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Tools and Technology

Assessing Expandable Global Positioning System Collars for Moose Neonates

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ABSTRACT Deploying Global Positioning System (GPS) collars on ungulate neonates would offer notable advantages to examining their life history and influence on population performance. During 2013 and 2014, we deployed expandable GPS collars on 74 moose (*Alces alces*) neonates in Minnesota, USA, to estimate survival and cause-specific mortality during their first year. Collars slipped from 10.5% and 62.5% of calves at 15.8 (±4.5 [SE]) and 27.9 (±8.1) days postcapture in 2013 and 2014, respectively, from premature deterioration of the breakaway mechanism or excessive band expansion. We conducted various controlled tests on the bands to quantify potential design flaws. We placed 8 bands (with GPS package) around a polyvinyl chloride (PVC) pipe outdoors (exposed to weather) with clear plastic tubing (sleeve) to prevent neck abrasions, 7 collars outdoors with no sleeve, and 7 collars indoors with no sleeve. We dropped each pipe 10 cm 50 times in the morning and in the afternoon daily for 4 weeks to simulate animal movement and test elastic memory. Circumference of bands from the 3 treatment groups increased 14.6 (±2.5), 8.5 (±2.9), and 3.9 (±2.4) cm, respectively, with 41.9% attributed to the sleeve, 26.9% to simulated animal movement, and 31.2% to weather exposure. Circumference of control group bands (indoors, not bounced) did not change. After design modifications were made to the collar, the band length increased only 1.5 ± 0.6 cm during a 4-week trial. Subsequently, we placed 6 of these collars on confined and sheltered Holstein dairy calves; 5 retained their collar during an 8-week test. After increasing the strength of the expandable loops via sewing, we placed 4 collars on pastured Angus beef calves. Three of 4 slipped their collars at 42.4 (±8.9) days. Our results indicate additional modifications of the band are needed before GPS-collaring of moose neonates is resumed.

KEY WORDS *Alces alces*, calves, expandable GPS collars, moose, neonates.

Ungulate calf production and recruitment (survival to 1 yr) are sensitive to many limiting factors and may have pronounced effects on population performance and dynamics (Gaillard et al. 1998, Raithel et al. 2007, Lenarz et al. 2010, Patterson et al. 2013). Declining ungulate populations have been associated with poor juvenile survival and predation as the primary cause of calf mortality (Hatter and Janz 1994, Pinard et al. 2012). In northeastern Minnesota, USA, the moose (*Alces alces*) population decreased an estimated 52% from 2006 to 2012 (Lenarz 2012), but little was known about calf production and recruitment or their influence on the population's trend. Fitting very-high-frequency (VHF) transmitters to moose neonates has facilitated the collection of valuable survival and cause-specific mortality data (Ballard et al. 1981, Keech et al. 2000, Patterson et al. 2013). In response to the declining trend in northeastern Minnesota, and the recent near disappearance of moose in the northwestern part of the state (Murray et al. 2006, Lenarz et al. 2009), the Minnesota Department of Natural Resources (MNDNR) launched aggressive survival and cause-specific mortality studies of adults and calves in northeastern Minnesota (Butler et al. 2013, Severud et al. 2015). The calf study contributed to pioneering the deployment of Global Positioning System (GPS) collars on moose neonates of GPS-collared dams, an effort considered essential to ensuring rapid, more conclusive mortality investigations (Severud et al. 2015). Importantly, during the study's first year (2013), approximately 50% of collared calves died within 50 days of birth; but during both

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2013 and 2014, study progress was sorely hampered by design flaws (e.g., premature expansion of bands and separation of breakaway mechanism) associated with fitting of collars (Severud et al. 2014).

Ensuring that expandable bands for marking ungulate juveniles are retained for intended periods of time has been a challenge since the earliest designs were reported (Fashingbauer 1962, Hamilton 1962). Steadily, improvements have included materials that better facilitated increased band circumference, accommodated breakaway mechanisms, and incorporated VHF transmitters (Steigers and Flinders 1980, Smith et al. 1998, Dick et al. 2013). Expandable VHF radiocollars have been deployed on neonates of white-tailed deer (*Odocoileus virginianus*; Merrill et al. 1998, Diefenbach et al. 2003, Carstensen et al. 2009), elk (*Cervus elaphus*; Smith et al. 1998, Dick et al. 2013), and pronghorn (*Antilocapra americana*; Keister et al. 1988), as well as on juvenile bobcat (*Lynx rufus;* Jackson et al. 1985) and black bear (*Ursus americanus*; Strathearn et al. 1984). Yet, intermittent problems of durability, retention (i.e., premature slipping), and neck abrasions associated with the expandable collars have persisted (Strathearn et al. 1984, Krausman et al. 2004).

Given inherent limitations of VHF telemetry as compared with GPS collars (Rodgers et al. 1996, Kochanny et al. 2009, Frair et al. 2010), attempts to realize the potential value of fitting GPS collars to neonates were inevitable (Kjellander et al. 2012, Severud et al. 2015). However, with increased collar capabilities came new, but similar, design challenges associated specifically with GPS package positioning, mass, interactions with band durability, weather conditions, and fit. Modifications and field-testing were required to assess the efficacy of the collars in fulfilling specific study objectives.

The overall purpose of the moose calf study was to estimate calf production, survival, and cause-specific mortality. Herein, our objectives were to 1) assess and document the efficacy and specific problems of the first GPS collars deployed on free-ranging moose neonates, 2) assess relative effects of physical disturbance (e.g., calf movement) and weather conditions on fit of these expandable collars over time, 3) test modifications to the collar's design prior to deployment on free-ranging moose neonates, and 4) contribute to the development of an improved GPS collar for moose neonates that would be retained for $\geq$1 year (recruitment).

STUDY AREA

Our 6,068-km^2 study area was located between 47°06′N and 47°58′N latitude and 90°04′W and 92°17′W longitude in the Northern Superior Upland (NSU) section of northeastern Minnesota (MNDNR 2015). Upland forests were dominated by trembling aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*), and conifers 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, yet there were limited elevation changes across the study area. In Ely, Minnesota, mean daily minimum and maximum temperatures varied between 2.7° C and 16.1° C, and 11.5° C and 25.0° C during May to August 2013, and between 4.5° C and 17.9° C, and 11.0° C and 23.2° C for the same interval in 2014 (Midwestern Regional Climate Center 2017). We conducted collar tests on dairy and beef calves in Scandia, Minnesota, on farms located at 45°19′N and 92°52′W and 45°18′N latitude and 92°52′W longitude.

METHODS

Moose Capture and Handling

One hundred eleven (84 females, 27 males) and 37 (25 females, 12 males) adult moose were captured and fitted with Iridium GPS Plus collars (Vectronic Aerospace GmbH, Berlin, Germany) during January–February 2013 and February 2014, respectively (Butler et al. 2013, Carstensen et al. 2014). The capture and handling protocols met American Society of Mammalogists guidelines (Sikes et al. 2011). We captured and GPS-collared 49 (25 females, 24 males) and 25 (11 females, 14 males) moose neonates during May–June 2013 and 2014; 9 calves were censored each year as a result of capture-induced abandonment (DelGiudice et al. 2014, 2015, 2018), and 1 in 2013 as a result of capture-related mortality. A second neonate died of a pre-existing condition within 4 hr of collaring in 2013 (DelGiudice and Severud 2016) and also was censored. Captures were helicopter-assisted in 2013 to facilitate efficient access to calving locations; whereas, in 2014, helicopters were removed from the capture protocol in an attempt to minimize capture-induced abandonment (DelGiudice et al. 2014, 2018).

GPS Collar Prototypes

Calves collared in 2013 were fitted with a GPS PLUS VERTEX Survey-1 GLOBALSTAR collar (Vectronic Aerospace GmbH, Berlin, Germany) as described by Severud et al. (2015). The collar (420 g, 2.6% of mean body mass at capture [BMC]) included an expandable band and 2 expansion loops, GPS–VHF package dimensions of $85 \times 60 \times 65$ mm, a 3.0-cm-wide polyester and elastane band with an initial band circumference of 35 cm, and fully expanded circumference of 65 cm (Fig. 1). The GPS–VHF package was programmed to record hourly locations for $\geq$1 year and transmit (via Globalstar satellite, 1-way communication) every third successful location-fix. All location-fixes were also stored on-board the collar. The expandable band included a cotton breakaway section designed to release the collar at approximately 400 days. Some calves experienced neck abrasions from the original band; therefore, the 2014.1 band included the following modifications by Vectronic: new polyester and elasthodiene band material with an increased width of 5.0 cm, increased number of expansion loops to 4,

Figure 1. GPS PLUS VERTEX Survey-1 GLOBALSTAR package (top) and expandable bands (bottom: left to right): 2013, 2014.1, 2014.2, 2015.1, and 2015.2, deployed and tested 2013–2015, in Minnesota, USA.

and added a smooth, clear plastic tubing (hereafter, sleeve) over the band in an attempt to prevent abrasions. Collar 2014.1 weighed 515 g (3.2% of mean BMC). The initial circumference was 35–40 cm and fully expanded to 110 cm (Fig. 1). The sleeve made for a poor fit and ostensibly was more visually conspicuous, so we removed the tubing from the band and reinforced the stitching on each expandable loop (Collar 2014.2); the resulting weight was 455 g (2.8% of mean BMC; Fig. 1). All collars were well below the 5–10% of body mass recommended by the American Society of Mammalogists (Sikes et al. 2011). Following 2014 captures and collar-testing, we made additional collar modifications to prevent premature expansion, including additional stitching, double-layering the elastic band, and improving fit by adding a flexible nylon belt (Collar 2015.1; Fig. 1). We further strengthened the collar band (2015.2) by adding progressive layers of stitching on each expansion loop (Fig. 1). The GPS and VHF components remained the same in all collar prototypes.

Accuracy of GPS Collar Location-Fixes

In summer 2013, we estimated mean linear error of location-fixes by deploying 3 calf collars beneath >80% canopy closure in each of the following National Land Cover Database cover classes for 3 days: deciduous forest, coniferous forest, mixed forest, scrub shrub, and woody wetlands (Fry et al. 2011). We confirmed cover classes in the field. We chose the aforementioned classes because of their prevalence in our moose study area, and they were commonly used by GPS-collared moose. For each cover type, we first recorded an averaged location-fix (i.e., collected locations until the GPS sample confidence reached 100%), at the specific location (focal point) using a handheld GPS unit (Garmin GPSMAP 62sc, Olathe, KS, USA), and then placed an adult Iridium GPS collar on the ground at this focal location to simulate a bedded moose. We then placed the next 2 adult collars 5 m and 10 m north of the focal location, respectively. We placed 1 calf collar 5 m, 10 m, and 15 m west of each adult collar. We then calculated an exact easting and northing coordinate for each collar from the focal location. Location error was estimated from the Euclidean distance between fixes and each individual collar's location. We also put 3 calf collars together in the open (0% closure) to estimate mean linear error. We performed this experiment twice under open canopy for 1 day each. We calculated the mean linear error for each collar, and subsequently compared errors by canopy type and closure.

Testing Calf GPS Collar Bands

During July–August 2014, we evaluated the efficacy of the 2014.1 and 2014.2 expandable bands by sliding 29 complete GPS collars around 2, 10.2-cm-diameter (32.0-cm-circumference, similar to average neck size of moose neonate) polyvinyl chloride (PVC) pipes, which rested on 2, 54-cm-tall metal stands (Fig. 2). We placed 14 and 15 collars indoors or outdoors (exposed to weather [e.g., precipitation, sunlight]), respectively. For the outdoor groups, 8 of the collars had the plastic sleeve on the dorsal side of the band. We tested 4 experimental groups: 1) indoors, not bounced, no sleeve); 2) indoors, bounced, no sleeve; 3) outdoors, bounced, no sleeve; and 4) outdoors, bounced, sleeve. We bounced (dropped) the PVC pipe with collars from a height of 10 cm 50× in the morning and afternoon daily during a 4-week trial period to simulate animal movement and test elastic memory. We measured total length (circumference; cm) of each expandable band, and took pictures prior to beginning the trials and again at the end of each trial-week.

On 9 June 2014, we placed 2014.2 collars on 2 Angus beef calves (≤4 months of age) to evaluate the expandable band on live animals. We placed calves together with other cattle in a large fenced pasture with access to an indoor barn. We made weekly visual observations to inspect fit of the 2 collars, but we did not make measurements until the collars were slipped, because calves were inaccessible.

We sewed additional expansion loops into the next generation (Collar 2015.1) of the expandable band and then repeated the PVC pipe-test in January–February 2015

Figure 2. Polyvinyl chloride (PVC) pipe bounce-test structure used to quantify environmental and animal movement effects on expansion of Global Positioning System (GPS) collar bands, 2014 to 2015, in northeastern Minnesota and St. Paul, USA. The PVC pipe was 10.2 cm in diameter, resting on 2 metal stands, each 54 cm tall.

in a greenhouse. There were 2 test groups: 1) not bounced, natural sunlight, no precipitation; and 2) bounced daily (as previously described), natural sunlight, and precipitation. We sprayed the collars heavily with water twice per week to simulate precipitation or swimming.

On 20 January 2015, we began a new 8-week trial, placing 2015.1 collars on 4 Holstein dairy calves (36.0 ± 10.5 [SE], 12.0–63.0 days old) held within individual 2 × 3-m pens. At 6 weeks, 2 calves were moved to slightly larger individual pens outdoors. We measured neck circumference where the collar fit on the calves, and then calculated the change in band length at the end of the test to examine how the collar expanded with animal neck growth.

Following the dairy calf trial, we made additional modifications to the expandable belt. On 30 March 2015, we again placed collars (2015.2) on 4 Angus beef calves at 8.5 days old (±2.0, 3–12 days old; Fig. 3). These calves were able to roam in a larger pasture than in 2014, which included a wetland, woodland, and brush. We made biweekly observations to assess overall collar fit, but calves were not approachable and we did not make band measurements until the collars were recovered. All moose calf handling protocols were approved by the Institutional Animal Care and Use Committee for the University of Minnesota (Protocol 1302-30328A). All animal handling (including bovine calves) followed guidelines of the American Society of Mammalogists (Sikes et al. 2011).

We used a simple linear regression to compare mean Euclidean location error by cover type and collar ID. We used logistic regression to test whether band length was affected by test method or time (week). We conducted all statistical analyses using Program R version 1.0.136 (R Core Team 2016). We used the R package "KMsurv" for the Kaplan–Meier estimator to estimate collar retention rate. We considered results significant at $P \leq 0.05$.

RESULTS

At a November 2013 field necropsy, we observed neck abrasions from collar wear on a moose calf killed by wolves and quickly recovered. We checked the remaining collared calves from helicopter in December 2013 and all appeared to be in good condition with no detectable signs of neck abrasions. Furthermore, shortly thereafter in early January 2014, 1 of the remaining 9 collared calves prematurely slipped its collar; upon recovery there was no sign of skin abrasion (e.g., tissue, blood, exudate) on that collar's band, as had been observed on the collar of the November mortality. However, as a precaution, during subsequent helicopter captures of adult moose in February 2014, we captured and removed collars from all 8 of the remaining collared calves. Ultimately, 7 of these 8 calves exhibited neck abrasions of varying severity. Interestingly, the seventh calf, and the largest of the group, exhibited no neck abrasions. A broad-spectrum antibiotic was administered to all of these captured calves, and our on-site veterinarian expected all to recover satisfactorily from their collar-caused wound (T.J. Kreeger, University of Minnesota, personal communication).

Figure 3. A 12-day-old Angus beef calf collared with the 2015.2 generation collar on 30 March 2015 in Scandia, Minnesota, USA. The collar was removed by the owner 332 days postcapture.

Four of 38 (10.5%) calves had their breakaway mechanism separate prematurely in 2013, whereas 10 of 16 (62.5%) slipped the collars over their head in 2014. Collar retention was 85.8% and 39.5% at 30 days in 2013 and 2014, respectively. Beyond 30 days, overall collar retention remained constant in 2013, whereas it declined to 0% by 93 days postcapture in 2014. The mean time from capture to when the collars were slipped in 2013 was 15.8 days (±4.5, 10–29 days) versus 27.9 days (±8.1, 7–93 days) in 2014.

Logistic regression on band length indicated significant group (treatment *vs.* control; $F_{3,112} = 65.05$, $P \leq 0.001$) and week ($F_{1,114} = 4.07$, $P = 0.05$) effects in the PVC bounce-test for the 2014.1 and 2014.2 collar designs, but group × week interactions had no effect on band length ($P > 0.07$). The 2014.1 bands (outdoors, bounced, sleeve) increased 14.6 cm (±2.5, 6–25 cm). The 2014.2 treatment group bands (outdoors, bounced, no sleeve; indoors, bounced, no sleeve) increased 8.5 cm (±2.9, 2.0–24.5 cm) and 3.9 cm (±2.4, 0–17 cm), respectively. The control group (indoors, not bounced, no sleeve) did not increase in length. The sleeve accounted for 41.9% of the expansion; weather exposure, 31.2%; and movement (bouncing), 26.9%. The generation 2014.2 collars ($n = 2$) remained on the beef calves for only 10.4 and 17.9 days, and increased band circumference by 31.0 cm and 32.5 cm, respectively.

After incorporating additional expansion stitching, the 2015.1 collar treatment group increased only 1.5 cm (±0.6, 0–4.5 cm) in the greenhouse over the 4-week trial. Three of 4 sheltered dairy calves retained their 2015.1 collars during the 8-week test; the band circumference increased by 13.1 cm (±2.7, 9.5–18.5 cm), whereas mean increase in neck circumference was 11.5 cm (±1.2, 9.5–13.5 cm). The only slipped collar occurred at approximately 6 weeks, increasing by 30.5 cm. The free-ranging beef calves slipped 3 of 4 generation 2015.2 collars at 42.4 days (±8.9, 29.1–59.4 days). The fourth collar remained on the calf for 332 days before being removed by the owner.

The GPS package exhibited occasional problems; 1 collar stopped transmitting and 4 did not transmit or collect location-fixes when placed in puddles or buried by predators.

In each of these cases, VHF was still functioning. The overall mean linear location error of GPS collars beneath closed canopy (40.3 m, 95% CL = 37.8, 42.8, range = 0–369 m) differed ($F_{1,\ 1153} = 23.3$, $P \leq 0.001$) from open canopy (24.9 m, 95% CL = 19.7, 30.1, range = 1–274.4 m). We noted GPS location error was not affected by collar ID ($F_{1,\ 978} = 0.64$, $P = 0.43$), cover type ($F_{4,\ 975} = 1.17$, $P = 0.32$), or collar ID × cover type ($F_{9,\ 970} = 1.3$, $P = 0.23$).

DISCUSSION

The original moose neonate collar design (2013) did not fully meet our requirements or expectations for fit, expansion, or retention. We removed 8 of these collars from calves at significant expense using helicopter-capture (US $1,600/calf) at approximately 9 months of age, because of earlier evidence of neck abrasions observed on a calf ($\sim$7 months of age) killed by wolves (Severud et al. 2015). Consequently, we also incurred a notable loss of location (movement), habitat use, and survival data; collars were expected to remain on surviving calves ≥1 year. Seven of the 8 recaptured calves exhibited neck abrasions. Collar-induced injuries ranging from slight abrasions to severe cuts through the dermis were observed on 8 black bears in Ontario, Canada; later handling showed the abrasions had healed within 3 weeks (Strathearn et al. 1984). Based on patterns of the neck abrasions on our calves, we postulated that the expandable band was not wide enough to adequately distribute pressure on top of the neck caused by the weight of the GPS package below the neck, particularly as they moved. Consequently, the edges of the narrow band gradually wore into the skin. Also, the circumference of the band did not expand to the specified 65 cm. We did not observe any neck abrasions following modifications to the 2013 collar (i.e., widening of the bands).

During both years, moose neonates slipped their collars relatively soon after capture (7–93 days). Similarly, mule deer (*O. hemionus*) and white-tailed deer neonates slipped their VHF collars at a mean 3 and 5 days postcapture, respectively (Grovenburg et al. 2014). Collars of 19 elk newborns were slipped at a mean 13 days postcapture (Smith et al. 1998). Retention rates of expandable VHF collars have varied markedly (36–100%) among ungulate species (Diefenbach et al. 2003, Dick et al. 2013, Grovenburg et al. 2014, Kalb and Bowman 2014). In cases where our collars were not retained, the breakaway mechanism separated prematurely (2013) or collars were slipped over the head (2014), as has occurred with elk neonates (Smith et al. 1998). Multiple alterations have improved the original expandable band, yet, additional modifications are required. The elasthodiene band material and stitching were too weak or lacked adequate elastic memory to withstand movement of the GPS-collared calves. The 2015.1 band was designed to alleviate this problem, but the bands continued to expand too readily, and the GPS collars were hanging loosely from the necks of confined dairy calves at the end of their trial. Ultimately, even incorporating additional loops and stitching to the band (2015.2) did not prevent premature slipping by 3 of the 4 free-ranging beef calves.

Our PVC bounce-test to simulate animal movement showed that the plastic sleeve, weather exposure, and movement all contributed to relatively rapid increases in band circumference, which led to premature slipping of GPS collars in 2014. Our trials showed the sleeve retained moisture on the band, leading to faster deterioration of the stitching. Keister et al. (1988) reported weather effects on collar retention for pronghorn neonates in Oregon, USA, when bands became brittle, cracked, and were lost. Our next band generation (2015.1) performed well on the PVC bounce-test, but inadequately during subsequent tests on dairy calves, indicating that fitting live animals with collar prototypes is essential prior to deploying them on free-ranging, wild ungulate neonates. Testing the 2015.1 collar design on dairy calves was valuable for measuring growth of the neck relative to band expansion, but assessing the influence of animal movement was limited, because owners had them confined to small individual pens. We tested band generations 2014 and 2015.1 outdoors and in a greenhouse, respectively, leading to the possibility of immediate environment as a source of variation between tests. The outdoor treatment group (2014) may have been more susceptible to band deterioration through extended periods of precipitation and moisture from dew, potentially overestimating the performance of the 2015.1 band, even though they were artificially sprayed with water 2 times/week.

Collar evaluation using various tests can be beneficial to align performance expectations with study objectives prior to deployment. Controlled trials, such as those using the PVC bounce-test, allowed us to quantify the influence and assess the importance of individual factors we expected were contributing to the premature failure of the neonate GPS collars, whereas trials involving free-ranging captive ungulates provided more realistic assessments of movements and potentially influential environmental factors (e.g., weather, vegetation, fences). Lack of proper testing can lead to poor retention of collars, loss of data, and wasted resources.

Extensive stitching patterns on expandable bands has increased retention rates of neonate collars (Smith et al. 1998, Grovenburg et al. 2014). All collars were retained on mule deer in the Sierra Nevada Mountains when stitching was strengthened and threaded in alternating patterns on each expandable loop (Grovenburg et al. 2014). We recommend this technique to allow the loops to break more gradually with the animals' growth. We also suggest expanding the nylon belt of the 2015.2 collar (only covered the dorsal part of the band) to encase the entire band, which will increase overall strength (Smith et al. 1998). Upon applying these modifications, we would suggest fitting this band, with GPS package, to free-ranging bovine calves.

Fitting moose neonates with GPS collars allowed us to monitor, in near real time, movements at a finer scale (1 location/hr) than was feasible previously using expandable VHF collars (Smith et al. 1998, Grovenburg et al. 2014). This permitted us to more effectively fulfill our study objectives of examining neonate–dam proximity; use of space, habitat, and other resources; survival and cause-specific mortality; and assess capture-induced abandonment (Severud et al. 2014, 2015, 2016; DelGiudice et al. 2015, 2018).

Our limited success with deploying these GPS-collars on moose neonates also contributed to a better understanding of dam movement behavior relative to the timing and location of calf mortality, particularly by predation, which led to an improved ability to detect such mortalities when the dam was GPS-collared, but the calf was not (Obermoller 2017). But critical data and opportunities were lost, and unexpected costs were incurred. Researchers cannot afford the iterative process of collar deployment, redesign, testing, and redeployment, particularly when studying a declining population and time is critical. The expandable GPS collars have thus far not allowed us to fully address the overall moose calf study objectives. With more advanced and proper testing and development, reliable, high-performing expandable GPS collars for neonates will prove to be invaluable in research and to management across species.

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