Wildlife Society Bulletin 39(3):616–625; 2015; DOI: 10.1002/wsb.558

Tools and Technology

Using GPS Collars to Determine Parturition and Cause-Specific Mortality of Moose Calves

WILLIAM J. SEVERUD,[1] *Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, 2003 Upper Buford Circle, Suite 135, Saint Paul, Minnesota 55108, USA*

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

TYLER R. OBERMOLLER, *Forest Wildlife Populations and Research Group, Minnesota Department of Natural Resources, 5463-C West Broadway Avenue, Forest Lake, Minnesota 55025, USA*

THOMAS A. ENRIGHT,[2] *Forest Wildlife Populations and Research Group, Minnesota Department of Natural Resources, 5463-C West Broadway Avenue, Forest Lake, Minnesota 55025, USA*

ROBERT G. WRIGHT, *Minnesota Information Technology Services, Minnesota Department of Natural Resources, 5463-C West Broadway Avenue, Forest Lake, Minnesota 55025, USA*

JAMES D. FORESTER, *Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, 2003 Upper Buford Circle, Suite 135, Saint Paul, Minnesota 55108, USA*

ABSTRACT Global positioning system (GPS) collars have been deployed on adult moose (*Alces americanus*) and other ungulates to study various aspects of their ecology, but until the current study they have not been fitted to moose neonates. The moose population in northeastern Minnesota, USA, has been declining since 2006, and information on neonatal survival and cause-specific mortality are needed. We monitored hourly movements of GPS-collared females for indications of calving. During 2 May–2 June 2013 we observed 47 of 73 collared females (50 known pregnant, 17 not pregnant, 6 unknown pregnancy status) make "calving movements" followed by a clustering of locations. After allowing a mean bonding time of 40.2 hr, we approached their calving sites and captured and GPS-collared 49 neonates from 31 dams. We closely monitored dam–calf movements and launched rapid investigative responses to calf mortality notifications to determine cause of mortality. Mean response time was 53.3 hr, but ranged from 0.3 hr to 579 hr, depending on collar accessibility and proper functioning of the GPS component. We censored capture-related mortalities and slipped collars. Twenty-five of 34 calves (74%) died of natural causes as of 31 December 2013, including 1 after natural abandonment, 1 after abandonment of unknown cause, 1 drowning, 1 unknown predator kill, 1 lethal infection from wolf (*Canis lupus*) bites, 4 black bear (*Ursus americanus*) kills, 12 wolf kills, and 4 "probable wolf kills." As this technology develops, the quantity and quality of survival, cause-specific mortality, movement, and habitat use data generated from intense monitoring of GPS-collared adults and offspring will have unprecedented value associated with management at the population and landscape scales. © 2015 The Wildlife Society.

KEY WORDS *Alces americanus*, calving, cause-specific mortality, GPS collars, Minnesota, moose, mortality, neonate, survival.

In the United States, Minnesota's northeastern (NE) moose (*Alces americanus*) population has been experiencing a downward decline from 2006 to 2014 (DelGiudice 2014). The state's northwestern (NW) population fell dramatically from approximately 4,000 to <100 animals from the mid-1980s to 2007 (Murray et al. 2006, Lenarz et al. 2009). From 2006 to 2014, the NE population has exhibited adult annual survival rates similar to those documented for the NW population during its decline (81%; Lenarz et al. 2009, M. Carstensen, Minnesota Department of Natural Resources [MNDNR], unpublished data). Lenarz et al. (2009) reported 89% of natural mortalities of collared adults as "unknown cause"; estimated calf survival was 40%, but causes of mortality were not investigated (Lenarz et al. 2010). Furthermore, calves were assumed to have died if their dam died, but this depends on timing of the dam's death relative to the calf's age (Jolicoeur and Crête 1988). Calf survival can markedly affect annual variation in population growth, especially in populations experiencing low and

Received: 9 October 2014; Accepted: 30 March 2015
Published: 21 July 2015

[1]*E-mail: seve0135@umn.edu*
[2]*Present address: Department of Wildlife, Sustainability, and Ecosystem Sciences, Tarleton State University, 1333 West Washington Street, Stephenville, TX 76402, USA.*

variable survival rates of calves (Gaillard et al. 2000, Raithel et al. 2007, Patterson et al. 2013). Recently, the MNDNR initiated aggressive studies of cause-specific mortality of adult moose and calves in NE Minnesota to address information needs and to facilitate a more effective management response to the declining population.

Very high frequency (VHF) collars were deployed in the aforementioned moose survival study (Lenarz et al. 2009, 2010) and others focused on moose calf survival and cause-specific mortality (Ballard et al. 1981, Osborne et al. 1991, Keech et al. 2011, Patterson et al. 2013). Observations of VHF-collared animals commonly are limited by overall frequency of fix locations (determined from the ground or fixed-wing) and flights biasing locations toward diurnal and fair weather conditions (Rodgers et al. 1996). Consequently, response times to mortality events are delayed. Using VHF collars also is time- and labor-intensive compared with GPS collars (Moen et al. 1996, Rodgers et al. 1996, Bowman et al. 2000). Global positioning system collars have been used on adult moose to examine habitat use, predation, fine-scale movement, migration, and parturition behavior (Moen et al. 1996, Rodgers et al. 1996, Welch et al. 2000, van Beest and Milner 2013, McGraw et al. 2014, White et al. 2014). We intensively monitored preparturient, GPS-collared females to facilitate GPS-collaring their neonates. Until the current study, expandable GPS collars have not been fitted to moose neonates, and had only recently been used in small numbers on other ungulate neonates in the wild (fallow deer [*Dama dama*], $n = 3$; Kjellander et al. 2012) or in captivity (domestic horse [*Equus caballus*], $n = 4$; Hampson et al. 2010). This technology allowed us to conduct cause-specific mortality investigations in a timelier manner than had been possible with conventional telemetry techniques (Barber-Meyer et al. 2008, Keech et al. 2011, Patterson et al. 2013).

The objectives of our study were to 1) describe the efficacy of using movement behavior of GPS-collared, adult female moose to determine timing and location of calving, facilitate neonate capture, and assess calf production, and 2) evaluate remote tracking of GPS-collared dams and neonates to expedite investigations of calf mortalities and assign cause of mortality with greater confidence.

STUDY AREA

We conducted this study in a 6,636 km^2 area of NE Minnesota, located between 47°00′N and 47°56′N, 89°57′W and 92°17′W (Fig. 1). The area was characterized as Northern Superior Uplands (MNDNR 2015) and was interspersed with lakes, wetlands, logging roads, and low-density human settlements. Stands of northern white cedar (*Thuja occidentalis*), black spruce (*Picea mariana*), and tamarack (*Larix laricina*) predominated in the lowlands, and balsam fir (*Abies balsamea*), jack (*Pinus banksiana*), eastern white (*P. strobus*), and red pines (*P. resinosa*) were most prevalent on the uplands, where mixed stands of trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*) also occurred. Open areas included lowland or upland deciduous shrub and sedge (*Carex* spp.) meadows (MNDNR 2015).

White-tailed deer (*Odocoileus virginianus*) populations occurred at prefawning densities of $\leq$4 deer/km^2 (Grund 2013). Major predators of moose in the area included gray wolves (*Canis lupus;* 3 wolves/100 km^2; Erb and Sampson 2013) and black bears (*Ursus americanus;* 23 bears/100 km^2; Garshelis and Noyce 2011). Moose had not been harvested in the state since 2012 (DelGiudice 2014).

METHODS

Adult Moose Capture and Handling

In January and February 2013, 111 adult moose (84 females, 27 males) were captured and handled as part of the MNDNR's study of cause-specific mortality (Butler et al. 2013). Capture and handling protocols met American Society of Mammalogists guidelines (Sikes et al. 2011). The capture crew fitted moose with Iridium GPS Plus collars (Vectronic Aerospace GmbH, Berlin, Germany). These collars have an expected life of 5 years and use Iridium satellite 2-way communication technology, which allows them to be reprogrammed remotely. Collars collected GPS locations every 4 hr 15 min and transmitted all recorded locations after 6 successful fixes along with the collar status (Normal or Mortality). When a collar entered mortality mode (triggered by limited motion for 6 hr), the accelerometer triggered a mortality schedule (immediate collection of 10 fixes to force a data transmission, followed by fixes acquired at 30 min intervals for 6 hr) and a notification was sent to the base station, which then generated both SMS (text message) and e-mail notifications to designated project staff. Alerts listed the collar serial number and time it entered mortality mode. Summer field tests demonstrated mean linear error ($\pm$ SE, range) of locations from adult collars of 3.7 m ($\pm$ 0.3, 0–17 m) under open canopy and 7.0 m ($\pm$ 0.3, 1–36 m) under dense canopy ($\geq$80% closure; W. J. Severud, unpublished data).

Minnesota Department of Natural Resources analyzed blood samples taken at time of capture for progesterone concentrations. Previously reported mean progesterone levels of pregnant females ranged from 6.1 ng/mL to 7.4 ng/mL, nonpregnant females 0.4 to 0.7 ng/mL, and 1 male 0.42 ng/mL; the pregnancy threshold was $\geq$2 ng/mL (Haigh et al. 1982, Testa and Adams 1998, Murray et al. 2006). Serum progesterone indicated a 75% pregnancy rate of all captured females that we tested, with mean $\pm$ standard deviation progesterone levels of pregnant females, nonpregnant females, and males of 4.8 ± 1.6 ($n = 58$), 0.4 ± 0.2 ($n = 19$), and 0.5 ± 0.7 ($n = 23$) ng/mL, respectively (E. A. Butler and M. Carstensen, Minnesota Department of Natural Resources, unpublished data).

Monitoring for Calving

We began monitoring 73 females on 1 May 2013 (50 pregnant, 6 unknown pregnancy status [no blood sample taken at capture], and 17 not pregnant); 11 of 84 collared females died between capture and initiation of monitoring (Butler et al. 2013). Female collars were remotely programmed to acquire fixes hourly during May and to transmit 4 times/day. We monitored female movements

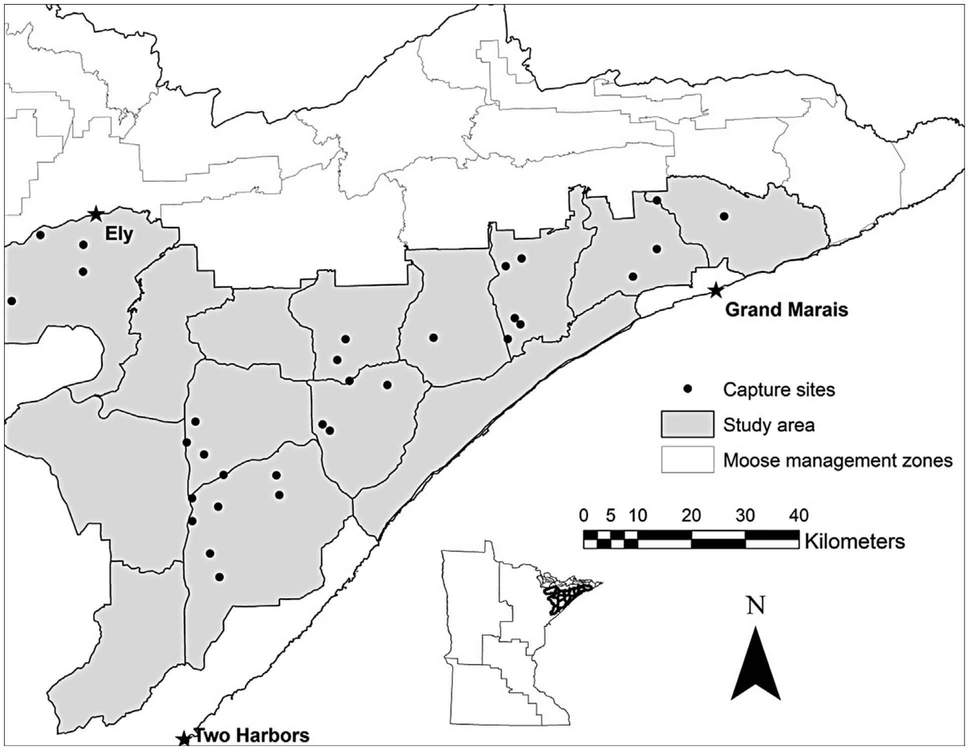

Figure 1. Capture sites ($n = 31$) of moose neonates (6,636 km^2 study area), 8–17 May 2013, northeastern Minnesota, USA.

during preparturition and calving, with particular attention paid to pregnant females. We looked for movement patterns indicative of calving (Welch et al. 2000), including a long-distance movement followed by localization (Bowyer et al. 1999, Testa et al. 2000, Poole et al. 2007, McGraw et al. 2014). Generally, parturition occurs within 12 hr after localizing (R. A. Moen, Natural Resources Research Institute, personal communication). We received automated reports by e-mail 6 times/day (0400, 0800, 1200, 1600, 2000, 2400 hr). Each e-mail included 2 files describing the most recent location of each animal (in csv and kml formats), in addition to a pdf report displaying movement and location metrics for each collared female. The reports contained a coarse-scale map of NE Minnesota with all females displayed and a summary table of all animal locations and distances moved in the past 24 and 48 hr. This table was followed by a separate page for each female that included the date and time of the last location, movement path over the past 5 days, movement path over the past 24 hr overlaid on Google Earth (earth.google.com) imagery, and a plot showing the 3 hr moving average of distances moved per hour (speed) over the previous 10 days. We monitored the distance plot for relatively large peaks in movements followed by a dampening of movement (i.e., localization). If a female's displacement was <100 m during a 36 hr interval after making a long-distance movement, the program flagged it as "localized," and its calf was determined "eligible" for capture. This gave females and calves ≥24–36 hr of bonding time. Once reports indicated a localized female, we checked the movement path using Vectronic's website (www.vectronic-wildlife.com) and graphed hourly movement rates in Excel (2010; Microsoft Corporation, Redmond, WA) using data sent to our base station and managed by GPS Plus X software (Vectronic Aerospace GmbH). Once the calf was collared, its collar was paired with its dam's collar so that proximity between them could be monitored as well. Calves then had similar reports generated automatically.

Calf Capture and Handling

A capture crew (Quicksilver Air, Fairbanks, AK) located eligible calves via helicopter and then landed to allow 1–2 handlers to disembark. Typically, handlers were able to easily approach and capture calves. Each calf was weighed (± 0.5 kg) by spring-scale, ear-tagged, and blood drawn. The crew recorded morphological measurements (hind foot length, upper and lower neck circumference, chest girth, total body length [± 1 cm]) and rectal temperature (± 0.1° F), and fitted GPS collars. The crew weighed calves in grain sacks ($n = 11$), but then switched to using a rope sling to limit transfer of scent from one calf to another ($n = 32$). Handlers did not wear gloves. We estimated age of calves (± 0.5 days) following Larsen et al. (1989). We used a fixed-wing aircraft as a spotter plane for the first 5 days of captures to record handling times, dam behavior, and status (e.g., percent hair loss due to winter tick [*Dermacentor albipictus*] infestation, aggressiveness). If twins were spotted, both were handled, collared, and released together to minimize the risk of capture-related abandonment (Keech et al. 2011). We placed collars in bags with vegetation, mud, and moisture for ≥24 hr before captures to mask human and collar scent. All calf captures and handling protocols followed requirements of the Institutional Animal Care and Use Committee for the University of Minnesota (Protocol 1302-30328A) and were consistent with guidelines recommended by the American Society of Mammalogists (Sikes et al. 2011).

Calf Collars

Calves were fitted with a GPS PLUS VERTEX Survey-1 GLOBALSTAR collar (Fig. 2) with expandable belt (420 g, box dimensions 85 × 59 × 75 mm, belt 3 cm wide, initial circumference 35 cm, fully expanded circumference 65 cm; Vectronic Aerospace GmbH), which recorded hourly locations for 1 year and transmitted (via Globalstar satellite 1-way communication) every third successful location. All locations also were stored on-board the collar. These collars were programmed by the vendor and could not be reprogrammed in-hand or remotely. Calf collar accelerometers used similar mortality delay, schedule, and notifications as the adult collars (see above). Text messages included the serial number of the calf's and dam's collar. The expandable collar material included stitched expansion loops and a breakaway section designed to deteriorate at approximately 400 days. Summer field tests demonstrated that mean linear error (± SE, range) of calf collar locations was 24.9 m (± 2.7, 1–274 m) under open canopy and 33.7 m (± 3.1, 1–236 m) under dense canopy (≥80% closure; W. J. Severud, unpublished data).

Dam–Calf Monitoring

Once calves were collared, we monitored dam–calf groups several times daily as updated locations were received by our base station. We examined proximity and synchrony of dam–calf GPS locations until fate was known (mortality, slipped collar, failed collar). When we received a mortality alert text message, a mortality response team initiated an investigation.

Figure 2. GPS (Global positioning system) PLUS VERTEX Survey-1 GLOBALSTAR collar with expandable belt (Vectronic Aerospace GmbH, Berlin, Germany) deployed on moose neonates ($n = 49$), 8–17 May 2013, northeastern Minnesota, USA.

Collars can be kept in active mode by motion caused by predators, scavengers, or moving water, and data transmissions can be blocked if satellite reception is poor (e.g., if collar is buried). We decided to rely on closer monitoring of dam–calf groups after we observed several dams moving from stationary calf collars, yet we did not receive a mortality alert text message. We consulted the Vectronic website each morning and reviewed raw data from the base station to see whether collars were actively transmitting or were in mortality mode. Collars that stopped transmitting may have been buried. These methods also allowed us to track capture-induced abandonment of calves by their dams (DelGiudice et al. 2015).

Mortality Investigations

To avoid disturbing a dam and any surviving calves, we checked the dam's most recent location before deploying a mortality response team. The dam's location or behavior around the time the calf's collar entered mortality mode could indicate whether the alert message was the result of a true mortality or a slipped collar. If a dam remained at the mortality site, we did not deploy a response team until it departed.

We used several sets of coordinates when navigating to a mortality site, including the most recent calf(ves) and dam locations, the locations at the estimated time of death, locations from the past 2 days (to assess whether the collar was moved from a mortality or kill site to its current location), and locations from the last time dam and calf were together. All locations were loaded into handheld GPS units (GPSmap 62sc; Garmin, Olathe, KS).

In addition to relying on GPS location data, we also homed in on VHF frequencies of the presumably dead calf, its dam and sibling (if a twin). Other equipment packed in for mortality investigations included a full field necropsy kit (M. Carstensen, unpublished data) to be used when the carcass could not be extracted from the field, as well as safety equipment (yellow vests, eyewear, bug suits, bear spray, and 12-gauge shotgun loaded with rubber shot, buck shot, and a slug). We were attempting to estimate cause-specific mortality and were alerted to mortalities 6 hr postmortem; therefore, we needed to anticipate potentially aggressive predators or scavengers defending fresh kills or carcasses (McNay 2002, Herrero et al. 2011), or dams protecting dead calves (LeResche 1968). Care was taken to haze off predators and scavengers when approaching the mortality site; bear repellent spray and firearms were available as a last resort for protection, but their use was not anticipated (Smith et al. 2008, 2012). We postponed investigations when predators were sighted on the carcass; return was dependent on the age and size of the carcass as an indication of how long the predator or scavenger might feed. Response crews consisted of ≥3 people.

While navigating to the mortality site, we used telemetry to correct for GPS error and confirm the collar was still in mortality mode (96 beats/min [bpm] vs. 48 bpm when in active mode). When our team arrived within 100 m of the presumed mortality site, we conducted a safety briefing. We distributed ourselves to optimize search effectiveness, but all group members stayed within earshot or line of sight. We searched for sign indicative of specific predators (e.g., wolves, bears) or of scavenging (Ballard et al. 1979). Characteristics of carcasses preyed upon by bears included peeled or inverted hide, cached body parts, selective feeding of viscera or sensory organs, and claw marks across the body. Wolves typically did not consume viscera (especially the rumen and its contents), chewed the ends of long bones, scattered remains over a large area, and inflicted puncture wounds on the head, neck, or hindquarters. Depredated carcasses exhibited subcutaneous hemorrhaging at wound sites or were surrounded by signs of a struggle (broken or matted vegetation, blood sprays on vegetation or collar). Scavenged carcasses may be surrounded by many pellets and smell of decay. Sternal or lateral carcass position of older and larger calves also may indicate predation or scavenging, respectively (M. W. Schrage, Fond du Lac Resource Management Division, personal communication). We looked for moose or predator hair, tracks, or scat. Photographs were taken before any evidence was handled. We photographed tracks and scat and collected scat and hair when predator identification was uncertain. Swabs also were available to sample for DNA from predator or scavenger saliva from wounds on the carcass (B. R. Patterson, Ontario Ministry of Natural Resources and Forestry, personal communication). We used the preponderance of evidence to assign causes of mortality.

Our primary field objective was to recover the entire carcass and deliver it to the University of Minnesota's Veterinary Diagnostics Laboratory (VDL) for necropsy. When the carcass could not be extracted and transported (as in the case of older or larger calves in remote areas), we conducted a detailed field necropsy. When scavenged or mostly consumed, we collected fresh organ and tissue samples and shipped them to the VDL as feasible (Butler et al. 2011).

Necropsies were thorough whether conducted in the field or at the VDL, although necropsies conducted by board-certified pathologists in a lab setting were more likely to yield detailed results. We scanned for external and internal abnormalities, collected tissue samples (stored fresh and in formalin) from most organs, weighed the carcass, and measured the same morphometrics we recorded at captures. Pathology and histology tests were conducted by the University of Minnesota's VDL and Clinical Pathology Laboratory. When the cause of death was unknown, we collected various samples for metagenomic testing (M. Carstensen, personal communication). We checked stomachs for curdled milk or vegetation; depending on a calf's age, these could yield insight into whether it was abandoned, refused milk by its dam, or unable to nurse. Pathologists looked for signs of capture myopathy (e.g., coffee-colored urine, white striations in muscle), but diagnosis is difficult, especially for extremely young animals (A. Wuenschmann, University of Minnesota VDL, personal communication).

When we found a GPS collar without a carcass or other evidence of predation, we backtracked to the last known locations of the calf and its dam to conduct an expanded search. The Iridium adult collars were more accurate than the Globalstar calf collars, so we used the dam's location from the approximate time of death of the calf to search for evidence of a mortality. Once the calf collar was located, we determined the collar to be slipped rather than associated with mortality when the breakaway section was frayed or the bolts holding the breakaway section were loose, coupled with both an absence of blood on the collar and lack of mortality evidence within a 30 m radius of the collar. Also, dams rarely fled the site of a slipped collar, whereas they typically fled when a calf was preyed upon.

RESULTS

Monitoring for Calving

We observed 48 of 73 (66%) monitored females localize during May–June. Of these 48, 47 (43 pregnant, 4 unknown pregnancy status) made a long-distance calving movement followed by localization (Fig. 3); the female that did not make a long-distance movement was pregnant. In total, 44 of 50 (88%) pregnant females localized. Four nonpregnant females localized during this time. Mean path length from start of the calving movement to localization was 5.4 km ($\pm$ 0.7, 0.4–22.7 km) and mean displacement was 2.1 km ($\pm$ 0.3, 0.05–13.4 km). These movements occurred over 14.4 hr ($\pm$ 1.5, 1.0–42.5 hr). Calving occurred during 2 May–2 June 2013. Mean and median calving date for all monitored females was 14 May ($\pm$ 0.9 days); 73% (35 of 48) of the calving localizations occurred 6–17 May. Overall, monitored females (pregnant and unknown pregnancy status) presumed to have calved localized for 3.3 days ($\pm$ 0.3, 1.1–14.7 days) at calving sites, but females whose calves we collared localized less than half as long at calving sites as did females whose calves we did not collar (Table 1). Of the 48 females that localized, 32 (67%) moved 415 m ($\pm$ 66.9, 42.5–1,821 m) to a secondary postparturition site before again localizing for 4.2 days ($\pm$ 0.5, 0.6–12.2 days). Females we approached to collar calves moved farther and remained at their secondary site longer, than did females we did not approach (Table 1). Of 32 females that moved to secondary localization sites, 22 had their calves captured. All dam–calf groups spent 6.1 days ($\pm$ 0.5, 1.1–14.7, $n = 48$) in postparturition areas (birth site plus subsequent localization). We observed no effect of capture on duration localized in postparturition areas (Table 1).

Our automated reports accurately flagged 14 dams as localized; we subsequently collared 24 of their calves. The reports flagged 1 dead moose, and 3 moose that localized after we collared their calves (i.e., 4 false positives). The reports did not flag 17 dams that we approached (based on our on-screen observations of their movements) for neonate capture, and 12 dams that appeared to have made movements indicative of calving (3 within the capture operation window), but were not approached (i.e., 29 false negatives). We do not know whether 2 females were flagged because reports were not generated for 2 days because of technical problems.

Calf Capture and Handling

We collared 49 calves of 31 dams during 8–17 May 2013. Mean bonding time (duration of localization before capture

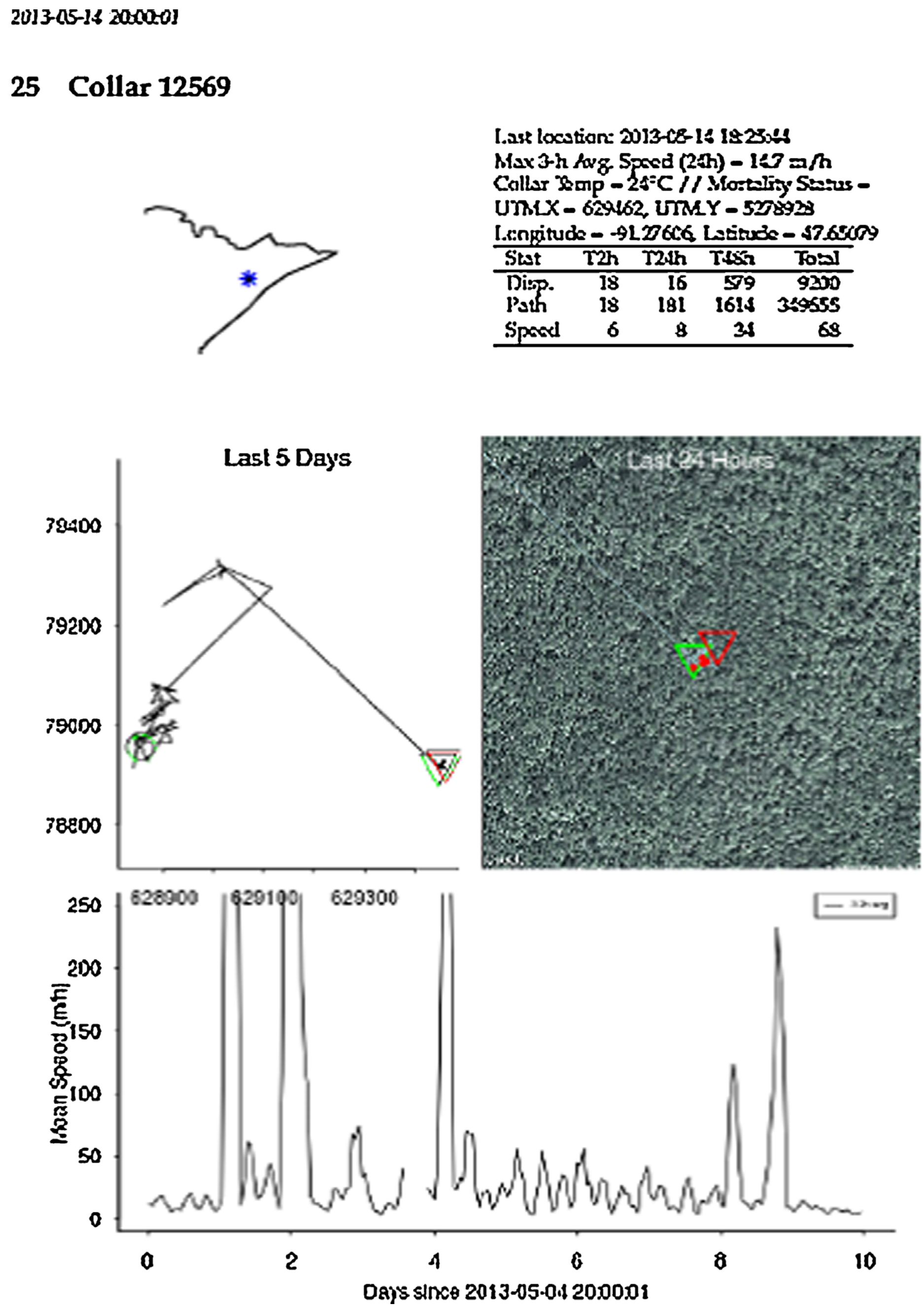

Figure 3. Example report for adult female moose number 12569 from 2000 hr, 14 May 2013, northeastern Minnesota, USA, showing movement paths for the past 5 days and 24 hr, and the 3 hr average distances moved per hour (speed). The green circle, green triangle, and red triangle represent the start of the 5-day period, the start of the 24 hr period, and the most recent location, respectively. Red dots depict the location when the collar was "localized." We approached this female at 7 days since 4 May (12 May), but she had not yet calved. She made a "calving movement" approximately 9 days after 4 May 2013 (14 May) and then localized. She was approached on 15 May and her twin calves were collared.

minus 12 hr) was 40.2 hr ($\pm$ 3.7, 21.9–132.4 hr, $n = 31$). Of the 31 dams, 28 were confirmed pregnant by serum progesterone during the previous winter, and 3 were unknown. In total, we approached 39 females for neonate capture; 31 of these were observed with $\geq$1 calf. Of the 8 females not observed with a calf, 1 female was dead, 4 were pregnant, and 3 were not pregnant. Two of these females (1 confirmed pregnant, 1 not pregnant) were revisited 1–2$\times$ with no calf spotted. Our monitoring (using automated flagging combined with examination of movement plots by eye) therefore accurately predicted calving for 31 of 38 live females (82%). Assuming the 4 pregnant females calved, but given that we could not find their calves, our success rate was 35 of 38 live females (92%). We approached 11 females (8 pregnant, 3 not pregnant) that had exhibited movement patterns indicative of calving, yet no calf was observed at first approach. We revisited 6 of these females (5 pregnant, 1 not pregnant) 1–3$\times$, because they were behaving as if a calf was nearby (e.g., reluctant to move away from the local area where observed, looking back at the area) or each female

Table 1. Time spent (days) at and distance traveled (m) between primary and secondary postparturition sites by female moose, May–June 2013, northeastern Minnesota, USA.

	Approached to collar calves					Not approached							
Variable	$\bar{x}$	**SE**	**Min.**	**Max.**	***n***	$\bar{x}$	**SE**	**Min.**	**Max.**	***n***	***t***	**df**	***P***
Duration at primary site (days)	2.4	0.2	1.4	6.5	31	5.1	0.7	1.1	14.7	17	3.5	19	≤0.01
Distance moved to secondary site (m)	504	88.2	62.0	1,821	22	220	56.1	42.5	654	10	−2.7	30	0.01
Duration at secondary site (days)	4.8	0.6	0.9	12.2	22	2.9	0.5	0.6	5.3	10	−2.3	28	0.03
Total localization (days)	5.8	0.6	1.5	14.0	31	6.8	0.9	1.1	14.7	17	0.9	32	0.35

remained localized following the first approach by the crew. During a subsequent observation the helicopter crew captured ≥1 calf with 4 of these 6 females, all known to be pregnant. Five females (3 pregnant, 2 not pregnant) were approached once with no calf observed and not revisited.

We captured 18 sets of twins and 13 singletons (58% twinning rate) throughout the capture operation; 7 of the singletons were captured in the last 2 days of the operation. Twins accounted for 71.4% of calves captured during the first 8 days, but only 30% during the final 2 days of the 10-day operation. Median calving date of our study cohort dams (the 31 whose calf[ves] we handled) was 12 May 2013 (range = 5–16 May) and the mean date was 11 May 2013 (± 0.6 days). In an effort to reduce handling time, the crew measured all morphometrics for only an initial subset of calves ($n = 11$). Overall, handling times averaged 9.1 min (± 2.27, 3–18 min, $n = 16$). Handling times averaged 12.3 min (± 0.3, 7–18 min, $n = 10$) for captures timed by the spotter plane (8–12 May), with singletons taking less time than twins (9.0 vs. 14.5 min). Handling times were reduced to 3.7 min later during 13–14 May (± 1.2, 3–5 min, $n = 6$, all twins) when handling times were recorded by the capture crew and handling protocols were shortened in an attempt to mitigate capture-related abandonment (DelGiudice et al. 2015).

Calf Collars

Of 38 mortalities we investigated on site, 11 of the collars failed to send a mortality alert text message. Three of these collars were buried, which blocked transmission of their mortality messages to the satellite base station (and stopped sending GPS fixes); 1 was on a drowned calf in flowing water (causing collar motion); 5 sent mortality transmissions to the base station, but the base station did not send an e-mail or text alert; and 2 simply did not send a mortality transmission to the base station. It is unknown whether the collars that never sent a mortality transmission to the base station were in VHF mortality mode, because this was not checked in the field in these instances.

On 26 November 2013, we investigated a calf mortality (systemic infection resulting from wolf-inflicted wounds). The expandable collar had caused abrasions on the dorsal aspect of the neck. On 17 January 2014, a collar dropped as designed, but prematurely. The band had expanded and there was no evidence of neck abrasion. One calf collar stopped transmitting GPS coordinates on 13 August 2013 (VHF was still functional). We captured this calf on 6 February 2014 to remove its collar and observed an expandable band-caused abrasion on the top of its neck. Consequently, we captured and removed all remaining collars (7–10 Feb 2014, $n = 7$). Neck abrasions were evident on 7 of 9 calves aged approximately 6.5–9 months old. The prognosis was good for the calves that exhibited abrasions in our study (T. J. Kreeger, University of Minnesota, personal communication).

Collars weighed 420 g, which was 2.6% of mean total body mass at capture (16.0 ± 0.3 kg, $n = 43$; Severud et al. 2014). Moose calves exhibit a self-accelerating growth phase during which they gain 1.3–1.6% body mass/day for the first 150–165 days of life (Schwartz 2007); however, we recovered 1.6- and 6.7-month-old carcasses that weighed 46.7 kg (with missing head and gastrointestinal tract) and 136.4 kg (intact but emaciated; W. J. Severud, unpublished data), representing a 0.9%/day and 2.4%/day growth rate, respectively. At a conservative rate of 0.9%/day growth, our collars would be <1% of mean body mass by 110 days, but at our observed 2.4%/day this would be at 43 days. In each case, collar mass was well below the 5–10% of body mass recommended by the American Society of Mammalogists (Sikes et al. 2011).

Mortality Investigations

Mean time elapsed between estimated death (backtracked 6 hr from when collar entered mortality mode) and mortality investigation (response time) was 53.3 hr (± 15.3, 0.3–579 hr, $n = 38$). This included slower response times due to extraordinary circumstances. One slipped collar was inaccessible for 24 days (located on an island with the surviving collared twin and dam); 1 collar was buried, unable to transmit, and failed to send text alerts; and 3 were associated with project staff taking mandatory time off because of human safety concerns. With these outliers and the capture-related mortalities excluded, the mean response time was 27.5 hr (± 2.9, 9.4−74 hr, $n = 22$). Response times were slower ($t_{17} = -2.10$, $P = 0.03$) when we investigated multiple mortality sites/day compared with a single site ($\bar{x}_{\text{multiple}} = 54.25 \pm 0.5$, 0.3–192 hr, $n = 16$ vs. $\bar{x}_{\text{single}} = 27.5 \pm 0.1$, 9.4–49 hr, $n = 21$). Mean distance from a collar's transmitted location when it entered mortality mode to the mortality site was 91 m (± 24.2, 4–502 m, $n = 33$). Mean distance from the UTM coordinates used for navigation (most recent location) to the mortality site was 69 m (± 15.2, 3.6–401 m, $n = 34$).

As of 31 December 2013, we documented 36 mortalities and 4 slipped collars; 9 collared calves remained "on air." Capture-related activities accounted for 11 of the mortalities, including 9 following abandonments, 1 accidental (stepped on by the dam), and 1 unknown cause (DelGiudice et al., 2015). Three of the 4 slipped collars came off when calves were 13–15 days old, and 1 at 31 days old. Of the remaining 25 natural mortalities, there was 1 death following natural abandonment (dam and calf were together after capture for 80 hr before abandonment), 1 following abandonment of unknown cause (together after capture for 17 hr), 1 drowning, 1 unknown predator kill, 1 lethal infection from a wolf bite, 4 bear kills, 12 wolf kills, and 4 "probable wolf kills." Histological and disease-screening results from the VDL revealed no contributing factors associated with the natural mortalities. After censoring capture-related mortalities and slipped collars, 25 of 34 calves (74%) died as of 31 December 2013, with 21 (84%) due to predation. About 50% of collared calves died before 50 days of age.

Dams fled from calf predation events (first location post–estimated time of death) 21× farther ($\bar{x} = 623 \pm 90$, 28–1,517 m, $n = 22$) than from slipped collars ($\bar{x} = 29 \pm 15.1$, 1–76 m, $n = 4$). A dam fled 2,476 m from the single drowned calf.

We retrieved 14 intact carcasses and 1 partial carcass (missing left kidney, gastrointestinal tract, part of liver,) and delivered them to the VDL for necropsy. Of these, causes of death included hypoglycemia due to capture-related abandonment ($n = 9$), capture-related mortality (1 unknown cause, 1 fractured skull resulting from trampling by dam), emaciation and infection likely resulting from wolf-bite (1), drowning (1), hypoglycemia due to abandonment of unknown cause (1), and bear predation (1). Hypoglycemic calves had no curdled milk in their abomasum, but often varying amounts of vegetation in their rumen, indicative of abandonment by their dams. Thirteen of the retrieved carcasses were of neonates (3–12 days old) and 2 were of calves 1.6 and 6.7 months old (bear kill and infection, respectively). Carcasses of wolf-killed calves were never retrieved because wolves typically consumed the entire carcass quickly or moved the collar enough to keep it in active mode and delay our investigation. We also retrieved an incidental (uncollared) intact carcass that died of infection likely due to a wolf-inflicted wound (3 months old).

DISCUSSION

Monitoring for Calving

Our monitoring method has served as the first large-scale attempt to monitor moose calving accurately without the use of more invasive methods (e.g., vaginal implant transmitters [VITs]). During a recent moose-calf mortality study in 2 locations in Ontario, Canada, 64 VITs were deployed in one study area and 67% of those VITs resulted in a successful assessment of calving, while 58% resulted in successful capture of neonates (difference due to calves that were stillborn or too mobile for capture). In the other study area, 35 VITs were deployed but resulted in only 1 successful capture. Calves in that area were not able to be captured from "most" females fit with VITs because of either maternal aggression or remote calving location (Patterson et al. 2013), but it was not reported how many of these 35 females were observed with a calf. Vaginal implant transmitters were also deemed costly and logistically difficult (Patterson et al. 2013). Thus, our approach provides a potentially significant improvement over the use of VITs.

Fitting GPS collars facilitated intense monitoring of both females and calves to meet several study objectives in a cost- and labor-effective manner. Localizations, detected by computer-monitoring of females, were a clear indication of calving, even though our automated female movement reports did not always flag females as "localized." Consequently, we often identified localized female patterns visually on the screen rather than by relying on the "localization flag" (i.e., moved <100 m in 36 hr after a long-distance move). Other studies have used movement patterns of ungulates to infer calving with varying success (Welch et al. 2000, Vore and Schmidt 2001, DeMars et al. 2013, Asher et al. 2014, McGraw et al. 2014).

In our study, almost all of the females made a long-distance calving movement prior to their localization, which is higher than in previous studies (NE Minnesota: 88%, McGraw et al. 2014, Alaska [USA]: 20%, Bowyer et al. 1999). However, the mean displacement and path length that we observed were similar to those reported by McGraw et al. (2014; 3 and 6 km, respectively). In Alaska, 20% of preparturient females made an average 7.3 km movement immediately before calving; however, that study used VHF collars, so shorter calving moves may have been within triangulation error ellipses and therefore masked (Bowyer et al. 1999). In another Alaskan study, female daily movements greatly increased 2 days prior to parturition, decreased to <120 m/day (close to expected GPS collar error) for 9 days after birth, and did not reach preparturition levels until calves were 26 days old (Testa et al. 2000). Mean displacement during the calving movement (4 km) was 2 × the distance we observed.

In our study, about two-thirds of the dams moved to a secondary postparturition site, which was similar to that found by McGraw et al. (2014). Overall, the limited distance of dam movements may be attributable to the relative immobility and vulnerability of their very young neonates (van Beest et al. 2011), but dams must forage to fulfill heightened nutritional demands of lactation and condition recovery following winter (Verme and Ullrey 1984, Robbins 2001, Schwartz 2007).

Calf Capture and Handling

As in our study, an Alaskan study observed twin births more frequently early in the calving period (Bailey and Bangs 1980). From 2004 to 2010, mean estimated twinning rate in NE Minnesota was 29% (±2.6, 18–39%; M. W. Schrage, unpublished data). In an earlier moose study (2011) in NE Minnesota, mean calving date, based on monitoring calving moves of GPS-collared females and subsequent localizations, was 14 May (range = 3–27 May), with 70% of births occurring during 9–20 May (McGraw et al. 2014). Calves were not approached or captured in that study. Our study cohort's mean calving date was earlier (captures restricted to 8–17 May), but was similar for all adult females monitored for calving in 2013.

Calf Collars

In our study, even though the collar was within acceptable weight ranges, the expandable band caused abrasions on the top of the neck of several calves. Lesions have been reported from ill-fitting collars on mule deer (*Odocoileus hemionus*) and bighorn sheep (*Ovis canadensis*), but all healed well (Krausman et al. 2004). The band was likely too narrow for the total weight of the GPS collar. We described this problem to the manufacturer and the band was redesigned for future studies.

Circumstances influencing proper collar and modem function precluded timely mortality notifications and investigations in several instances. When we did not receive mortality alert text notifications or did not investigate because of personnel safety issues, our mean response time essentially doubled. Our response times were close to daily monitoring of VHF collars (Barber-Meyer et al. 2008, Patterson et al. 2013), but only if daily flights are possible given fair weather and working equipment. Some collars did not send a text message after a mortality; consequently, we began to also closely monitor the status of female–calf(ves) collars using the GPS Plus X software and proximities using the Vectronic website to determine possible mortalities. Working with the vendor, we determined that our modem power was not strong enough, which was potentially inhibiting transmission of mortality text notifications. An antenna booster greatly improved cellular signal strength, and since then we have not documented further problems. Additionally, the Globalstar satellite system is not as comprehensive as the Iridium system (Tomkiewicz et al. 2010), and therefore is not as reliable. Bears caching collars or calves drowning and remaining in flowing water may either keep a collar from transmitting or keep it in normal mode because of motion. Similarly, predators or scavengers may "play" with the collar and keep it in normal mode long after mortality has occurred. In some cases, predators moving collars likely also accounted for long distances between where we located a collar and where the mortality event occurred; but in most cases, collars were recovered in close proximity to mortality sites. Exceptions included a bear caching a head (with the collar) 400 m from the mortality site, and wolves moving a collar 500 m around the shore of a permanent wetland. These noteworthy field observations will be of value in how we monitor calves and their dams from the beginning of future capture operations. Arriving at mortality sites in a timely manner allowed retrieval of entire carcasses and afforded more certainty when assigning mortality cause.

Mortality Investigations

Our observed natural mortality rate was similar to estimates in NE Minnesota (60%; Lenarz et al. 2010), but much higher than a recent study in Ontario (36%; Patterson et al. 2013). In our study, about half of the collared calves died before 50 days of age, consistent with studies of moose and other ungulate neonates demonstrating the highest hazard in the first months of life where predators are present (Ballard et al. 1991, Testa et al. 2000, Carstensen et al. 2009, Patterson et al. 2013).

Just as fitting GPS collars to dams proved highly valuable in allowing us to locate parturition sites, capture and GPS-collar neonates, subsequently monitor movements of both, and respond rapidly to investigate mortalities, this technology and associated monitoring tools should prove to be of significant value in closely examining other aspects of ungulate ecology and management. Species inhabiting heavily forested landscapes or that are otherwise cryptic during calving could be monitored in this manner, and population demographics such as calving rate and neonatal survival can be more accurately assessed by reducing bias in analyses. Intensive monitoring made possible by GPS collars offers a greater quantity and higher quality of data from which to synthesize valuable information and enhance our understanding of ecological relations critical to management. This can be done in an unprecedented, comprehensive, and efficient manner.

ACKNOWLEDGMENTS

Many thanks to K. Foshay, B. Betterly, J. Lodel, Quicksilver Air, M. Schrage, R. Moen, A. McGraw, J. Terry, K. Miedke, A. Jones, S. Larson, E. Hildebrand, M. Carstensen, M. Dexter, D. Pauly, E. Butler, A. Wuenschmann, A. Armien, D. Ryan, B. Patterson, J. Crouse, and Minnesota Department of Natural Resources (MNDNR) spotter plane pilots, A. Buchert and L. Ettl. Funding was provided by MNDNR Section of Wildlife's Wildlife Populations and Research Unit, the Wildlife Restoration (Pittman–Robertson) Program, and the Minnesota Deer Hunters Association. The University of Minnesota Department of Fisheries, Wildlife, and Conservation Biology provided technical and other support. WJS received financial support provided by the Albert W. Franzmann and Distinguished Colleagues Memorial Award. Thank you to Associate Editor A. Rodgers, B. Patterson, and 2 anonymous reviewers for feedback that strengthened the manuscript.

LITERATURE CITED

Asher, G. W., A. J. Wall, K. T. O'Neill, R. P. Littlejohn, A. Bryant, and N. Cox. 2014. The use of GPS data to identify calving behaviour of farmed red deer hinds: proof of concept for intensively managed hinds. Applied Animal Behaviour Science 154:93–103.

Bailey, T. N., and E. E. Bangs. 1980. Moose calving areas and use on the Kenai National Moose Range, Alaska. Alces 16:289–313.

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.

Ballard, W. B., J. S. Whitman, and D. J. Reed. 1991. Population dynamics of moose in south-central Alaska. Wildlife Monographs 114.

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.

Bowman, J. L., C. O. Kochanny, S. Demarais, and B. D. Leopold. 2000. Evaluation of a GPS collar for white-tailed deer. Wildlife Society Bulletin 28:141–145.

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.

Butler, E., M. Carstensen, and G. D. DelGiudice. 2011. Proposal title: determining causes of death in declining moose population. Environmental and Natural Resources Trust Fund-LCCMR. Wildlife Populations and Research Unit, Minnesota Department of Natural Resources, St. Paul, 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.
DelGiudice, G. D. 2014. 2014 aerial moose survey. Minnesota Department of Natural Resources, St. Paul, USA.
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. DOI: http://dx.doi.org/10.1093/jmammal/gyv105
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.
Gaillard, J. M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367–393.
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.
Grund, M. 2014. Monitoring population trends of white-tailed deer in Minnesota - 2014. Status of Wildlife Populations. Minnesota Department of Natural Resources, St. Paul, USA.
Haigh, J. C., E. H. Kowal, W. Runge, and G. Wobeser. 1982. Pregnancy diagnosis as a management tool for moose. Alces 18:45–53.
Hampson, B., J. Morton, P. Mills, M. Trotter, D. Lamb, and C. Pollitt. 2010. Monitoring distances travelled by horses using GPS tracking collars. Australian Veterinary Journal 88:176–181.
Herrero, S., A. Higgins, J. E. Cardoza, L. I. Hajduk, and T. S. Smith. 2011. Fatal attacks by American black bear on people:1900–2009. Journal of Wildlife Management 75:596–603.
Jolicoeur, H., and M. Crête. 1988. Winter survival and habitat use of orphaned and non-orphaned moose calves in southern Quebec. Canadian Journal of Zoology 66:919–924.
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.
Kjellander, P., I. Svartholm, U. A. Bergvall, and A. Jarnemo. 2012. Habitat use, bed-site selection and mortality rate in neonate fallow deer *Dama*. Wildlife Biology 18:280–291.
Krausman, P. R., V. C. Bleich, J. W. Cain, III, T. R. Stephenson, D. W. DeYoung, P. W. McGrath, P. K. Swift, B. M. Pierce, and B. D. Jansen. 2004. Neck lesions in ungulates from collars incorporating satellite technology. Wildlife Society Bulletin 32:987–991.
Larsen, D. G., D. A. Gauthier, and R. L. Markel. 1989. Causes and rate of moose mortality in the southwest Yukon. Journal of Wildlife Management 53:548–557.
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.
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.
McNay, M. E. 2002. Wolf–human interaction in Alaska and Canada: a review of the case history. Wildlife Society Bulletin 30:831–843.
Minnesota Department of Natural Resources (MNDNR). 2015. Ecological Classification System. Minnesota Department of Natural Resources, St. Paul, Minnesota, USA. <http://www.dnr.state.mn.us/ecs/index.html>. Accessed 27 May 2015.
Moen, R., J. Pastor, Y. Cohen, and C. C. Schwartz. 1996. Effects of moose movement and habitat use on GPS collar performance. Journal of Wildlife Management 60:659–668.
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.
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.
Poole, K. G., R. Serrouya, and K. Stuart-Smith. 2007. Moose calving strategies in interior montane ecosystems. Journal of Mammalogy 88:139–150.
Raithel, J. D., M. J. Kauffman, and D. H. Pletscher. 2007. Impact of spatial and temporal variation in calf survival on the growth of elk populations. Journal of Wildlife Management 71:795–803.
Robbins, C. T. 2001. Wildlife feeding and nutrition. Second edition. Academic Press, San Diego, California, USA.
Rodgers, A. R., R. S. Rempel, and K. F. Abraham. 1996. A GPS-based telemetry system. Wildlife Society Bulletin 24:559–566.
Schwartz, C. C. 2007. Reproduction, natality, and growth. 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., G. D. DelGiudice, T. R. Obermoller, K. J. Foshay, and R. G. Wright. 2014. Using GPS collars to determine moose calving and cause-specific mortality of calves in northeastern Minnesota: progress report on second field season. Pages 40–56 *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.
Sikes, R. S., W. L. Gannon, and The Animal Care and Use Committee of the American Society of Mammalogists. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235–253.
Smith, T. S., S. Herrero, T. D. Debruyn, and J. M. Wilder. 2008. Efficacy of bear deterrent spray in Alaska. Journal of Wildlife Management 72:640–645.
Smith, T. S., S. Herrero, C. S. Layton, R. T. Larsen, and K. R. Johnson. 2012. Efficacy of firearms for bear deterrence in Alaska. Journal of Wildlife Management 76:1021–1027.
Testa, J. W., and G. P. Adams. 1998. Body condition and adjustments to reproductive effort in female moose (*Alces alces*). Journal of Mammalogy 79:1345–1354.
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.
Tomkiewicz, S. M., M. R. Fuller, J. G. Kie, and K. K. Bates. 2010. Global positioning system and associated technologies in animal behaviour and ecological research. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2163–2176.
van Beest, F. M., and J. M. Milner. 2013. Behavioural responses to thermal conditions affect seasonal mass change in a heat-sensitive northern ungulate. PLoS ONE 8:e65972.
van Beest, F. M., I. M. Rivrud, L. E. Loe, J. M. Milner, and A. Mysterud. 2011. What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? Journal of Animal Ecology 80:771–785.
Verme, L. J., and D. E. Ullrey. 1984. Physiology and nutrition. Pages 91–118 *in* L. K. Halls, editor. White-tailed deer: ecology and management. Stackpole, Harrisburg, Pennsylvania, USA.
Vore, J. M., and E. M. Schmidt. 2001. Movements of female elk during calving season in northwest Montana. Wildlife Society Bulletin 29:720–725.
Welch, I. D., A. R. Rodgers, and R. S. McKinley. 2000. Timber harvest and calving site fidelity of moose in northwestern Ontario. Alces 36:93–103.
White, K. S., N. L. Barten, S. Crouse, and J. Crouse. 2014. Benefits of migration in relation to nutritional condition and predation risk in a partially migratory moose population. Ecology 95:225–237.

Associate Editor: Rodgers.