, wolves killed calves into the winter (Patterson et al. 2013). The cumulative incidence function for both bear and wolf predation in my study increased rapidly during the first 30 days of calf life (Fig. 4), emphasizing that these calves were particularly vulnerable to predation at a young age. On December 19, 2014, wolves in the Upper Midwest were relisted as a Threatened Species (Mech 2017), precluding the use of annual wolf harvests as a management tool, which would have the potential to increase moose calf survival and recruitment. In western Alaska, annual calf

mortality from predation, largely considered additive, decreased substantially when predators were removed (Keech et al. 2011). Elevated predator densities may continue to impact survival of calves in northeastern Minnesota (Vucetich et al. 2011, Sand et al. 2012, Mech and Fieberg 2014).

Neonatal ungulate survival can dramatically influence population dynamics (Unsworth et al. 1999). Calf survival to 30 days has been consistently low, 67% in the present study (2016), compared to 58 and 68% in in 2013-2014 (pooled) and 2015, respectively (Severud et al. 2015*b*). In 2015 and 2016, without GPS collars on calves, survival of twins may have been overestimated, because cows rarely made the mortality movement with a surviving calf present. Annual survival was similar for all years (2013–2016), ranging between 29 and 40% (Severud et al. 2015*b*), 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 (2013–2016, M. Carstensen, MNDNR, unpublished data), was moderately depressed and less variable. These demographics likely account for the sluggish performance, but recent stability of this population compared to its sharp decline from 2009 to 2012 (DelGiudice 2017).

Calves of cows selecting calving sites with greater cover and less edge were more likely to avoid wolf predation and survive (Langley and Pletscher 1994, Bowyer et al. 1999, Scarpitti et al. 2007, Severud 2017). In 2016, 4 of 13 (30.8%) calves were killed at or near (<50 m) their calving site. However, previously (2013–2014) the calving site was a haven for moose calves (Severud 2017). Increased wolf numbers in the study area may

explain an increased incidence of wolf-caused mortalities at calving sites (Mech et al. In press, Erb and Sampson 2013, Erb et al. 2016). Alternatively, my 2016 study cohort (i.e., sample size) may not be representative of the population in this regard.

Despite a moratorium on capturing and GPS-collaring moose neonates in 2016, monitoring dams for calving and mortality movements, field investigations, and relatively brief seasonal helicopter calf surveys, allowed me to collect valuable reproductive, survival and cause-specific mortality data that have contributed to our improved understanding of their impacts on the performance and trajectory of the population in northeastern Minnesota. Continuing to study reproductive success, cause-specific mortality, and recruitment as the population varies will be of critical value to the ability of management to support the long-term persistence of moose in northeastern Minnesota.

Figure 1. Percent of mortality ( $n = 15$ ) of moose calves attributable specific causes in northeastern Minnesota, May 2016–January 2017.

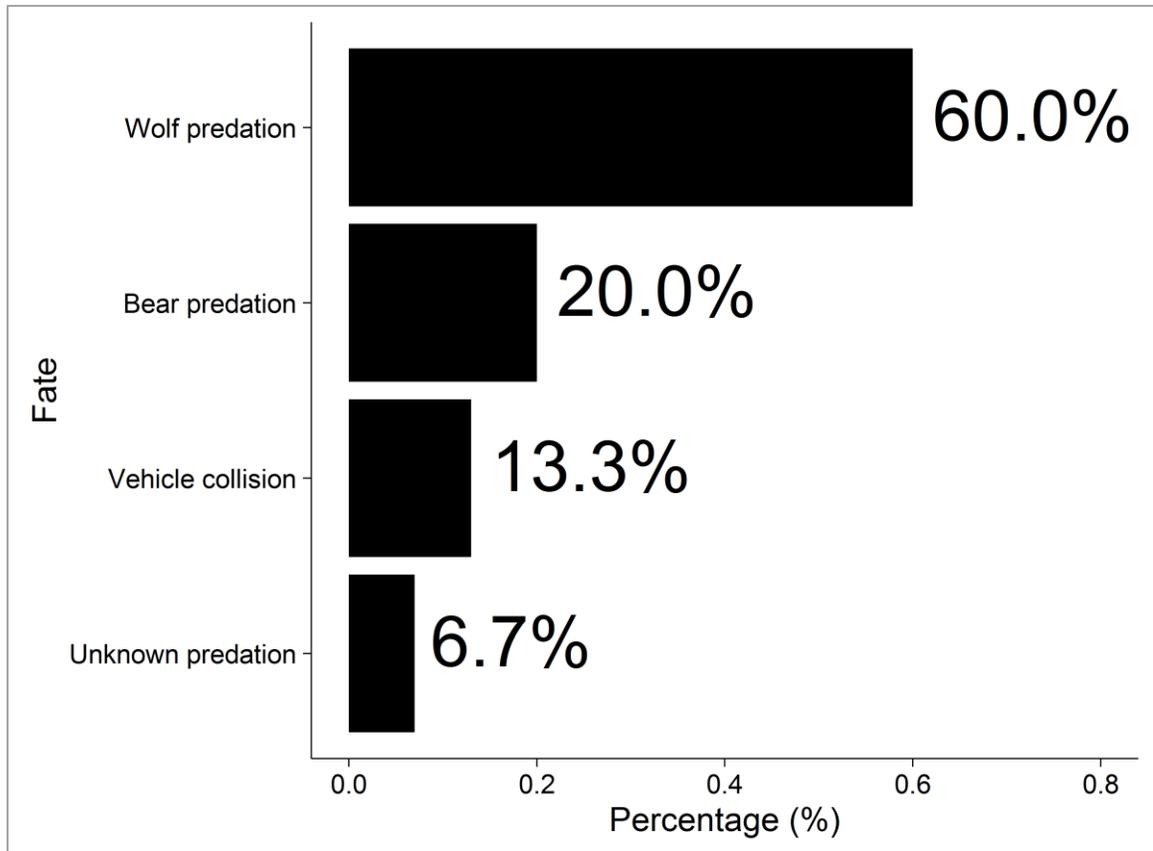


Figure 2. The Kaplan-Meier survival curve for known fates of moose calves ( $n = 36$ ) in northeastern Minnesota, May 2016–April 2017. Gray shading represents 95% confidence intervals.

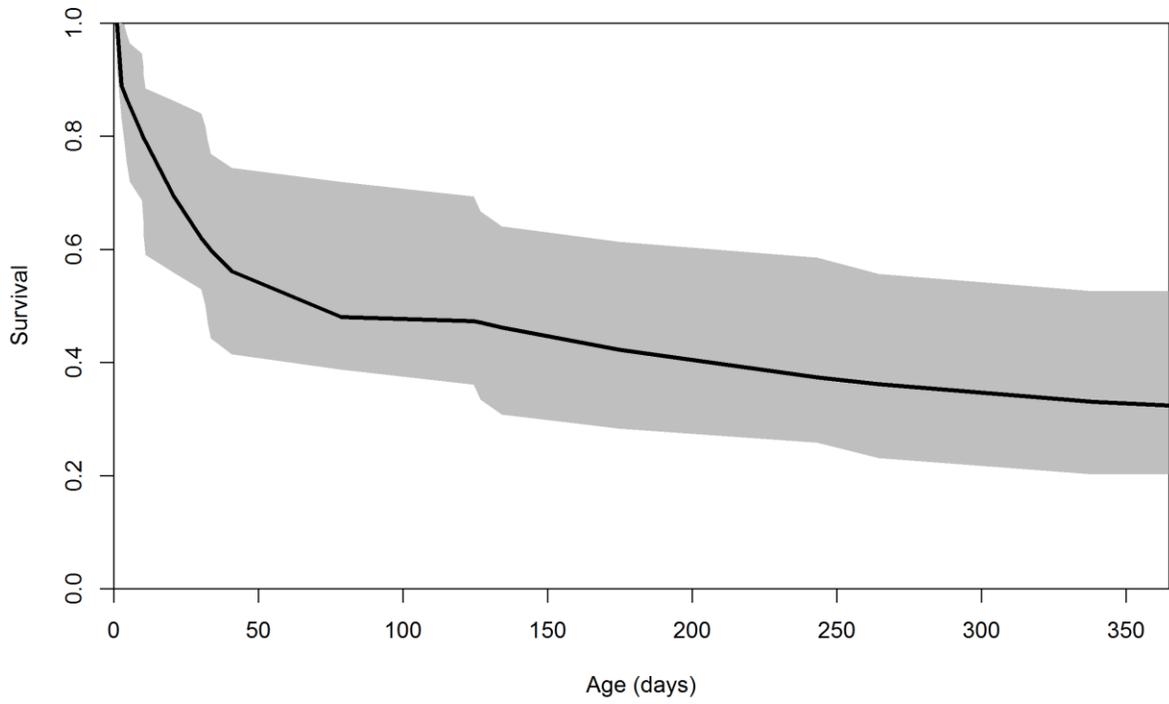


Figure 3. Empirical hazard function for known fates of moose calves ( $n = 36$ ), northeastern Minnesota, May 2016–April 2017. Gray shading represents 95% confidence intervals.

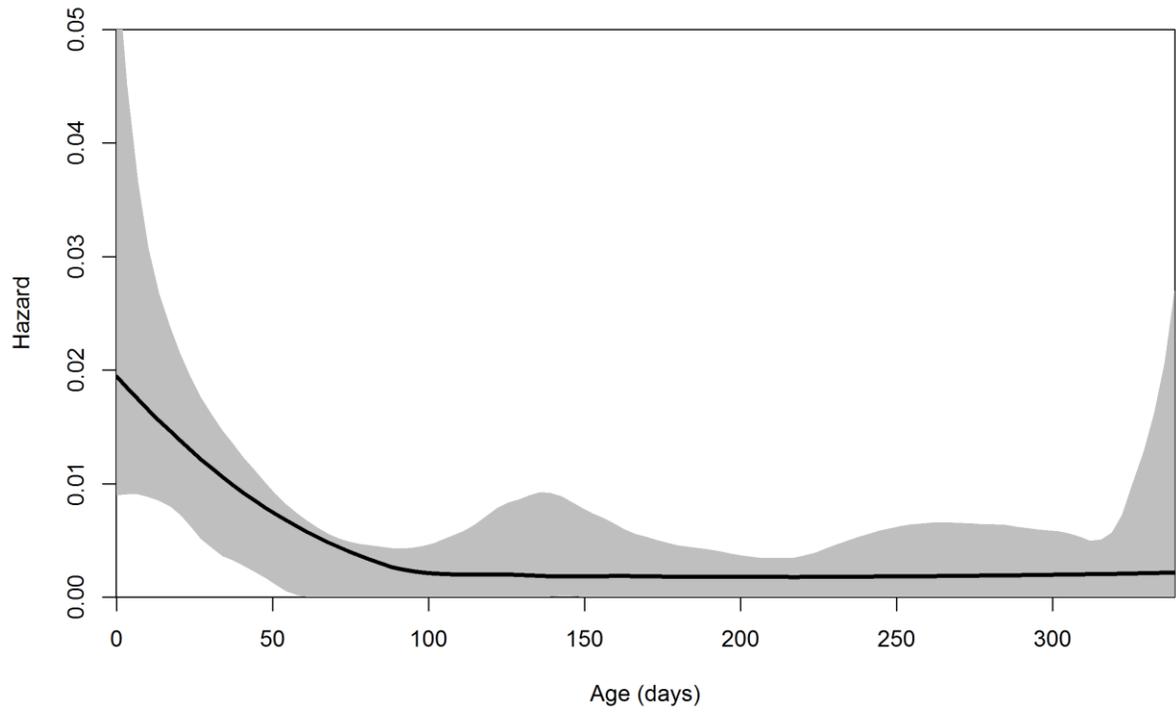
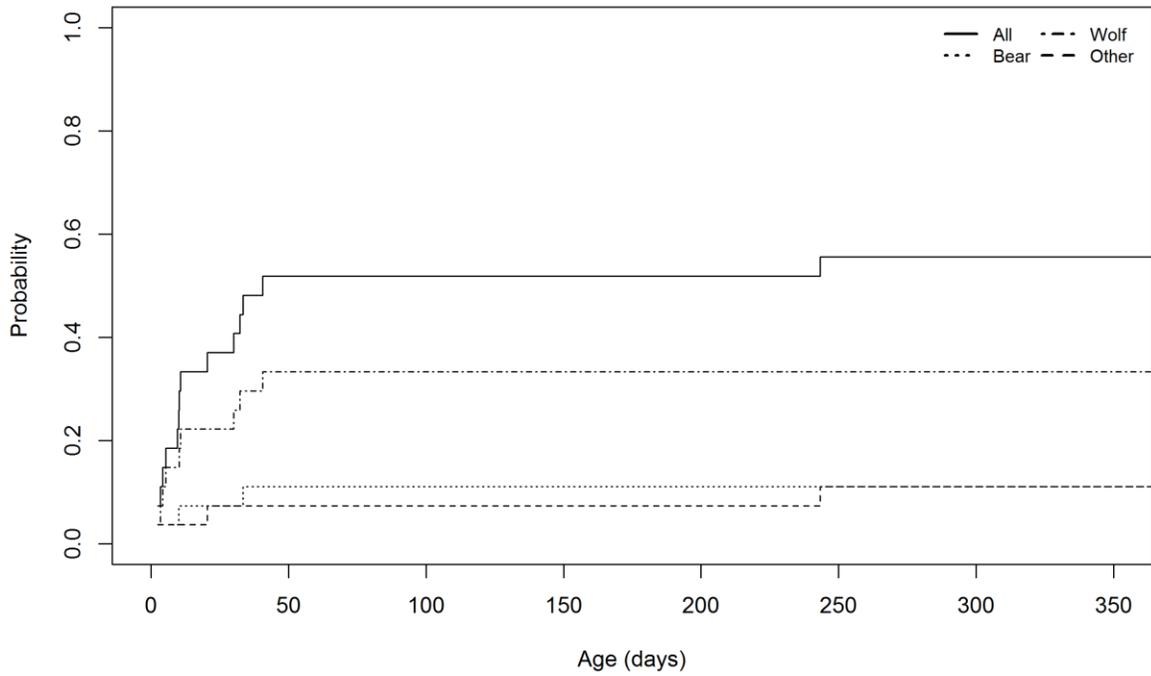


Figure 4. Cumulative incidence function for cause-specific mortality of moose calves ( $n = 15$ ), northeastern Minnesota, May 2016–April 2017. Causes of mortality include wolf (9) and black bear (3) predation, and other (vehicle collision [2] and unknown predator [1]).



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