The Journal of Wildlife Management 82(2):287–298; 2018; DOI: 10.1002/jwmg.21374

Featured Article

Gaining a Deeper Understanding of Capture-Induced Abandonment of Moose Neonates

GLENN D. DELGIUDICE,[1] *Forest Wildlife Populations and Research Group, Minnesota Department of Natural Resources, 5463-C West Broadway Avenue, Forest Lake, MN 55025, USA*

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

TYLER R. OBERMOLLER,[2] *Forest Wildlife Populations and Research Group, Minnesota Department of Natural Resources, 5463-C West Broadway Avenue, Forest Lake, MN 55025, USA*

VÉRONIQUE ST-LOUIS, *Wildlife Biometrics Unit, Section of Wildlife, Minnesota Department of Natural Resources, 5463-C West Broadway Avenue, Forest Lake, MN 55025, USA*

ABSTRACT Capture-induced abandonment of ungulate neonates has been poorly understood until recently, likely often underestimated, and anecdotally reported to occur at variable rates. This complex maternal behavior adversely affects the accuracy, efficiency, cost-effectiveness, and consequently the overall value of behavioral and survival studies. To follow-up on a previous study where we reported an 18.4% rate of abandonment of moose (*Alces alces*) neonates following helicopter-assisted capture in Minnesota, USA, we tracked the movement behavior of 12 and 13 moose neonates fitted with global positioning system (GPS) collars during 8–15 May 2014 (phase 1) and 21 May–19 June (phase 2), respectively. These efforts were part of an overall study of reproductive success and cause-specific mortality in Minnesota's remaining viable but declining moose population. During phase 1, 7 (3 M, 4 F) of 12 (6 M, 6 F) neonates were abandoned by 5 of 9 dams. Our capture-induced abandonment contingency plan and monitoring of hourly location fixes of the GPS-collared newborns and their dams allowed us to recover 6 of the 7 abandoned neonates alive and in good condition. During phase 2, we reduced our capture team from 3 to 4 to 2 persons and limited handling to fitting the GPS collar and sexing the neonate ($\bar{x} = 0.7$ min). Capture-induced abandonment decreased to 1 of 10 dams abandoning a set of twins. Mean distance of dams to capture site (calving site) 1 hour pre- and 1 hour post-capture did not indicate a predisposition to abandonment. However, differences in distances of dam to capture site, dam to neonate(s), and neonate to capture site over 48–96 hours post-capture suggested a clear pattern of capture-induced abandonment. None of the birth, capture, neonate, or dam characteristics examined indicated a predisposition to capture-induced abandonment at the study cohort level. However, minimizing capture-induced abandonment through rapid handling of neonates will greatly increase the overall value of field studies that rely on the capture of animals.

KEY WORDS abandonment, *Alces alces*, calves, capture-induced abandonment, GPS collars, moose, moose neonates, movement behavior.

Knowledge of annual survival and recruitment of free-ranging animals and factors influencing these drivers of population performance is important to sound wildlife management. Adult survival has the greatest influence on population growth rates (λ) of ungulates, but low and variable annual recruitment also affects population stability and dynamics (Gaillard et al. 1998, Heppell et al. 2000, Caswell 2001, Raithel et al. 2007, Lenarz et al. 2010). In 2013, prompted by a steadily decreasing moose (*Alces alces*) population in northeastern Minnesota, USA, we initiated a study to examine calf production, recruitment, and cause-specific mortality (DelGiudice 2013, Severud et al. 2015*a*). Because natural hazards are greatest for ungulates through their first 30–90 days of life, neonate capture and radio-collaring are critical to such studies (Ballard et al. 1981, Keech et al. 2000, Carstensen et al. 2009, Patterson et al. 2013, Severud et al. 2015*a*). But these operations have been associated with variable and unpredictable risks of capture-induced abandonment and mortality (Ballard et al. 1979, Livezey 1990, Keech et al. 2011, Patterson et al. 2013, DelGiudice et al. 2015).

Received: 16 February 2017; Accepted: 13 August 2017

[1]*E-mail: glenn.delgiudice@state.mn.us*
[2]*Present Address: Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, 2003 Upper Buford Circle, Suite 135, Saint Paul, MN 55108, USA.*

Not all abandonment is induced by human disturbance. Natural abandonment by moose and other ungulate dams has been documented and may be a source of neonate mortality but may be a relatively rare event (Franzmann and Schwartz 1986). However, abandonment, whether natural or capture-induced, may be underestimated because of the elusive nature of calving behavior, challenging observational conditions, limitations of very high frequency (VHF) telemetry for fine-scale, non-invasive monitoring of neonates and their dams, and a restricted ability of biologists to recognize it when it occurs (Livezey 1990, Child 2007). There has been speculation about factors predisposing neonates to capture-induced abandonment, but until recently, our understanding for most animal species relied primarily on anecdotal accounts.

In 2013, for the first time worldwide, we fit moose neonates with expandable global positioning system (GPS) collars, which facilitated rapid detection and investigation of calf mortalities (Severud et al. 2015*a*). Additionally, dams of these neonates were GPS-collared previous to the calving season (Butler et al. 2013). The collars of both were programmed to collect synchronous hourly location fixes during the calving and neonatal period, from which we could monitor maternal movements and proximity to neonates, ultimately allowing us to recognize and characterize capture-induced abandonments with greater confidence (DelGiudice et al. 2015, Severud et al. 2015*a*). During this first neonate capture season, 9 of 49 (18.4%) neonates were abandoned by 7 of 31 (22.6%) dams within 48 hours of capture and handling over a 10-day, helicopter-assisted capture operation (DelGiudice et al. 2015). The temporal pattern of the intermittent abandonments was largely uninformative, and there were no differences in birth, capture, or physical characteristics of abandoned versus non-abandoned neonates, and no effect of dam age. This study suggested that capture-induced abandonment involved far more complex behaviors than indicated by the brief accounts reported previously. For example, on average, approach for neonate capture did not induce abandoning dams to initially flee any farther from their neonates than non-abandoning dams. But they moved farther away with time and often made return visits during the 48-hour post-capture period from as far as 2.2 km. Additionally, after 6 hours post-release, abandoned calves remained closer to their capture sites than those not abandoned (DelGiudice et al. 2015).

There is a general growing interest in better understanding the influence of human disturbance, whether associated with research operations, hunting, or other recreational activities, on important drivers of population performance (Neumann et al. 2009, Ciuti et al. 2012, Johnsen 2013). Capture-induced abandonment of offspring commonly leads to mortality by a number of proximate causes, and not recognizing it can result in underestimating its occurrence and bias analyses of natural survival (Livezey 1990, Frid and Dill 2002, Gilbert et al. 2014, Chitwood et al. 2017). This may be particularly true for highly mobile animals such as moose and other ungulates, and in locations where predators strongly influence their movements, habitat use, and survival of their neonates (Bowyer et al. 1999, Frid and Dill 2002, Kittle et al. 2008, Balogh 2012, Bastille-Rousseau et al. 2016).

To enhance our understanding of capture-induced abandonment of moose neonates after our 2013 study, we modified our capture and handling approach in a way that would potentially minimize its occurrence and contribute to development of an effective abandonment contingency plan (Severud et al. 2016). We hypothesized that the helicopter component of our neonate capture operations was the primary factor inducing abandonment by dams in our study. Using only ground captures (i.e., no helicopter-assistance), our objectives were to compare the abandonment rates of our original, helicopter-assisted capture and handling approach from 2013 (DelGiudice et al. 2015) with rates associated with our less invasive approach, re-examine potential contributing factors (e.g., bonding time, capture-date, handling time, number of handlers, dam age) on abandonment, and quantify differences in movements of abandoning versus non-abandoning dams and their neonates post-capture ($\geq$48 hr).

STUDY AREA

We captured calves on a 6,068-km^2 study area located between 47°06′N and 47°58′N latitude and 90°04′W and 92°17′W longitude in northeastern Minnesota. This region has been characterized as the Northern Superior Upland (Minnesota Department of Natural Resources [MNDNR] 2015), which includes bogs, swamps, lakes, and streams; lowland stands of northern white cedar (*Thuja occidentalis*), black spruce (*Picea mariana*), and tamarack (*Larix laricina*); and upland balsam fir (*Abies balsamea*), jack pine (*Pinus banksiana*), white pine (*P. strobus*), and red pine (*P. resinosa*). Trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*) often are intermixed with conifers.

Behavior of ungulate species, particularly of dams rearing offspring, may be influenced by hunting activity, predators, and indirectly by the presence of alternative prey species (Livezey 1990, Frid and Dill 2002, Johnsen 2013). Because of the steady moose decline in this region, state and tribal harvests were suspended in 2013 until further notice. Gray wolves (*Canis lupus*) and black bears (*Ursus americanus*) are the most common predators of moose, and can have a pronounced impact on calves (Fritts and Mech 1981; Lenarz et al. 2009; Patterson et al. 2013; Severud et al. 2015*a*,*b*); wolf densities across northern Minnesota have been estimated at 3/100 km^2, whereas bear densities on our study area were estimated at 23/100 km^2 (Garshelis and Noyce 2011, Erb et al. 2015; D. L. Garshelis, MNDNR, unpublished data). White-tailed deer (*Odocoileus virginianus*) are managed at pre-fawning densities of $<$4/km^2, and are primary prey of wolves (Nelson and Mech 1986, DelGiudice et al. 2002, MNDNR 2011). Black bears and wolves also are major predators of deer fawns throughout summer (Kunkel and Mech 1994, Carstensen et al. 2009). Maximum daily temperatures have been generally increasing at Ely, Minnesota from 1960 to 2007 (Lenarz et al. 2010). Mean daily minimum and maximum temperatures ranged from −16.6°C to 21.1°C and −6.7°C to 33.3°C, respectively, during April to July 2014 at Ely, and from −11.7°C to 12.2°C and −0.6°C to 29.4°C at Grand Marais, Minnesota (Midwestern Regional Climate Center 2015), both located within the study area.

METHODS

Monitoring Female Movements, Calf Capture, and Handling

On 1 May 2014, we began computer-monitoring the locations of 70 adult female moose that had been captured and fitted with Iridium GPS collars (Vectronic Aerospace GmbH, Berlin, Germany) during late January–February 2013 or early February 2014 as part of a companion study of adult survival and cause-specific mortality (Butler et al. 2013, Carstensen et al. 2014). Age was determined for 54 of 70 adults by extraction of a last incisor and counting cementum annuli (Sergeant and Pimlott 1959; M. Carstensen, MNDNR, unpublished data). Additional details of adult captures and handling are presented elsewhere (Butler et al. 2013, Carstensen et al. 2014). The collars were re-programmed to collect hourly fixes (originally 1 fix/4 hr) during May–late June with 4 data transmissions daily, which permitted us to monitor their movements in near real time. As in the 2013 calving season, our initial monitoring objective was to record when and where pregnant females made a calving movement (i.e., an atypical, long-distance movement [0.4–22.7 km over a mean of 14.4 hr]; Severud et al. 2015*a*) that ended with a localization pattern of 1–15 days of spatially clustered locations (Bogomolova and Kurochkin 2002, Poole et al. 2007, DeMars et al. 2013, McGraw et al. 2014, Severud et al. 2015*a*). We employed 3 different monitoring approaches: a base station computer, a web-mapping service, and automated reports. The base station, collar vendor-provided software, and a shared network drive afforded full-time access to raw and processed (distance moved between locations) location data. The full-time web-mapping service, provided by the collar vendor, enabled us to view raw location data overlaid on Google Earth (Google, Mountain View, CA, USA) imagery. The 2014 automated reports, updated every 12 hours, plotted mean hourly distances moved for up to 10 days at a time, GPS locations and paths of movement for the most recent 5 days, and other movement metrics (Severud et al. 2015*a*). In 2013, we successfully predicted 92% of the calving activity of 73 GPS-collared adult females using this 3-pronged monitoring approach (Severud et al. 2015*a*).

As in 2013, we allowed the dams and calves a minimum of 24–36 hours of bonding time. We assumed the dam gave birth sometime within 12 hours of the start of localization, then allowed another 24 hours before designating that the calf was eligible for capture and handling (Severud et al. 2015*a*). Total allowed bonding time included any additional time elapsed beyond the initial 36 hours to the time of actual capture.

Our 2014 capture season involved 2 phases (8–15 May and 21 May–19 Jun). During phase 1, a 3–4-person (a fifth on 1 occasion) capture and handling team approached calving (birth) sites (center of the post-calving movement localization) on the ground. We captured, handled, and released twins together (Keech et al. 2011, DelGiudice et al. 2015). Because there was no apparent effect of handling time ($\bar{x} = 9.1$ min, 95% CL = 7.2, 11.4) in 2013 on whether neonates were abandoned or not, we adopted the same handling protocol during phase 1 of 2014, with the exception of excluding blood-sampling for all but the first dam's twins (DelGiudice et al. 2015, Severud et al. 2015*a*, DelGiudice and Severud 2016). Handling included weighing the calf by spring-scale to the nearest 0.5 kg, recording various morphological measurements and a rectal temperature ($\pm 0.05^{\circ}$C [SE]), fitting an expandable GPS collar (520 g; VERTEX Plus Survey-1 Globalstar, Vectronic Aerospace GmbH, Berlin, Germany), and examining the calf for injuries or abnormalities. The Globalstar GPS calf collars fitted in 2014 were the same as in 2013, except we modified the collar band material to minimize the risk of potential abrasions to the back of the neck (T. R. Obermoller, MNDNR, unpublished data). We programmed GPS collars to take fixes hourly and transmit every third successful fix; all fixes were stored on board. A more detailed description of the collar is provided by Severud et al. (2015*a*). During the field phase of capture operations, we considered dams to be with their neonates when they were $\leq$256 m away, the mean distance non-abandoning dams were from their calves during 48 hours post-capture in 2013 (DelGiudice et al. 2015). We classified dams that were >256 m from their neonates, but then moved to $\leq$256 m, as returned. Time spent >256 m away from their neonates and weather conditions were primary criteria for planning and initiating recoveries of abandoned neonates (Severud et al. 2016).

Intermittent capture-induced abandonments of neonates during phase 1 prompted us to discontinue operations after 8 days (8–15 May) to reconsider our capture approach and handling protocol. Because we considered GPS-collaring neonates of paramount importance for subsequent monitoring of their proximity to dams and movements, and for immediate notification of mortalities, we reduced our capture team to 2 people. We also limited handling to fitting the GPS collar, sexing each neonate, and visually scanning for injuries or abnormalities. Additionally, we removed a plastic sleeve fitted around the top of the expandable calf collars in an attempt to make them appear less obtrusive and conspicuous to the dams. As a precautionary measure, we also used a commercial scent-blocking product on handlers' clothes, gloves, and on collars. We stored collars in accumulated forest ground debris before taking them into the field. We continued to capture and collar twins simultaneously, 1 team member per calf. Phase 2 captures began on 21 May; we approached 1 dam with an eligible neonate(s) per day. We would not attempt an additional capture until our monitoring documented that the dam was with ($\leq$256 m) or had returned to its calf or calves following capture and release. All captures and handling protocols adhered to requirements of the Institutional Animal Care and Use Committee for the University of Minnesota (Protocol 1302-30328A) and followed guidelines of the American Society of Mammalogists (Sikes and the Animal Care and Use Committee of the American Society of Mammalogists 2016).

Data Analysis

Previously, we concluded that abandonment and differences in maternal movement behavior (e.g., dam-to-capture site, dam-to-neonate distances) induced by helicopter-assisted capture of neonates reflected pronounced differences in perceived disturbance of abandoning versus non-abandoning dams (DelGiudice et al. 2015). We calculated the mean distance in 6-hour segments using the location fixes of the dam's original times and interpolating from the neonate's hourly locations or location of the calving site (DelGiudice et al. 2015), but herein, we expanded our assessment of disturbance of dams induced by neonate capture. First, we tested for more subtle potential differences in disturbance of non-abandoners (only) and their calves relative to the different capture and handling approaches of phases 1 and 2 described above. We fit generalized estimating equation (GEE) models and selected a first-order autoregressive correlation structure to account for temporal correlation between observations from the same individual (Liang and Zeger 1986, DelGiudice et al. 2015). But we observed no significant differences between phases in dam-to-capture site ($\chi^2_1 = 1.314$, $P = 0.252$), dam-to-neonate ($\chi^2_1 = 1.034$, $P = 0.309$), or neonate-to-capture site ($\chi^2_1 = 0.456$, $P = 0.500$) distances from 6-hour bin averages up to 96 hours post-capture of neonates. Given the absence of an effect of capture phase on these distances, we subsequently pooled data across phases, and we used GEE models to test for differences in dam-to-capture site and dam-to-neonate distances between dams that did and did not abandon out to 96 hours post-capture. We extended our monitoring 48 hours beyond what we reported for helicopter-assisted captures (DelGiudice et al. 2015). We treated the 6-hour segments as continuous (i.e., 16 consecutive time periods) and tested for overall difference in distances between abandoners and non-abandoners. We used a similar approach to quantify differences in neonate-to-capture site distance between neonates that were and were not abandoned.

We used generalized linear mixed models to determine whether differences in bonding or handling times, estimated birth date, age of the dam, or phase (combined capture and handling approach) influenced capture-induced abandonment status (yes or no). We employed 1-sided Fisher's exact tests to assess the association between the abandonment status of individual neonates and 3 metrics of physical development or viability, including body mass, hind foot length (HFL), and body (rectal) temperature. We also predicted that neonates of body mass <15.1 kg (95% lower CL), HFL <42.3 cm, or exhibiting a body temperature <37.7°C (hypothermic) would be abandoned at a greater frequency than seemingly more developed or healthier individuals. Because evidence has suggested twins (1 or both) may be more predisposed to capture-induced abandonment than singletons (DelGiudice et al. 2015; M. A. Keech, Quicksilver Air, personal communication), we also used a 1-sided Fisher's to determine if this pattern was statistically supported by our data. We employed 2-sided Fishers exact test to determine if sex predisposed a neonate to being abandoned. We conducted all statistical analyses in R (R Core Team 2017) with the R packages exact2 × 2 (Fay 2010) for Fisher's exact tests and geepack (Yan 2002, Yan and Fine 2004, Højsgaard et al. 2006) for the GEE models. We considered tests significant at $\alpha = 0.05$.

During both capture phases, we used the mean distance of non-abandoning dams from their neonates (calculated from hourly fixes) during the 96 hours post-capture as a revised threshold distance to conclude that a dam (non-abandoning or abandoning) had made a return visit or was with its neonate(s). We compared mean (95% CL) number of return visits of abandoners versus non-abandoners, proportion of time dams spent within that threshold distance (i.e., time with neonates), distance returned (i.e., distance between dam and neonate 1 hr prior to returning), and dam-to-neonate distance of abandoners and non-abandoners once returned.

RESULTS

During phase 1 (8–15 May 2014), our initial approach to ground captures resulted in 7 (3 M, 4 F) of 12 (6 M, 6 F) neonates ultimately being abandoned by 5 of 9 dams in apparent response to capture operations (Fig. 1). Three of the abandoned neonates were singletons, and 2 dams abandoned both of their twins. Capture-induced abandonments began with a set of twins on the first day of operations, after which we discontinued captures for several days to reconsider our protocol (Fig. 1). At this time we removed blood sampling from the field methods and resumed operations on 12 May with a single neonate capture and no abandonment. However, abandonments continued intermittently during phase 1 through 15 May (Fig. 1). Our capture-induced abandonment contingency plan and monitoring of hourly location fixes of the GPS-collared newborns and their dams allowed us to recover 6 of the 7 abandoned neonates alive and in good condition (Severud et al. 2016). We transported these neonates to the Minnesota Zoo, where presently (11 Sep 2017) at >3 years old they are alive and well. Dam 13771 of the seventh abandoned neonate (13091), a male singleton, made several return visits (≤256 m) to the calf post-capture. However, it was unknown whether they had actually reunited and engaged in a nursing bout. That calf died at an estimated 4 days old, about 68 hours post-capture, 25 hours after the dam's third return visit, and during the morning of the same day we had planned to make a live recovery (Severud et al. 2016). Results of a necropsy conducted at the University of Minnesota Veterinary Diagnostic Laboratory (VDL) included an empty gastrointestinal tract and indicated that neonate 13091 died of nutritional deprivation.

During phase 2 (21 May–19 Jun) our 2-person team and abbreviated ($\bar{x} = 0.7$ min, range $= 0.2-2.2$ min; Severud et al. 2016) handling protocol limited capture-induced abandonment to just 1 (12608) of 10 dams abandoning 2 of 13 (8 M, 5 F) neonates, constituting a significant ($Z = -2.71$, $P = 0.007$) effect of capture phase (i.e., protocol). The abandoned twins (13096 and 13107) were both female. The dam was observed during the capture and release of the neonates, but because of a subsequent pause in transmission

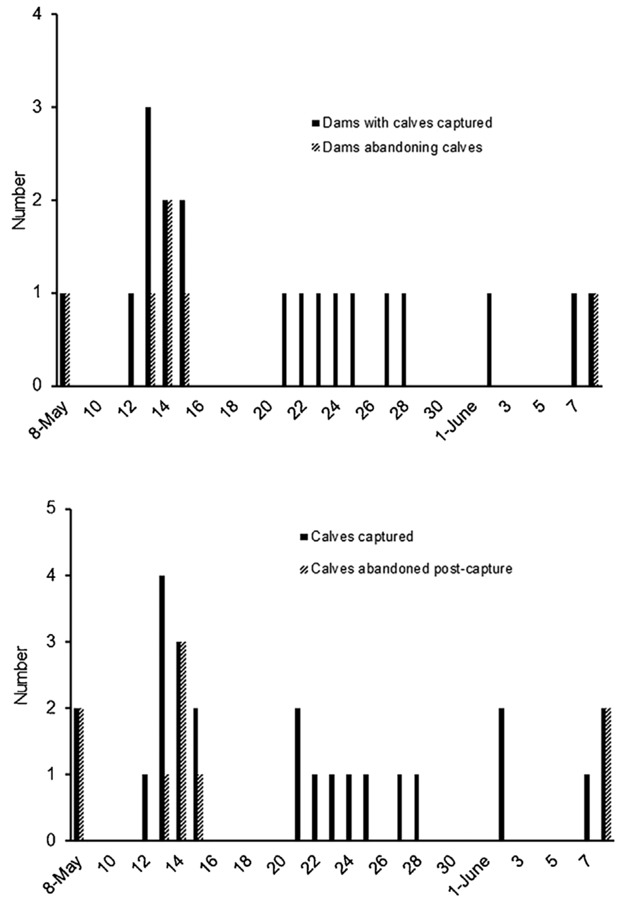

Figure 1. Temporal distributions of the number of moose dams whose neonates were captured, handled, and released compared to those that abandoned neonates (top) and the number of neonates captured, handled, and released compared to those that were abandoned in response to capture operations (bottom), northeastern Minnesota, USA, 8–15 May (phase 1) and 21 May–19 June 2014 (phase 2).

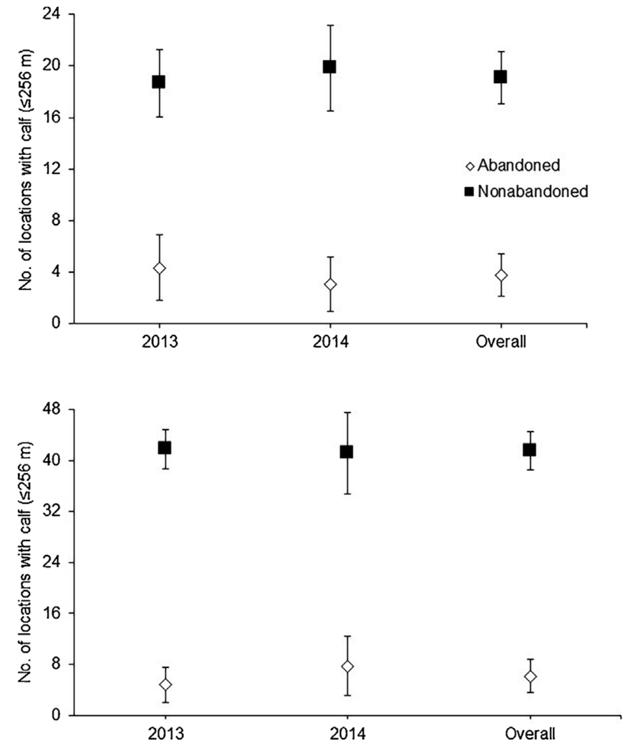

Figure 2. Mean (±95% CL) number of hourly locations of abandoning and non-abandoning moose dams that occurred ≤256 m from their neonates within 24 hours (top) and 48 hours (bottom) post-capture, northeastern Minnesota, USA, 8–19 May 2013 (helicopter-assisted) and 8 May–21 June 2014 (no helicopter assistance).

of her GPS-fixes, her location was temporarily unknown to us. Once fix transmissions resumed, abandonment was indicated, but she had made 2 return visits to within an average 86 m of the neonates. We delayed retrieval of the neonates so as not to further disturb the dam. Upon recovering the neonates (116 hr post-capture, 63 hr after the dam had last been <256 m), 1 (13107) was dead and the other was viable, in good condition, and transported to a licensed captive facility where it thrived for just over 2 years (Severud et al. 2016). Necropsy evidence from the VDL similarly indicated that neonate 13107 died of nutritional deprivation.

Characterizing Capture-Induced Abandonment

Dams that did not abandon their neonates in response to capture were located ≤256 m of them for a mean 82.7% and 85.7% of their hourly fixes ≤24 and 48 hours post-capture, respectively, compared to 12.9% and 16.2% for abandoning dams (Fig. 2). This was consistent with movement behavior of abandoning and non-abandoning dams following helicopter-assisted captures (Fig. 2). Actual mean distance of all non-abandoning dams from their neonates during the 48 and 96 hours post-capture in 2014 was 107 m (95% CL = 85, 129 m; $n = 16$ dam-neonate pairs) and 102 m (95% CL = 89, 115 m; $n = 16$ dam-neonate pairs), respectively.

Overall, there was neither a difference in mean distance between dams and capture sites (also the calving site) immediately (1 hr) prior to neonate capture for abandoners (20.3; 95% CL = 5.0, 35.6; range = 3–57 m) and non-abandoners (20.5; 95% CL = 10.7, 30.3; range = 4–66 m) nor 1 hour post-capture (149; 95% CL = 27.3, 271; range = 8–414 m vs. 84, 95% CL = 37.0, 131; range = 4–214 m). However, dam-to-capture site distance during the 96 hours post-capture was affected by group (abandoned vs. non-abandoned; Wald $\chi^2_1 = 20.71$, $P \leq 0.001$) and time (Wald $\chi^2_1 = 4.85$, $P = 0.028$) but not group × time (Wald $\chi^2_1 = 0.665$, $P = 0.415$; Fig. 3). The latter implies that over time, individuals that abandoned did not move away from neonate capture sites at a faster rate than individuals that did not abandon; slopes of the 2 groups differed but not significantly (Table 1, slope of 16.8 for non-abandoners, 42.6 for abandoners; Fig. 3). We also observed a difference in mean distance to capture sites between neonates abandoned and not abandoned (Wald $\chi^2_1 = 23.39$, $P \leq 0.001$), a time effect (Wald $\chi^2_1 = 6.409$, $P = 0.011$), and group × time interaction (Wald $\chi^2_1 = 6.552$, $P = 0.010$; Fig. 4). Immediately after capture, neonates not abandoned were an average 46.0 m farther from their capture sites than abandoned neonates. With time, the non-abandoned neonates moved away from the capture site at a significantly faster rate (16.0 m/6-hr interval) than neonates that were abandoned.

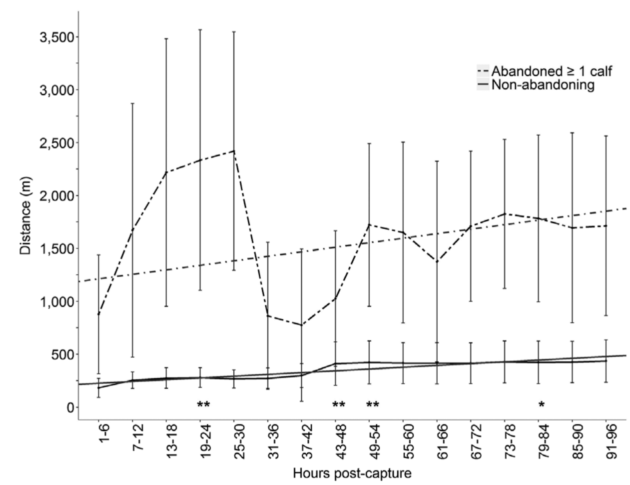

Figure 3. Mean (±95% CL) moose dam-to-capture site distances up to 96 hours post-capture for dams that abandoned at least 1 of their neonates (i.e., 1 twin, both twins, or a singleton; $n = 6$) and dams that did not abandon ($n = 12$), northeastern Minnesota, USA, 8 May–23 June 2014. We used generalized estimating equation models to test for differences between groups and present the modeled regression lines for abandoning (intercept = 1,169.7, slope = 42.6) and non-abandoning dams (intercept = 210.1, slope = 16.8). We treated the 6-hour segments as continuous. Each asterisk represents when we recovered and removed an abandoned neonate from the landscape. Once removed, we no longer included subsequent hourly dam-to-capture site distances for that neonate's dam.

The latter remained the same average distance over the 96 hours post-capture (Table 1 and Fig. 4), until they were recovered ($\bar{x} = 50.9 \pm 11.7$ [SE] hr post-capture, $n = 7$), or as in 2 cases, died. Consequently, post-capture dam-neonate distance differed between those abandoned and not abandoned (Wald $\chi^2_1 = 85.3$, $P \leq 0.001$), was influenced by time (Wald $\chi^2_1 = 3.798$, $P = 0.051$), and exhibited a group × time interaction (Wald $\chi^2_1 = 20.68$, $P \leq 0.001$; Fig. 5). Results from the model indicate that during the first time interval (1–6 hr), dams that abandoned were 1,355 m farther away from their neonate(s) than individuals that did not abandon, and afterwards moved away from them at a significantly faster rate ($\bar{x} = 85.83$ m/6-hr interval faster) than individuals that did not abandon (a slope approaching zero; Table 1 and Fig. 5). Over the 96 hours post-capture, the mean distance per 6-hour interval of non-abandoners from their neonates was ≤134 m, and most often 100 m (Fig. 5).

Four of 6 abandoning dams made ≥1 return visit ($\bar{x} = 1.5 \pm 0.50$, range = 1–3) to 4 of 9 neonates during the 96-hour post-capture monitoring period using the mean distance of non-abandoners from their neonates (102 m) as the threshold indicating return. We recorded return visits for individual dams only when their neonates were present on the landscape (i.e., not after retrieval) during the 96-hour period. For all 9 abandoned neonates, dams were with them (≤102 m) for a mean 3% (±1%, range = 0–10%) of their post-capture interval. All non-abandoners (16) made ≥1 return visit ($\bar{x} = 5.1 \pm 0.56$, range = 1–9), and were with their neonates for a mean 74% (±6%, range = 30–100%) of the 96 hours post-capture. Overall, abandoners returned to within a mean 60.0 m (95% CL = 31.1, 88.9; range = 28–98 m) and non-abandoners returned to within a mean 45.7 m (95% CL = 36.3, 55.1; range = 2–76 m) of their neonates. However, abandoners were on average 792 m (95% CL = 177, 1,406; range = 112–1,591 m) from their neonates 1 hour prior to returning versus 170 m (95% CL = 133, 207; range = 124–420 m) for non-abandoners.

Table 1. Coefficient estimates (SE) from the generalized estimating equations models testing how the relationship between dam-to-neonate capture site (hereafter capture site), neonate-to-capture site, and dam-to-neonate distances and time period differ between abandoning and non-abandoning dams (A and C) or between abandoned and non-abandoned calves (B) up to 96 hours post-capture, northeastern Minnesota, USA, 8 May–23 June 2014. We treated time as a continuous variable (1–16) that corresponds to 16, 6-hour bins over which we averaged the distances. We accounted for temporal correlation in the data using a first-order autoregressive correlation structure for each dam or calf. The Wald statistic and associated *P*-value indicate if the coefficient is significantly different from zero.

	Estimate	SE	Wald	P (>|W|)
(A) Dam-to-capture site				
Intercept[a]	210.1	33.0	40.5	≤0.001
Abandoners[b]	959.6	173.9	30.5	≤0.001
Time period[c]	16.8	6.1	7.7	0.006
Abandoners × time period[d]	25.9	31.7	0.7	0.415
(B) Neonate-to-capture site				
Intercept[a]	163.2	24.3	45.0	≤0.001
Abandoned[b]	−46.0	9.0	26.2	≤0.001
Time period[c]	16.0	6.0	7.2	0.007
Abandoned × time period[d]	−15.9	6.2	6.6	0.010
(C) Dam-to-neonate				
Intercept[a]	84.4	25.3	11.1	0.001
Abandoners[b]	1,355	219.8	38.0	≤0.001
Time period[c]	−0.0	4.2	0.0	0.996
Abandoners × time period[d]	85.8	18.9	20.7	≤0.001

[a] The intercept corresponds to the modeled (A) dam-to-capture site, (B) neonate-to-capture site, or (C) dam-to-neonate distances in the first time period for non-abandoning dams (A and C) or non-abandoned neonates (B).

[b] Modeled difference in (A) dam-to-capture site, (B) neonate-to-capture site, or (C) dam-to-neonate distances in the first time period between abandoning and non-abandoning dams (A and C), or abandoned and non-abandoned neonates (B). Non-abandoner dams (A and C) and non-abandoned calves (B) are used as the reference.

[c] Slope of the modeled relationship between (A) dam-to-capture site, (B) neonate-to-capture site, or (C) dam-to-neonate distances and time period for non-abandoning dams (A and C) or non-abandoned neonates (B).

[d] Difference in slopes of the modeled relationships of (A) dam-to-capture site, (B) neonate-to-capture site, or (C) dam-to-neonate distances as a function of time period between abandoning and non-abandoning dams (A and C) or between abandoned and non-abandoned calves (B).

There was no significant difference ($P \geq 0.742$) between neonates abandoned and not abandoned in mean estimated birth date (19 May 2014 ± 2.3 days, range = 5 May–17 Jun, $n = 25$) or age of their dams (7.0 ± 0.8, range = 1–12 yr, $n = 17$). Five of 6 dams that abandoned their neonates did so during phase 1 with the larger handling teams and more protracted protocols, but there was no difference in handling times of abandoned versus non-abandoned neonates in phase 1 ($\bar{x} = 7.5 \pm 0.59$, range = 4.9–10.4 min); we recorded handling times for 8 of 12 neonates handled in this phase. We observed a difference ($Z = -2.05$, $P = 0.040$) in mean bonding times of abandoned versus non-abandoned calves (42 ± 5.8, range = 12–65 hr, $n = 9$ vs. 55 ± 4.5, range = 31–98 hr, $n = 16$). There

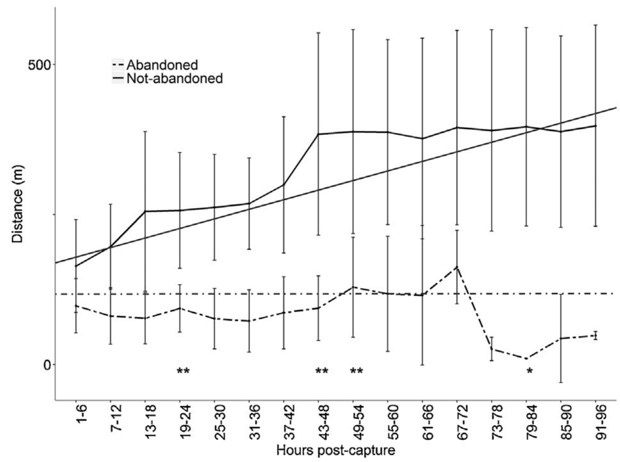

Figure 4. Mean (±95% CL) moose neonate-to-capture site distances up to 96 hours post-capture for neonates that were ($n = 9$) and were not ($n = 15$) abandoned, northeastern Minnesota, USA, 8 May–23 June 2014. We used generalized estimating equation models to test for differences between groups and present the modeled regression lines for abandoned (intercept = 117.4, slope = 0.1) and non-abandoned (intercept = 163.2, slope = 16.0) calves. We treated the 6-hour segments as continuous. Each asterisk represents when we recovered and removed an abandoned neonate from the landscape. Once removed, we no longer included subsequent hourly neonate-to-capture site distances for that neonate.

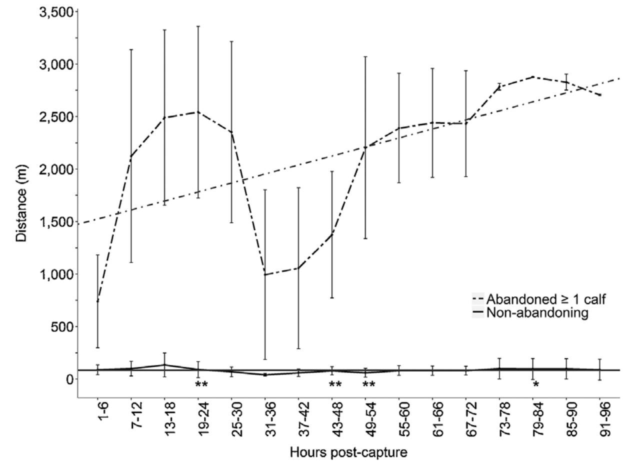

Figure 5. Mean (±95% CL) moose dam-to-neonate distances up to 96 hours post-capture for abandoned ($n = 9$) and non-abandoned ($n = 15$) neonates, northeastern Minnesota, USA, 8 May–23 June 2014. We used generalized estimating equation models to test for differences between groups and present the modeled regression lines for dams that abandoned at least one calf (intercept = 1,439.4, slope = 85.8) and non-abandoning dams (intercept = 84.4, slope = −0.02). We treated the 6-hour segments as continuous. Each asterisk represents when we recovered and removed an abandoned neonate from the landscape. Once removed, we no longer included subsequent hourly dam-to-neonate distances for that neonate.

was no effect of sex (odds ratio [OR] = 0.243; 95% CL = 0.037, 1.385; $P = 0.115$) or twinning (OR = 0.242; 95% CL = 0.373, ∞; $P = 0.257$) on capture-induced abandonment. At the study cohort level, smaller neonates by body mass (OR = 0.301; 95% CL = 0.020, ∞; $P = 0.955$) or HFL (OR = 1.181; 95% CL = 0.064, ∞; $P = 0.721$) were not predisposed to capture-induced abandonment, and there was no difference in mean body mass (16.2 ± 0.49, range = 14.0–19.5 kg, $n = 12$) or HFL (43.4 ± 0.51, range = 40.5–46.5 cm, $n = 12$) between those abandoned and not abandoned. However, 2 of 6 of the neonates below the 95% lower confidence limit of body mass (15.1 kg) and 1 of 3 below the 95% lower confidence limit of HFL (42.3 cm) for all neonates were abandoned. Additionally, low rectal temperature (OR = 1.540; 95% CL = 0.089, ∞; $P = 0.636$) did not contribute to abandonment and did not differ (38.5 ± 0.38, range = 36.5–41.7°C, $n = 12$) between neonates abandoned and not abandoned, but 2 of 3 neonates with rectal temperatures <37.7°C (95% lower CL) and both neonates with temperatures >39.3°C (95% upper CL) were abandoned.

DISCUSSION

Capture-induced abandonment of ungulate neonates by their dams is not uncommon, but until recently, the mostly anecdotal reports have provided only a limited understanding or characterization of this maternal behavior (Livezey 1990, Bertram and Vivion 2002, Keech et al. 2011, Patterson et al. 2013). This has made it difficult for biologists to consider potential predisposing factors (e.g., handling time) in an effort to mitigate the risk of abandonment during capture operations, immediately recognize abandonment as it occurs post-capture, or consider recovery of otherwise viable abandoned young. Our examination of captured-induced abandonment of moose neonates demonstrated how frequent, noninvasive monitoring of GPS-collared newborns and their dams facilitated confident detection of abandonment as it occurred and yielded insights that could motivate and assist biologists in minimizing abandonment risk and successfully retrieving viable young (DelGiudice et al. 2015, Severud et al. 2016).

Our initial effort (2013) increased our understanding of this complex maternal behavior relative to circumstances surrounding helicopter-assisted, neonate capture operations (DelGiudice et al. 2015). But in our follow-up study reported here, the increased incidence of capture-induced abandonment during phase 1 of ground-capture operations (5 of 9 dams) compared to 2013 (7 of 31 dams; DelGiudice et al. 2015) suggested that helicopter assistance may not have been the primary factor contributing to abandonment for potentially predisposed dams. The size of the capture team or duration of handling may have been equally if not more important. Although phase 1 neonate handling followed the same protocol as in 2013, our 3–4-person capture teams rather than the 2-person teams of 2013 may have negated the potential benefit of removing helicopter-induced disturbance. In Alaska, helicopters are employed for more efficient access to neonates and to haze off aggressive dams, commonly encountered during handling (Ballard et al. 1979, Keech et al. 2011; R. Swisher, Quicksilver Air, personal communication). We included the additional 1–2 persons for our phase 1 ground captures to fulfill that latter function and contribute to handling efficiency when we encountered twins, but ultimately the larger team may have contributed to the increased incidence of capture-induced abandonment. This conclusion was further supported when during phase 2, limiting our team to 2 persons and handling time to an average 0.7 minutes (range = 0.2–2.2 min; Severud et al. 2016), only 1 (of 10) dam abandoned twins following capture. Evidence indicates that human disturbance stimuli are analogous to predation risk, where number, distribution, or behavior of predators alone or via interaction with other factors affect perceived risk (i.e., attack and capture probabilities) and induce similar responses by prey; the greater the perceived risk, the stronger the response (Abrams 1993, Hugie and Dill 1994, Frid and Dill 2002). Because human hunters have been a threat to large vertebrates such as moose over evolutionary time and presently, Frid and Dill (2002) suggested that disturbance stimuli associated with humans approaching on foot may be indistinguishable by prey from true predatory stimuli. Despite helicopter-assistance, Ballard et al. (1979) markedly reduced capture-induced abandonment of moose neonates by similarly minimizing handling time and limiting handlers to ≤2 persons.

The average 48-hour distance of non-abandoners from their neonates (256 m) following helicopter-assisted captures in 2013 was a useful threshold for distinguishing between abandoners and non-abandoners then (DelGiudice et al. 2015) and following ground captures (Fig. 2), despite the shorter corresponding average distance (107 m) of non-abandoners in 2014. This was particularly beneficial in that the 256-m threshold was integral to developing our abandonment contingency plan prior to initiating ground captures, and subsequently guided our largely successful recovery efforts in 2014 (Severud et al. 2016). Using the more relevant non-abandoners' average 96-hour dam-to-neonate distance (102 m) following ground captures also yielded consistent differences between abandoners and non-abandoners that further contribute to our previously limited understanding of return visits, variations in behavior relative to capture and handling approach, and the dam's decision process when rejecting neonates.

Characterizing Capture-Induced Abandonment

Similar to our study of neonate abandonments induced by helicopter-assisted captures, movements of dams and neonates were the 2 informative behavioral components associated with ground-capture-induced abandonment. However, differences in the movement behavior of abandoning and non-abandoning dams were not immediately apparent. Their almost identical mean distances (~20 m) to neonatal capture (birth) sites 1 hour pre-capture indicated a similar level of maternal attentiveness prior to capture disturbance. This was consistent with 1-hour pre-capture (helicopter-assisted) distances of abandoners (35 ± 25 m) and non-abandoners (24 ± 4.3 m) in 2013, suggesting that during both years a predisposition to this behavior was not indicated by an apparent lack of maternal interest prior to disturbance. Mean distances between neonates not approached for capture and their GPS-collared dams (2013) ranged from 27–108 m for at least 84 hours of their calving localization (DelGiudice et al. 2015). Bogomolova et al. (1992) reported dams stayed within 50 m of their calves for 5–7 days postpartum.

Studies have reported numerous response similarities of prey animals to human-disturbance stimuli and predation risk (Hediger 1934 cited in Walther 1969, Berger et al. 1983, Gill et al. 1996, Frid and Dill 2002). Fleeing (i.e., flight) and ultimately abandoning parental investment were the 2 most apparent antipredator responses we observed in our moose dams. Unexpectedly, in our study area of relatively high wolf and black bear densities and predation pressure on calves (Severud et al. 2015*a*, b), only 5 (3 in phase 1, 2 in phase 2) of 19 dams initially stood their ground and exhibited aggression (e.g., pinned ears, roaring, charges) toward our handlers. Aggressive dams have been more commonly encountered during helicopter-assisted captures and handling of neonates in Alaska (M. A. Keech, Quicksilver Air, personal communication). Most of our dams fled, but similar initial flight distances (1 hr post-capture) of ultimately abandoning and non-abandoning dams from ground capture sites, as from helicopter-assisted capture sites, reflected no immediate tendency toward abandonment. Overall, 15 of 19 dams (abandoning and non-abandoning) remained within 128 m at 1 hour post-capture during both phases; 2 of the 4 dams beyond 128 m ultimately abandoned neonates, whereas 2 did not. Additionally, more subtle effects of capture disturbance were not reflected by the similar initial flight distances of non-abandoners of phases 1 and 2. Initial flight distances may be influenced by factors other than the actual disturbance (capture and handling). For example, aspects of flight by prey have been influenced by the directness and speed of predator (or handler) approach, their numbers, frequency of disturbance by predators, resource quality at the site of disturbance (i.e., poorer the quality, the greater probability of flight) and in surrounding habitats, and the proximity to refuge (Walther 1969, Ydenberg and Dill 1986, Bonenfant and Kramer 1996). Although greater flight distances immediately post-capture were therefore not reflective of higher abandonment rates, the lower abandonment rate during the second phase did meet our expectation.

Cumulative evidence suggests that the visual and auditory disturbance stimuli immediately associated with captures were not the predominant factors inducing maternal abandonment behavior, but perhaps residual effects on individual neonate behavior contributed to their dams' growing hesitancy to accept (Goldberg and Haas 1978). In a low predator (wolves and brown bears [*U. arctos*]) density but high fall moose hunting pressure area of Norway, Johnsen (2013) reported that no dams defended their neonates by aggressive behavior during early June ground checks (no captures) for calves. Rather dams fled an average 1,363 m (117–7,326 m) over a 2-hour period post-disturbance. Although abandonments and returns were not reported or discussed, the decision to flee from perceived risk (predation or human-disturbance induced) must balance the benefits of prolonging their own survival with the cost of energy expenditure for locomotion and possible loss of their offspring (Frid and Dill 2002).

As with helicopter-assisted captures of moose neonates, movements associated with dam-to-capture site, neonate-to-capture site, and dam-to-neonate distances 48–96 hours after capture were most informative in determining the incidence and temporal pattern of abandonments induced by ground captures. We postulated that the greater distances of abandoners to neonatal capture sites and to their neonates compared to non-abandoners by 6 hours post-capture reflects a more heightened agitation or stress response to the capture disturbance and relative to their avoidance reaction (Bodie 1979). This presumed elevated agitation was associated with a greater and highly variable rate of movement during the first 30 hours post-capture relative to the disturbance sites and to their neonates throughout the 96-hour post-capture period (Figs. 3 and 5). Consistent with an apparent intention to abandon, these dams largely maintained a greater average distance from the capture sites compared to non-abandoners. However, on average, not moving any farther from the disturbance sites after 30 hours post-capture and no longer moving at a faster rate than non-abandoners may indicate that their initial capture-induced agitated state was subsiding (i.e., "settling down," Johnsen 2013:6). In contrast, helicopter-assisted captures appeared to have a longer-lasting effect on movement behavior of abandoning dams because they continued to move farther from the capture sites and their neonates throughout the 48-hour monitoring period (DelGiudice et al. 2015).

Anecdotal evidence from several ungulate studies suggested that neonates that remained closer to release sites post-capture were more likely to be abandoned (Trainer et al. 1981, 1983; Livezey 1990). Our observations indeed indicate that investigating differences in average distances of abandoned and non-abandoned neonates to capture sites may be key to understanding what prompts and reinforces certain dams to continue to invest in their offspring as opposed to abandoning. The greater average distance from capture sites (46 m) by the first hour post-capture of neonates not ultimately abandoned versus those abandoned, and movement in the direction of their dams reflects a greater apparent viability. Throughout the 96 hours post-capture, our consistent hourly monitoring showed that these neonates continued to move at a faster rate and remained farther from their capture sites than abandoned neonates, whereas the latter moved less and remained the same average distance from capture sites until recovery or death (Fig. 4). These differences were very consistent with those we observed following helicopter-assisted captures, except the difference in the neonate-to-capture site distance was not evident as quickly following that disturbance. Neonates that were not ultimately abandoned had moved farther from their capture sites by 7–12 hours post-capture (DelGiudice et al. 2015). The greater mobility of the non-abandoned neonates allowed them to remain close to their dams throughout the post-capture monitoring period. Presumably this reinforces nurturing behavior by the dams and increased neonatal fitness, whereas it seems that the sedentary status of the abandoned neonate(s), continued nutritional deprivation, and weakening condition would reinforce its dam's decision to abandon (Verme 1962, Langenau and Lerg 1976). This was reflected by their faster movements and increasing distances from neonates over the 48–96 hours post-capture. However, it is plausible that in some cases the abandonment process and associated nutritional deprivation of a neonate(s) remaining at or close to its capture site, which was also the birth-site, began prior to capture.

Return visits of dams to their neonates (i.e., moving from >102 m to ≤102 m), whether ultimately abandoning or not, allows us to better understand the complexities of abandonment behavior. The average distance of non-abandoners from their neonates, shorter following ground captures (107 and 102 m at 48 and 96 hr) than helicopter-assisted captures (256 m at 48 hr), provided a useful threshold indicative of a consistent commitment to maternal investment following the capture disturbance. The number of return visits of all 16 non-abandoners varied markedly (1–9) among individuals during our 96-hour post-capture monitoring period, primarily because a number of individuals remained within 102 m of their neonates most of the time, whereas others tended to move farther than the threshold (up to 1,060 m), periodically returning to care for their young (Reese and Robbins 1994, Bubenik 2007). The distance dams move from their neonates and the number of return visits is likely influenced by habitat composition in the vicinity of calving sites as moose seek and select habitats that are rich in forage quality but with low risk of predation or other disturbances (Edwards 1983, Gilliam and Fraser 1987, Berger 1991). The spatial and temporal aspects of dam and neonate movements interpreted through their distances to fixed sites of disturbance (capture) and to one another (moving) allowed us to assess their immediate and more prolonged responses to the predator-like disturbance associated with ground captures, and to one another based on changes in proximity. Because we know from our own data sets that dams can move long distances in a brief period (e.g., 1 hr), we acknowledge that the hourly fixes we collected may have missed an undeterminable number of returns by abandoners and non-abandoners. Nonetheless, we observed noteworthy patterns. Abandoning and non-abandoning dams, for example, returned to within a similar average distance of their neonates (58 vs. 46 m), but abandoners traveled a markedly farther distance in the hour of their return (up to 1,612 vs. 1,060 m) and proportionately spent far less time close to their newborns. This would suggest that the abandoning dams rarely engaged in nursing bouts upon their return. This characterization of return visits appears to underscore the hesitancy of abandoners over time to accept (or reject) their offspring. These dams appear to be struggling with their maternal instincts. We observed similar patterns following helicopter-assisted captures, with the exception that we detected return visits by only 5 of 24 non-abandoners and there was no difference in the average number of return visits of abandoners and non-abandoners that made them during the 48 hours post-capture (DelGiudice et al. 2015). This was largely attributable to most of the non-abandoning dams spending more time within the 256-m threshold, whereas the abandoners spent more time farther than 256 m.

Potential Predisposing Factors

We examined birth, capture, neonate, and dam characteristics for their potential in predisposing neonates to abandonment induced by ground captures, just as we had done relative to helicopter-assisted captures (DelGiudice et al. 2015), because these had most commonly been the subject of previously reported anecdotal accounts and speculation (Livezey 1990, Keech et al. 2011, Patterson et al. 2013). Most typically, capture-induced abandonment has not been the focus of reported research. We again observed little evidence to support the influence of these factors at the study cohort level, but this may be partly attributable to marginal sample sizes. Based on our findings herein and previously reported, and the collective accounts of others, we maintain that at the individual level, such factors as dam age (e.g., previous experience rearing young) or condition and metrics of neonate viability (e.g., rectal temperature) immediately prior to capture should not be discounted but further evaluated.

The overall difference in bonding time that we observed between neonates abandoned and not abandoned was likely of little biological significance alone, as indicated by similar mean bonding times of these groups (39.4 ± 7.2 vs. 41.3 ± 2.6 hr) during phase 1 when most of the abandonments occurred. This comparison is consistent with our findings relative to helicopter-assisted captures (40.6 hr; DelGiudice et al. 2015). Estimated allowed bonding times associated with capture-induced abandonment of ungulate neonates have been variable (Livezey 1990); recommendations from other studies should be followed with caution because findings may easily be confounded by other intrinsic and extrinsic factors.

Additional work involving other species, capture and handling approaches, and varying environmental conditions should further expand our knowledge of abandonment behavior and help to reduce its occurrence at a greater scale. Our phase 2 results and findings of Ballard et al. (1979) indicate that limiting the number of handlers and spending minimal time with the animal has notable potential for minimizing capture-induced abandonment of neonates, with or without helicopter assistance. Of course, minimizing handling time sacrifices potentially valuable data that importantly inform the role of neonate condition on survival and population performance. Ballard et al. (1979:377) argued that at times important data should "...outweigh the risk and disadvantages of a high abandonment rate." We think our current, more in-depth understanding of capture-induced abandonment, facilitated by cutting-edge GPS-collar technology, will permit additional research to identify options to modestly extend handling times for important data collection, while minimizing the potential for apparent diminished viability (i.e., movements) and abandonment.

MANAGEMENT IMPLICATIONS

Our results indicate that capture-induced abandonment of ungulate neonates is the result of a complex decision process of dams that may be influenced by cues associated with movement behavior of the newborns. Relative to our 2 neonate capture approaches (3 including our previous study), intense monitoring of movements and proximity of GPS-collared moose neonates and dams in northeastern Minnesota permitted us to characterize abandonment, recognize it as it occurred, and ultimately minimize its occurrence by reducing handling time and number of handlers. However, just as the incidence of capture-induced abandonment may vary with species, location, and capture approach, so too might the characterization of abandonment behavior. Finally, it is difficult to know whether the abandonment decision process may have begun before the approach of our capture teams, and so was of a more natural origin. That is, we do not know if capture was the ultimate or only the proximate cause of abandonment. This has implications as to whether specific data should be included or censored from subsequent survival and cause-specific mortality analyses. Continued study of ungulate abandonment, capture-induced and natural, facilitated by GPS-collar technology, will further expand our understanding of this behavior and best support decision-making in management focused on population performance.

ACKNOWLEDGMENTS

Numerous individuals contributed to this study in various ways as we applied what we had learned from our initial examination of abandonment induced by helicopter-assisted capture, including K. J. Foshay, L. M. Ross, M. J. Haas, A. Wuenschmann, A. G. Armien, J. H. Giudice, B. R. Patterson, M. Carstensen, E. C. Hildebrand, M. H. Dexter, R. A. Moen, A. M. McGraw, R. G. Wright, J. D. Forester, M. W. Schrage, Vectronic Aerospace, M. A. Larson, L. J. Cornicelli, J. M. Rasmussen, T. J. Kreeger, J. A. Crouse, and J. H. Weickert. The University of Minnesota's Department of Fisheries, Wildlife, and Conservation Biology provided technical and other support. Funding was provided by the MNDNR Section of Wildlife and Wildlife Populations and Research Unit, Minnesota Environmental and Natural Resources Trust Fund (ENRTF), and the Wildlife Restoration (Pittman–Robertson) Program, with supplemental support from the Minnesota Deer Hunters Association.

LITERATURE CITED

Abrams, P. A. 1993. Why predation rate should not be proportional to predator density. Ecology 74:726–733.

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

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

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

Bastille-Rousseau, G., N. D. Rayl, E. H. Ellington, J. A. Schaefer, M. J. L. Peers, M. A. Mumma, S. P. Mahoney, and D. L. Murray. 2016. Temporal variation in habitat use, co-occurrence, and risk among generalist predators and a shared prey. Canadian Journal of Zoology 94:191–198.

Berger, J. 1991. Pregnancy incentives, predation constraints and habitat shifts: experimental and field evidence for wild bighorn sheep. Animal Behaviour 41:61–77.

Berger, J., D. Daneke, J. Johnson, and S. H. Berwick. 1983. Pronghorn foraging economy and predator avoidance in a desert ecosystem: implications for the conservation of large mammalian herbivores. Biological Conservation 25:193–208.

Bertram, M. R., and M. T. Vivion. 2002. Moose mortality in eastern interior Alaska. Journal of Wildlife Management 66:747–756.

Bodie, W. L. 1979. Factors affecting pronghorn fawn mortality in central Idaho. Thesis, University of Montana, Missoula, USA.

Bogomolova, E. M., and Y. A. Kurochkin. 2002. Parturition activity of moose. Alces Supplement 2:27−31.

Bogomolova, E. M., J. A. Kurochkin, and P. K. Anokhin. 1992. Observations of moose behavior on a moose farm. Alces Supplement 1:216.

Bonenfant, M., and D. L. Kramer. 1996. The influence of distance to burrow on flight initiation distance on the woodchuck, *Marmota monax*. Behavioral Ecology 7:299–303.

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

Bubenik, A. B. 2007. Behavior. Pages 173–221 *in* A. W. Franzmann, and C. C. Schwartz, editors. Ecology and management of the North American moose. Second edition. University of Colorado Press, Boulder, USA.

Butler, E., M. Carstensen, E. Hildebrand, and D. Pauly. 2013. Determining causes of death in Minnesota's declining moose population: a progress report. Pages 97–105 *in* L. Cornicelli, M. Carstensen, M. D. Grund, M. A. Larson, and J. S. Lawrence, editors. Summaries of wildlife research findings 2012. Minnesota Department of Natural Resources, St. Paul, USA. http://www.dnr.state.mn.us/publications/wildlife/research2012.html. Accessed 19 Jul 2017.

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

Carstensen, M., E. C. Hildebrand, D. C. Pauly, R. G. Wright, and M. H. Dexter. 2014. Determining cause-specific mortality in Minnesota's northeast moose population. Pages 133−143 *in* L. Cornicelli, M. Carstensen, M. D. Grund, M. A. Larson, and J. S. Lawrence, editors. Summaries of Wildlife Research Findings 2013, Minnesota Department of Natural Resources, St. Paul, USA. http://www.dnr.state.mn.us/publications/wildlife/research2013.html. Last accessed 19 Jul 2017.

Caswell, H. 2001. Matrix population models, construction, analysis, and interpretation. Sinauer Associates, Inc., Sunderland, Massachusetts, USA.

Child, K. N. 2007. Incidental mortality. Pages 275–301 *in* A. W. Franzmann, and C. C. Schwartz, editors. Ecology and management of the North American moose. Second edition. University of Colorado Press, Boulder, USA.

Chitwood, M. C., M. A. Lashley, C. S. DePerno, and C. E. Moorman. 2017. Considerations on neonatal ungulate capture method: potential for bias in survival estimation and cause-specific mortality. Wildlife Biology 23: in press. https://doi.org/10.2981/wlb.00250.

Ciuti, S., T. Muhly, D. Paton, A. McDevitt, M. Musiani, and M. Boyce. 2012. Human selection of elk behavioural traits in a landscape of fear. Proceedings of the Royal Society B-Biological Sciences 279:4407–4416.

DelGiudice, G. D. 2013. 2013 Aerial moose survey. Technical report. Minnesota Department of Natural Resources, St. Paul, USA.

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

DelGiudice, G. D., and W. J. Severud. 2016. Blood profiles and associated birth characteristics of free-ranging moose (*Alces americanus*) neonates in a declining population in northeastern Minnesota. Alces 52:85–99.

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

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

Edwards, J. 1983. Diet shifts in moose due to predator avoidance. Oecologia 60:185–189.

Erb, J., C. A. Humpal, and B. A. Sampson. 2015. Minnesota wolf population update 2015. Technical report. Minnesota Department of Natural Resources, St. Paul, USA.

Fay, M. P. 2010. Confidence intervals that match Fisher's exact or Blaker's exact tests. Biostatistics 11:373−374.

Frid, A., and D. L. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6:11. http://www.ecologyandsociety.org/vol6/iss1/art11/. Accessed 21 Nov 2016.

Franzmann, A. W., and C. C. Schwartz. 1986. Black bear predation on moose in a highly productive versus marginal moose habitats on the Kenai Peninsula, Alaska. Alces 22:139−154.

Fritts, S. H., and L. D. Mech. 1981. Dynamics, movements, and feeding ecology of a newly protected wolf population in northwestern Minnesota. Wildlife Monographs 80.

Gaillard, J.-M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution 13:58–63.

Garshelis, D. L., and K. V. Noyce. 2011. Status of Minnesota black bears, 2010. Final report. Minnesota Department of Natural Resources, St. Paul, USA.

Gilbert, S. L., M. S. Lindberg, K. J. Hundertmark, and D. K. Person. 2014. Dead before detection: addressing the effects of left truncation on survival estimation and ecological inference for neonates. Methods in Ecology and Evolution 5:992–1001.

Gill, J. A., W. J. Sutherland, and A. R. Watkinson. 1996. A method to quantify the effects of human disturbance on animal populations. Journal of Applied Ecology 33:786–792.

Gilliam, J. F., and D. F. Fraser. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. Ecology 68:1856–1862.

Goldberg, J. S., and W. Haas. 1978. Interactions between mule deer dams and their radio-collared and unmarked fawns. Journal of Wildlife Management 42:422–425.

Heppell, S. S., H. Caswell, and L. B. Crowder. 2000. Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. Ecology 81:654–665.

Højsgaard, S., U. Halekoh, and J. Yan. 2006. The R Package geepack for generalized estimating equations. Journal of Statistical Software 15:1−11.

Hugie, D. M., and L. M. Dill. 1994. Fish and game: a game theoretic approach to habitat selection by predators and prey. Journal of Fish Biology 45:151–169.

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

Keech, M. A., R. T. Bowyer, J. M. Ver Hoef, R. D. Boertje, B. W. Dale, and T. R. Stephenson. 2000. Life-history consequences of maternal condition in Alaskan moose. Journal of Wildlife Management 64:450–462.

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

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

Kunkel, K. E., and L. D. Mech. 1994. Wolf and bear predation on white-tailed deer fawns in northeastern Minnesota. Canadian Journal of Zoology 72:1557–1565.

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.

Langenau, E. E., and J. M. Lerg. 1976. The effects of winter nutritional stress on maternal and neonatal behavior in penned white-tailed deer. Applied Animal Ethology 2:207–223.

Liang, K.-Y., and S. L. Zeger. 1986. Longitudinal data analysis using generalized linear models. Biometrika 73:13−22.

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

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

Midwestern Regional Climate Center. 2015. cli-MATE, MRCC application tools environment. http://mrcc.isws.illinois.edu/CLIMATE/. Accessed 19 Jul 2017.

Minnesota Department of Natural Resources [MNDNR]. 2011. Minnesota moose research and management plan. Final Plan, Division of Fish and Wildlife, St. Paul. http://files.dnr. state.mn.us/fish_wildlife/wildlife/moose/management/mooseplan-final.pdf. Accessed 19 Jul 2017.

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 19 Jul 2017.

Nelson, M. E., and L. D. Mech. 1986. Mortality of white-tailed deer in northeastern Minnesota. Journal of Wildlife Management 50:691−698.

Neumann, W., G. Ericsson, and H. Dettki. 2009. The non-impact of hunting on moose *Alces alces* movement, diurnal activity and activity range. European Journal of Wildlife Research 55:255–265.

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. Pletcher. 2007. Impact of spatial and temporal variation in calf survival on the growth of elk populations. Journal of Wildlife Management 71:795–803.

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

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

Sergeant, D. E., and D. H. Pimlott. 1959. Age determination in moose from sectioned incisor teeth. Journal of Wildlife Management 23:315–321.

Severud, W. J., G. D. DelGiudice, and T. R. Obermoller. 2016. Minimizing mortality of moose neonates from capture-induced abandonment. Alces 52:73–83.

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

Severud, W. J., G. D. DelGiudice, T. R. Obermoller, R. J. Ryan, and B. D. Smith. 2015*b*. An alternate method to determine moose calving and cause-specific mortality of calves in northeastern in Minnesota. Pages 93–108 *in* L. Cornicelli, M. Carstensen, M. D. Grund, M. A. Larson, and J. S. Lawrence, editors. Summaries of Wildlife Research Findings 2014, Minnesota Department of Natural Resources, St. Paul, USA. http://files. dnr. state.mn.us/publications/wildlife/research2014/binder.pdf. Accessed 19 Jul 2017.

Sikes, R. S., and the Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663−688.

Trainer, C. E., J. C. Lemos, T. P. Kistner Jr., W. C. Lightfoot, and D. E. Toweill. 1981. Mortality of mule deer fawns in southeastern Oregon, 1968–1979. Oregon Department of Fish and Wildlife Research Report 10, Portland, USA.

Trainer, C. E., M. J. Willis, G. P. Keister Jr., and D. P. Sheehy. 1983. Fawn mortality and habitat use among pronghorn during spring and summer in southeastern Oregon, 1981–1982. Oregon Department of Fish and Wildlife Research Report 12, Portland, USA.

Verme, L. J. 1962. Mortality of white-tailed deer fawns in relation to nutrition. Pages 15–38 *in* L. E. Foote, planning committee chairman. Proceedings of the first national white-tailed disease symposium. Southeastern Section of the Wildlife Society, University of Georgia, Athens, USA.

Walther, F. R. 1969. Flight behaviour and avoidance of predators in Thomson's gazelle (*Gazella thomsoni*: Guenther 1884). Behaviour 34:184–221.

Yan, J. 2002. Geepack: yet another package for generalized estimating equations. R-News 2/3:12−14.

Yan, J., and J. P. Fine. 2004. Estimating equations for association structures. Statistics in Medicine 23:859−880.

Ydenberg, R. C., and L. M. Dill. 1986. The economics of fleeing from predators. Advances in the Study of Behavior 16:229–249.

Associate Editor: Christopher Jacques.