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Monitoring movement behavior enhances recognition and understanding of capture-induced abandonment of moose neonates

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Capturing and collaring mammalian newborns is a valued technique in studies focused on survival, cause-specific mortality, maternal investment, and other aspects of animal behavior and ecology. Abandonment of ungulate neonates has been highly variable and often may be underestimated due to limited understanding of this maternal behavior. In a study of survival and cause-specific mortality of GPS-collared moose (*Alces americanus*) calves in a declining population in northeastern Minnesota, 9 of 49 (18.4%) neonates (25 females and 24 males) were abandoned postcapture (8–17 May 2013) by 7 of 31 (22.6%) mothers. During the 1–6-h-interval postcapture, nonabandoning and abandoning mothers were similar distances from their calves. However, for nonabandoning mothers, from 13 to 48 h postcapture mean 6-h-interval distances to their calves steadily approached 0 m, whereas for abandoning mothers, mean distances to their calves continued to increase from 7 to 48 h. Five of the 7 abandoning mothers stayed with their calves immediately after capture for up to 11 h before leaving. Additionally, 5 abandoning mothers and 5 that did not abandon returned a mean 1.4 and 1.3 times, respectively, but abandoning mothers were notably farther from their calves just 1 h prior to returning than nonabandoning mothers. There were no differences in birth date, capture date, bonding or handling times, metrics of body size, or rectal temperature of neonates abandoned versus not abandoned, or in mean age of their mothers. Our study improves understanding of capture-induced abandonment and postcapture behavior of mothers that abandoned and mothers that did not. Employment of GPS collars and associated monitoring technology will continue to enhance our recognition and understanding of human-induced abandonment as it occurs for many species, allow rapid mortality investigations, limiting introduction of biases into analyses due to inaccurate data, and should help to minimize the occurrence of human-induced abandonment.

Key words: abandonment, *Alces americanus*, calves, capture-induced abandonment, GPS collars, human-induced abandonment, moose neonates

Human-induced maternal abandonment of juveniles has occurred in numerous wildlife species, from waterfowl (Anatidae) and game birds to bears (*Ursus* spp.) and ungulates (Mickelson 1975; Horton and Causey 1984; Livezey 1990; Linnell et al. 2000). To examine maternal investment, survival strategies, movement behavior, and habitat use, researchers rely on the valuable techniques of capturing and collaring newborns, but abandonment is the most common cause of marking-induced mortality of ungulate neonates (Livezey 1990). Growing research has shown that human-caused disturbance stimuli, analogous to predation risk, has consequences related to mothers becoming increasingly preoccupied with antipredator behavior (i.e., scouting) rather than with the fitness-enhancing activities of foraging and parental investment in their neonates (Gill and Sutherland 2000; Frid and Dill 2002; Johnsen 2013). Natural abandonment of neonatal ungulates has been documented, but it is relatively rare, whereas capture-related abandonment of neonates has ranged up to 28% for North American moose (*Alces americanus*) and as high as 40% among other ungulates (Hines 1975; Livezey 1990; Keech et al. 2011). A literature review by Livezey (1990) revealed that human-induced abandonment was highly variable and probably underestimated in many studies due to a lack of appropriate technology for closely monitoring the status of calves and mothers postcapture.

Suspected causes of capture-induced abandonment of newborn ungulates include insufficient or interrupted bonding time, confused recognition of neonates, stress associated with capture and handling, high population density, poor nutritional condition of calves or mothers, and young or old age of mothers (Livezey 1990; Keech et al. 2011; Patterson et al. 2013). Unfortunately, most accounts have been anecdotal or at the individual level, inconsistent among studies, and speculative with little supportive data presented. Interestingly, a recent study of white-tailed deer (*Odocoileus virginianus*) in north-central Minnesota reported no evidence of capture-induced abandonment or influence of numerous potential predisposing factors for 89 neonates radiocollared over 5 spring seasons (Carstensen Powell et al. 2005).

At least 3 factors may influence the accuracy of assessing human-induced abandonment of newborns: 1) it is not the focus of studies and therefore is not assigned high priority with respect to time, effort, and resources; 2) identification of abandonment is difficult because predators, scavengers, and decomposition remove evidence of abandonment, or other proximate causes of death (e.g., poor condition, hypothermia) obscure the ultimate cause of death (Livezey 1990); and 3) limitations of commonly used very high frequency (VHF) telemetry have precluded frequent, noninvasive monitoring of newborns and mothers necessary to detect abandonments as they occurred. Additionally, in a number of studies, the absence of radiocollars on some or all mothers hampered close monitoring of their proximity to neonates; determinations of whether abandonment occurred relied on infrequent, chance observations of apparent reunions of mothers and calves (Franzmann and Schwartz 1986; Carstensen Powell et al. 2005; Keech et al. 2011).

We launched a study of moose calf survival and cause-specific mortality and fitted GPS collars to moose neonates for the 1st time worldwide. We programmed collars to obtain hourly location fixes (Severud et al., in press). In a companion study, all mothers of these neonates were fitted 3 months earlier with GPS collars that were programmed to obtain hourly fixes during the calving season (Butler et al. 2013). Hourly fixes and multiple data transmissions per day allowed us to identify capture-induced abandonments in real time. Herein, our goal was to use the intense calf and mother monitoring capability afforded by GPS collars, and capture and handling data (Severud et al., in press) to improve our understanding of this human-induced disturbance of maternal instinct, specifically, to enhance our recognition and understanding of capture-induced abandonment both spatially and temporally. Furthermore, we examined the potential influence of capture-related factors (e.g., capture date, bonding time) and neonate characteristics (e.g., sex, litter size, body mass) on the tendency of mothers to abandon their neonates. Based on anecdotal data, other researchers postulated that twins, smaller, or less viable neonates are more vulnerable to capture-induced abandonment (Livezey 1990; Keech et al. 2011). Consequently, we predicted that twins and neonates of smaller body mass, shorter hind foot length, or lower rectal temperature would face greater risk of abandonment.

Materials and methods

Study area.—Calf captures were conducted 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 is the Northern Superior Upland region (Minnesota Department of Natural Resources [MNDNR] 2015), characterized by a variety of wetlands, including bogs, swamps, lakes, and streams; lowland stands of northern white cedar (*Thuja occidentalis*), black spruce (*Picea mariana*), and tamarack (*Larix laricina*); and upland conifers, including 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*) occur on the uplands, often intermixed with conifers.

The moose population in northwestern Minnesota decreased from just over 4,000 in the mid-1980s to less than 100 by 2007 (Murray et al. 2006; Lenarz et al. 2009). The northeastern moose population decreased (51%) from 8,840 (2006) to 4,350 moose in 2014 (DelGiudice 2014). In 2013, the State and Tribal harvests were suspended until further notice.

Gray wolves (*Canis lupus*) and black bears (*Ursus americanus*) are predators of moose (Fritts and Mech 1981; Lenarz et al. 2009; Patterson et al. 2013). Most recently, the wolf density in northern Minnesota was estimated at 3.4 wolves/100 km^2 (Erb and Sampson 2013). Mean black bear density in Bear Management Unit 31 (most of the study area) in 2008 was 23 bears/100 km^2 (Garshelis and Noyce 2011). White-tailed deer share most of the study area with moose, are managed at pre-fawning densities of < 4 deer/km^2, and are primary prey of wolves (Nelson and Mech 1986; DelGiudice et al. 2002; MNDNR 2011). Black bears and wolves also are a major source of mortality of deer neonates throughout summer (Kunkel and Mech 1994; Carstensen et al. 2009).

Lenarz et al. (2010) reported a general increase in maximum daily temperatures at Ely, Minnesota from 1960 to 2007. Mean daily minimum and maximum temperatures ranged from −5.2°C to 13.3°C and 3.3°C to 24.6°C, respectively, during April to July 2013 at Ely, Minnesota (Midwestern Regional Climate Center 2015).

Monitoring cow movements and calf capture.—On 1 May 2013, Iridium GPS collars (Vectronic Aerospace GmbH, Berlin, Germany) previously placed on adult females were reprogrammed from recording 1 fix/4 h to an hourly fix rate. We began monitoring movements of 50 and 17 GPS-collared adult female moose determined to be pregnant and nonpregnant, respectively, by serum progesterone concentrations (≥ 2.0 ng/ml—Testa and Adams 1998) from blood collected during late January–early February captures (Butler et al. 2013). A last incisor was also extracted from most adults for aging by counting cementum annuli (Sergeant and Pimlott 1959). Additional details of adult captures are presented by Butler et al. (2013). We similarly monitored 6 collared adult females not blood-sampled during winter capture and so were assigned a pregnancy status of "unknown." Our primary monitoring objective was to record when and where individual pregnant females increased locomotor activity reflected by their "calving movement," a variable atypical, long distance movement that ends with localization (i.e., spatial clustering of locations) for up to 7–15 days (Bogomolova and Kurochkin 2002; Poole et al. 2007; Severud et al., in press). Mean fix accuracy of adult collars was 3.7 m (± 0.3 *SE*, range = 0–17 m) in the open and 7.0 m (± 0.3, range = 1–36 m) under ≥ 80% canopy closure (Severud et al., in press). Additional details of the monitoring process are provided in Severud et al. (in press).

Adult location fixes, and subsequently calf fixes, were transmitted 4 and 8 times/day, respectively, to our base station (Severud et al., in press). We used 3 different and complementary approaches for monitoring the hourly locations and movements of mothers and their GPS-collared neonates: a base station computer, a web-mapping service, and automated reports. The base station provided full-time access to raw and processed (distance moved between locations) location data through collar vendor-provided software and a shared network drive. The full-time web-mapping service also was provided by the collar vendor and enabled us to view raw location data over Google Earth (Vectronic Aerospace GmbH 2014) maps and imagery. The automated reports, updated every 4 h, plotted mean hourly distances moved for up to 10 days at a time and GPS locations and paths of movement for the most recent 5 days, and they provided calculations of speed and displacement distance (Severud et al., in press).

We assumed that once females made their calving movement then localized, the birthing process began, and they calved within 12 h (Hydbring et al. 1999; Bogomolova and Kurochkin 2002; Asher et al. 2014). We then allowed an additional 24 h for bonding between the mother and its calf or calves. Once monitored mothers were allowed 24 h for bonding beyond the initial 12 h of localization, calves were identified as "eligible" for capture. Maximum allowed bonding time was calculated from that 24 h and any additional hours that elapsed by the time of capture. Each morning our team provided the commercial capture crew (Quicksilver Air, Inc., Fairbanks, Alaska) with a list of females (identification numbers and VHF radio frequency) and their most recent GPS coordinates. The capture crew located specified mothers and captured and collared their calves as time and conditions allowed on a daily basis.

The helicopter capture crew located the target mother from the air and then landed some distance away to allow handler(s) to disembark and approach the calves on foot. Then from overhead, with 2-way communication, the helicopter pilot guided the handler(s) into the calf or calves before again landing out of sight. The calf-handling protocol included fitting a 420 g GPS collar (GPS PLUS VERTEX Survey-1 GLOBALSTAR with expandable belt; Vectronic Aerospace GmbH, Berlin, Germany); fixing ear tags; collecting 25 ml of blood by syringe from the jugular vein into ethylenediaminetetraacetic acid tubes for hematology and into 2 serum tubes for chemistry profiles; weighing the calf to the nearest 0.5 kg with a spring scale; measuring morphological characteristics by tape measure (± 1 cm; hind foot length, body length, girth, and neck circumference) and rectal temperature (± 0.1°F) by digital thermometer; and a physical examination to document injuries or abnormalities. Calf collars had a mean location fix accuracy of 25 m (± 2.7) and 34 m (± 3.1) within open and dense vegetative cover types, respectively, and were programmed to record 1 fix hourly and in synchrony with the hourly fixes of the mothers' GPS collars (Severud et al., in press). We planned to limit time expended for capturing calves while dealing with aggressive mothers to 10 min. Only 4 of 31 mothers actually exhibited overt aggression, and most calves did not move more than 10 m from where they were first observed to where they were captured and handled. The handling protocol was designed to require about 5–6 min per calf to limit separation from the mother (Keech et al. 2011). Our intention was to maximize our knowledge of overall health at birth, survival, and cause-specific mortality of moose neonates by handling both twins simultaneously when encountered. Further, handling both twins limited the risk of the mother abandoning the twin being handled with the one not being handled (Keech et al. 2011). Ultimately, the handling crew captured, handled, and released all twins together. When handling was complete, the handler(s) trekked out to the sitting helicopter. 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 et al. 2011).

Data analysis.—In our analyses of movement data we compared 1) initial flight distances of abandoning and nonabandoning mothers in response to neonate captures, 2) maximum distances moved by mothers from the capture sites and their recently collared neonates, and 3) movements made by abandoned and nonabandoned calves relative to their capture sites during 48 h postcapture. Furthermore, we examined whether mothers returned to visit their calves. We used generalized estimating equation (GEE) models (Liang and Zeger 1986) to test for differences in postcapture mother-to-capture site and mother-to-calf distances between mothers that did and did not abandon. For the mother-to-capture site analysis, we conducted an additional analysis by splitting the "mothers that abandoned" category into 2 groups: mothers of twins that abandoned only 1 twin and mothers that abandoned all calves (either both twins or 1 singleton). In addition to testing for an overall difference in distances between these 2 (or 3) groups, we also tested at which point in time this difference became significant. We used a similar approach to quantify differences in calf-to-capture site distances between calves that were and were not abandoned. We chose GEE models to account for the repeated nature of the observations (i.e., because mothers or calves are observed repeatedly, data from the same mother or calf are not independent). These models are attractive because they are robust to potential misspecification of the correlation structure and departure from normality (Liang and Zeger 1986). We selected a 1st-order autoregressive correlation structure (AR1) to account for temporal correlation between observations from the same individual. For the mother-to-capture site analysis with mothers that abandoned split into 2 groups, we used mixed-effects models with mother ID as a random effect, because the number of mothers in each group was likely too small to fit GEEs. Mother-to-capture site, mother-to-calf, and calf-to-capture site distances were calculated as the difference in mean location of a mother (or calf) and mean location of its calf (or location of the capture site) in 6-h windows (1–6, 7–12, 13–18, 19–24, 25–31, 37–42, and 43–48 h postcapture). Mother-to-calving site distances for mothers whose calves were not approached for capture were calculated as the difference in mean location of mother and calving site (mean location of postcalving movement localization) in the same 6-h windows after the 12-h interval for calving and additional allowed bonding time of 24 h.

We employed 1-sided Fisher's exact tests to assess the association between the abandonment status of individual neonates and 3 measures of body development or viability: body mass, hind foot length, and body temperature. Specifically, we predicted that neonates of < 15.4 kg (lower 95% confidence limits [*CL*]), with hind foot length < 45.7 cm, or exhibiting a body temperature < 38.6°C (hypothermic) were abandoned at a greater frequency than healthier individuals. We also compared mean birth date, capture date, bonding and handling times, body mass, hind foot length, and rectal temperature of neonates abandoned versus not abandoned by 95% *CL* to determine their potential as predisposing factors. We similarly compared mean ages of abandoning and nonabandoning mothers. We tested for an association between the abandonment status (yes or no) of females or calves and different categorical variables using Fisher's exact tests. Specifically, we used a 2-sided test to determine if sex was associated with the abandonment status of individual neonates. We used a 1-sided test to determine if a mother of twins was more likely to abandon at least 1 of its neonates than a mother of a singleton.

All statistical analyses were conducted in R (R Core Team 2014) with the R package "exact2x2" (Fay 2010) for Fisher's exact tests, "geepack" (Yan 2002; Yan and Fine 2004; Højsgaard et al. 2006) for GEE models, and "nlme" (Pinheiro et al. 2013) for mixed-effects models. We considered tests significant at $\alpha = 0.05$.

Results

During 8–17 May 2013, 9 of 49 (18.4%) captured and GPS-collared moose neonates (25 females and 24 males) were abandoned postcapture by 7 of 31 (22.6%) GPS-collared mothers; these neonates subsequently died. Capture-induced abandonments occurred intermittently throughout the 10-day capture operation without exhibiting a particularly striking temporal pattern (Fig. 1).

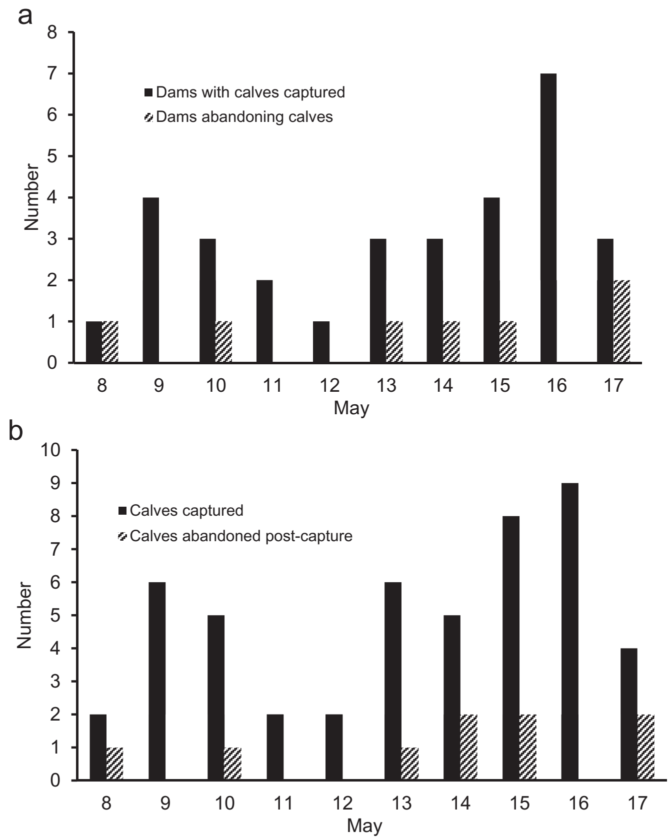

Fig. 1.—Temporal distributions of a) the total number of moose (*Alces americanus*) mothers whose newborn calves were captured, handled, and released compared to those that abandoned their calf(ves) and b) the total number of newborn calves captured, handled, and released compared to those that were abandoned apparently in response to capture operations, 8–17 May 2013, northeastern Minnesota.

The overall twinning rate (58.1%) was higher than we expected in a declining population. There was an apparent but nonsignificant influence of twinning on capture-related abandonment (odds ratio [*OR*] = 0.495, 95% *CL* = 0.724, ∞, $P = 0.104$), whether 1 or both twins of a litter were abandoned. Coincident with capture and handling, 6 of 18 mothers (33.3%) of twins abandoned their calves (1 or both), whereas only 1 of 13 mothers (7.7%) of singletons abandoned its calf.

Sex of neonates had no effect (*OR* = 0.460, 95% *CL* = 0.088, 2.522; $P = 0.464$) on capture-induced abandonment. Furthermore, there was no significant difference in the mean age of mothers that abandoned neonates (7.8 years, 95% *CL* = 4.0, 11.6, range = 2–12 years, $n = 5$) versus those that did not (5.7 years, 95% *CL* = 4.3, 7.1, range = 2–14 years, $n = 21$). Two of 7 abandoners and 3 of 24 nonabandoners did not have a last incisor extracted during adult capture.

Movement data.—Mothers of neonates not approached for capture, but that had localized after a calving movement, remained close to their calving sites (6-h means of 27.3 m, 95% *CL* = 17.9, 36.7–108 m, 95% *CL* = −15.0, 231 m, $n = 11$) up to 48 h beyond the presumed 12-h calving period and additional 24-h bonding time. The initial flight distance of mothers with the approach of the helicopter and handling of calves by the capture team, roughly indicated by the 1st hourly postcapture location of GPS-collared mothers, was a mean 257 and 183 m for mothers that ultimately did not abandon versus those that did, respectively. Mother-capture site distance was affected by group (abandoned versus nonabandoned; Wald $\chi^2_1 = 19.8$, $P < 0.0001$) and Group × Time (Wald $\chi^2_7 = 39$, $P < 0.0001$), but not by time (Wald $\chi^2_1 = 4.1$, $P = 0.7700$) up to 48 h postcapture (Fig. 2a). Abandoning mothers had moved farther ($P < 0.0039$; Appendix I) away from the capture site than nonabandoning mothers starting at 13–18 h after capture. When we split the group of mothers that abandoned at least 1 of their calves into 2 groups, i.e., abandoned all of their neonates (both twins or a singleton) or 1 twin, we observed a significant group effect ($F_{2, 26} = 16.9$, $P < 0.0001$) and a significant interaction of Group × Time ($F_{14, 182} = 7.7$, $P < 0.0001$), but no time effect ($F_{7, 182} = 0.80$, $P = 0.5912$). On average, mothers not abandoning their neonates did not move any farther from the capture site than they had during the first 6 h postcapture (Fig. 2b). However, by the 13–18-h interval, mothers that abandoned all calves moved increasingly farther from the capture site out to 48 h postcapture (Appendix II) compared to nonabandoning mothers ($P < 0.0001$; Fig. 2b). Mothers that abandoned only 1 twin did not move as far as mothers abandoning all of their neonates, but their mother-capture site distance was greater (Appendix II) than for nonabandoning mothers by the 25–30-h interval ($P = 0.0087$; Fig. 2b).

Postcapture mother-neonate distance differed for calves that were abandoned versus those that were not (Wald $\chi^2_1 = 35.8$, $P < 0.0001$), was affected by time (Wald $\chi^2_7 = 22.2$, $P = 0.0024$), and there was a significant Group × Time interaction (Wald $\chi^2_7 = 108.3$, $P < 0.0001$; Fig. 3). During the 1–6-h-interval postcapture, nonabandoning and abandoning mothers were similar distances from their calves ($\beta = 103.7$, $SE = 212.2$, $P = 0.625$; Fig. 3). However, for nonabandoning mothers, from 13 to 48 h postcapture, all mean distances to their calves differed ($P \leq 0.0468$; Appendix III) from their reference distance (498 m) and steadily approached 0 m, whereas for abandoning mothers, these mean distances increased from 7 to 48 h postcapture (Fig. 3).

We noted a difference between abandoned and nonabandoned neonates in mean distances to capture sites (Wald $\chi^2_1 = 5.9$, $P = 0.0150$), a time effect (Wald $\chi^2_7 = 32.3$, $P < 0.0001$), and a significant Group × Time interaction (Wald $\chi^2_7 = 39.4$, $P < 0.0001$; Fig. 4). Neonates abandoned and not abandoned were similar distances from their capture sites up to 6 h postcapture, but after 6 h abandoned neonates remained closer to their respective capture sites than those not abandoned ($P \leq 0.0200$; Appendix IV).

Movements of mothers postcapture were even more complex than indicated by distance between mothers and neonates or their capture sites. Five of the 7 abandoning mothers stayed with their calves immediately after capture for 1–11 h

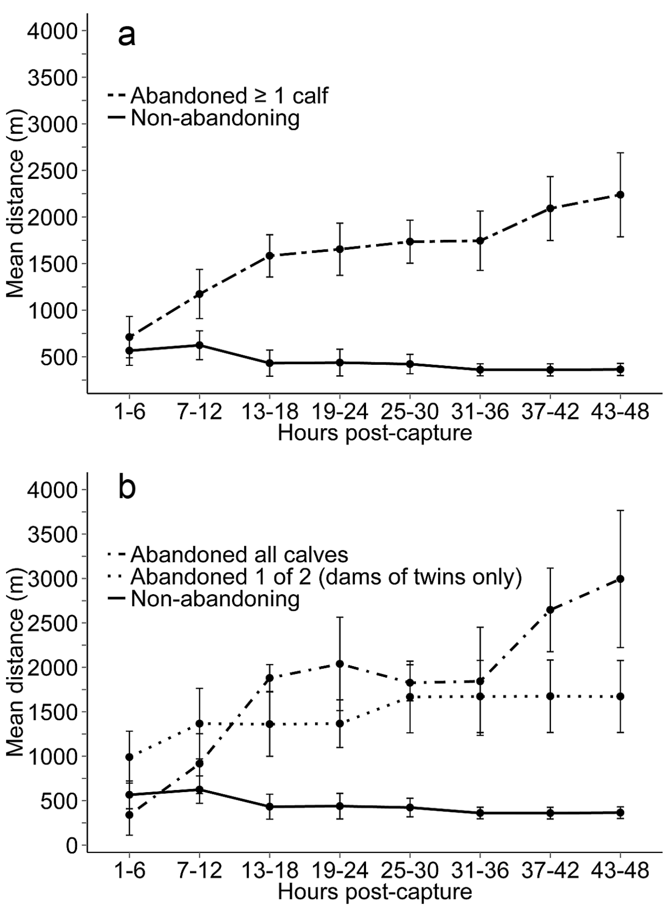

Fig. 2.—Mean (± *SE*) moose (*Alces americanus*) mother-to-capture site distances up to 48 h postcapture for a) mothers that abandoned at least 1 of the newborn calves (i.e., 1 twin, both twins, or a singleton; $n = 7$) and mothers that did not abandon ($n = 22$) and for b) mothers that abandon all newborn calves (i.e., both twins or a singleton; $n = 3$), mothers of twins that abandoned only 1 of the 2 calves ($n = 4$), and mothers that did not abandon ($n = 22$), 8–17 May 2013, northeastern Minnesota. For a given mother, the distance to the capture site was calculated at eight, 6-h blocks by averaging the hourly locations of the mother over each block and calculating the Euclidean distance between that average location and the capture site.

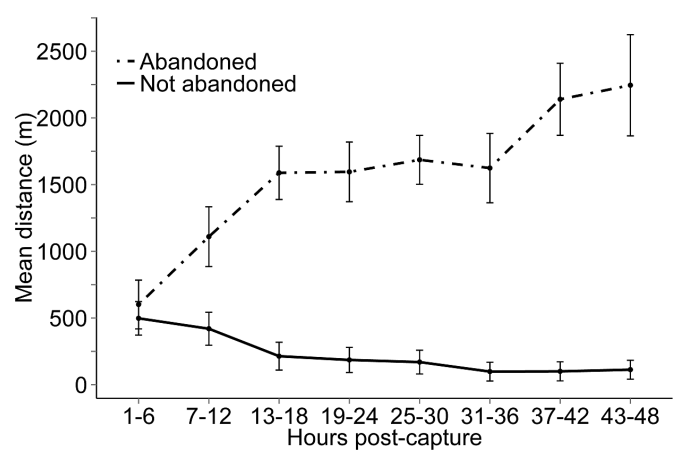

Fig. 3.—Mean (± *SE*) moose (*Alces americanus*) mother-to-calf distances up to 48 h postcapture for abandoned ($n = 9$) and nonabandoned ($n = 37$) newborn calves, 8–17 May 2013, northeastern Minnesota. For a given mother, the distance to its calf was calculated at eight, 6-h blocks by averaging the hourly locations of the mother and its calf over each block and calculating the Euclidean distance between these 2 averaged locations.

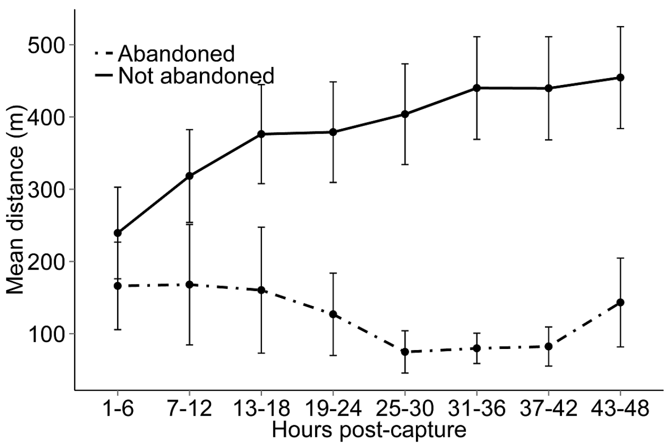

Fig. 4.—Mean (± *SE*) newborn moose (*Alces americanus*) calf-to-capture site distances up to 48 h postcapture for calves that were abandoned (*n* = 9) and calves that were not abandoned (*n* = 37), 8–17 May 2013, northeastern Minnesota. For a given calf, the distance to the capture site was calculated at eight, 6-h blocks by averaging the hourly locations of the calf over each block and calculating the Euclidean distance between that average location and the location of the capture site.

($\overline{X}$ = 5.8, 95% *CL* = 1.49, 10.1 h) before leaving. Determined by hourly fixes, these mothers were 106 m (95% *CL* = 72, 140, range = 78–174 m) from their calves. We used overall mean distance of nonabandoning mothers from their calves during the first 48 h postcapture (256 m) as a threshold distance to indicate that mothers essentially were within reasonable proximity to their calves or reunited at varying points in time. Paradoxically, these abandoning movements included varying numbers of returns by mothers to their calves postcapture (until death of the calf). Five abandoning mothers (included 4 of 5 that did not leave their neonate[s] immediately postcapture) and 5 that did not abandon returned 1.4 (95% *CL* = 1.01, 1.79, range = 1–2) and 1.3 times (95% *CL* = 0.71, 1.89, range = 1–3), respectively. Though they shared similar aspects of this postcapture movement behavior, abandoning mothers were notably farther from their calves just 1 h prior to returning ($\overline{X}$ = 1,560 m, 95% *CL* = 1,170, 1,950, range = 1,105–2,223 m) than nonabandoning mothers ($\overline{X}$ = 582 m, 95% *CL* = 425, 739, range = 402–812 m). However, the proximity of abandoning and nonabandoning mothers to their calves was similar once they returned ($\overline{X}$ = 98 m, 95% *CL* = 47, 149, range = 33–163 m versus $\overline{X}$ = 80 m, 95% *CL* = 21, 139, range = 14–162 m). Upon returning, abandoning mothers did not stay with their calves as long as nonabandoning mothers ($\overline{X}$ = 1.5 h, 95% *CL* = 1.1, 1.9, range = 1–2 h versus $\overline{X}$ = 4.7 h, 95% *CL* = 2.5, 6.9, range = 1–7 h, respectively). Mean distance from capture sites to mortality sites of abandoned calves was 150 m (95% *CL* = −7, 308, range = 4–752 m).

Capture and neonate characteristics.—Characteristics of captures and neonates at both the individual and study cohort level appeared to have little influence on this human-induced abandonment. There was no difference in mean birth date ($\overline{X}$ = 11 May, 95% *CL* = 10, 12 May, range = 5–16 May), capture date ($\overline{X}$ = 13 May, 95% *CL* = 12, 14 May, range = 8–17 May), minimum bonding time ($\overline{X}$ = 40.6 h, 95% *CL* = 34.4, 46.8, range = 21.9–132 h), or handling time ($\overline{X}$ = 9.1 min, 95% *CL* = 7.2, 11.4, range = 3–18 min) for calves abandoned versus those not abandoned. Smaller neonates by body mass (*OR* = 0.452, 95% *CL* = 0.059, ∞, *P* = 0.912) or hind foot length (*OR* = 1.644, 95% *CL* = 0.360, ∞, *P* = 0.377) were not more prone to being abandoned, and there was no difference in mean body mass ($\overline{X}$ = 16.0 kg, 95% *CL* = 15.4, 16.6, range = 12.0–20.5 kg) or hind foot length ($\overline{X}$ = 46.2 cm, 95% *CL* = 45.8, 46.6, range = 42.0–49.0 cm) of neonates abandoned versus not abandoned. Only 2 of 18 (11.1%) calves with the lightest body mass (12–15 kg; below the 95% lower confidence limit [*LCL*]) were abandoned, whereas 4 of 16 (25.0%) neonates with the shortest hind foot length (42–45.5 cm; below the 95% *LCL*) were abandoned. Lower rectal temperatures (*OR* = 0.3187, 95% *CL* = 0.013, ∞, *P* = 0.946) did not predispose calves to abandonment, and there was no difference in mean temperatures ($\overline{X}$ = 38.7°C, 95% *CL* = 38.4, 38.9°C, range = 37.7–39.7°C) of calves abandoned and not abandoned. Necropsies of abandoned calves at the Veterinary Diagnostic Laboratory of the University of Minnesota (St. Paul) yielded no macroscopic or microscopic findings indicative of a specific cause of death or contributing factors other than lack of curdled milk in the abomasum; hypoglycemia was indicated.

Mean mortality time postcapture for abandoned calves was 56 h (95% *CL* = 47, 65, range = 43–86 h); 1 of 9 calves was recovered alive, but it died while in transport to the Minnesota Zoo. Mean body mass loss from capture to necropsy was 14.2% (95% *CL* = 10.3, 18.1, range = 4.8–23.0%, *n* = 8).

Discussion

Until now a limited characterization of postcapture movement behavior and spatial dynamics of mothers and their neonates has been at least partially responsible for the narrow understanding of capture-induced abandonment. Our recent ability to intensely, but less invasively, monitor GPS-collared moose neonates of GPS-collared mothers over a 6,000-km^2 study area has shown that human-induced abandonment is a far more complex and prolonged behavior than the mother immediately fleeing and permanently separating itself from its newborn calves in response to human disturbance. We characterized capture-induced abandonment as involving 2 primary behavioral components, one associated with the mothers' movements and the other with those of the neonates. It also appears from our analysis that the degree of commitment to abandon, i.e., "hesitant acceptance" (Goldberg and Haas 1978:424), during the 48 h postcapture may be reflected by 1) whether or not the mother stays with its calf(ves) for a period of time immediately following capture and handling, 2) whether or not it abandons all of its calves (both twins or a singleton), 3) how far it moves from the source of disturbance (e.g., capture site) and neonates over time, and 4) whether it makes return trips to them for brief periods (≤ 2 h) during the interval between disturbance (e.g., capture) and permanent separation or death of the neonate by neglect.

The defensive and occasionally aggressive response of moose mothers to humans documented in Alaska and Canada (Ballard et al. 1979; Keech et al. 2000; Patterson et al. 2013) was less common during our captures (only 4 of 31 mothers). Most mothers fled as the helicopter initially approached or as it hovered overhead to assist the disembarked handler(s) locate and approach the calves (Mark A. Keech, Quicksilver Air, Inc., Fairbanks, Alaska, pers. comm., 8–17 May 2013). Most female moose (88%) also fled when approached by humans on the ground (without helicopter assistance) during calving and hunting seasons in Norway (Johnsen 2013). However, this initial flight response did not appear to be a critical determinant of whether a mother would ultimately abandon its neonates in our study; the mean estimated flight distance was actually farther, albeit nonsignificantly so, for those that did not abandon (257 versus 183 m). Notably farther initial flight distances of moose mothers from wolf and bear predation events of their neonates ($\overline{X}$ = 623 m, 95% *CL* = 447, 799 m) have been documented (Severud et al., in press).

In our study, the 2 ends of the abandonment behavior continuum were represented by 1) mothers that ultimately abandoned all of their calves and had a propensity to move increasingly long distances and farthest from their neonates' capture sites (up to a mean of 2,239 m) over 48 h postcapture and 2) nonabandoning mothers, which had moved their farthest (up to a mean of 738 m) within 12 h postcapture and then steadily began returning to the capture sites and their newborns. The capture disturbance undoubtedly induced all of these movements as mothers whose neonates were not approached for capture on average remained closest to their calving sites (≤ 108 m) over the same time period. Indeed, Bogomolova et al. (1992) reported captive moose mothers within 50 m of their calves for 5–7 days postpartum. During June ground checks for moose neonates (no captures) in Norway, Johnsen (2013:6) reported an initial mean flight distance of GPS-collared females of 1,364 m (range = 117–7,326 m) with a mean "settling down" time of 2 h. The stronger "avoidance reactions" (Bodie 1979:57) of abandoning mothers in our study likely reflected their varied but pronounced levels of agitation and stress from the capture disturbance, and perhaps, from a diminished or confused recognition of their young (Livezey 1990; Johnsen 2013). Interestingly, a more moderate degree of this maternal behavior was indicated by mothers abandoning only 1 of their twin neonates; these mothers did not differ in distance to the capture site compared to nonabandoning mothers until at least 19 h postcapture when these abandoning mothers also then began to move farther away.

Mobility of individual calves subsequent to capture may be as key to their fate as maternal movement behavior. By 7–12 h postcapture, calves ultimately not abandoned had moved farther from their capture sites ($\overline{X}$ = 318 m) than abandoned calves, the distance to which then stabilized as their mothers gradually returned to them over the next 36 h. Tendency of these neonates to be more mobile, and to move in the general direction of their mothers, may signal enhanced viability, prompting greater maternal investment (Langenau and Lerg 1976). Nonabandoned white-tailed deer fawns remained within a mean 162 m of their capture sites for at least 24 h (Carstensen Powell et al. 2005), which was more similar to abandoned moose calves in this study. However, as with nonabandoned moose calves, the mothers of these nonabandoned fawns largely stayed closer (within 200 m) to them and their capture sites than mothers that abandoned in the present study. Nonabandoned mule deer (*O. hemionus*) newborns made long movements (0.5–2 km) within 2 days of release, whereas abandoned neonates tended to remain close (≤ 10–300 m) to release sites (Livezey 1990). As with abandoned moose calves in our study, abandoned neonates of other ungulate species that died shortly after capture typically were discovered in close proximity to their capture sites (Trainer et al. 1983; Carstensen Powell et al. 2005).

Whereas abandoned calves in our study remained closer to the site of disturbance than nonabandoned neonates did, distance to their mothers steadily increased. However, the initial abandonment response did not appear to be spontaneous or absolute, as indicated by 5 of the 7 abandoning mothers reuniting with their calves immediately following capture for up to 11 h. This apparent indecision (hesitant acceptance) was further reflected over 48 h postcapture by 5 of the 7 mothers making 1–2 return trips to their calves before ultimately abandoning them. Four of these 5 mothers exhibited both aforementioned behaviors. Livezey (1990) cited cases of mule deer and white-tailed deer mothers running away and returning 3–10 times, but there was no reference to timeframes or distances. In our study, hesitant acceptance manifested in this way was not as commonly or as strongly exhibited by nonabandoning mothers before permanently reuniting with their neonate(s), but interestingly, mother-calf distances were similar for nonabandoning ($\overline{X}$ = 80) and abandoning mothers (98 m) during these return visits. The most striking feature about abandoning mothers was that they moved much farther distances (up to 2,223 m) than nonabandoning mothers (up to 812 m) in the hour just prior to reuniting with their calves, but their stay was much briefer ($\overline{X}$ = 1.5 versus 4.5 h). This pattern suggests that the instinct to accept their neonates was overwhelming enough to prompt multiple long distance returns, but ultimately, compelling factors unknown to us convinced them to reject their calves.

A number of studies have relied on daily visual or VHF telemetry checks of ungulate neonates and mothers reuniting postcapture to detect capture-induced abandonment (Ballard et al. 1979; Franzmann and Schwartz 1986; Keech et al. 2011). However, considering the complexity and variability of movement behavior associated with the capture-induced abandonment we observed, these monitoring approaches may not be intense or accurate enough to reliably assign capture-induced abandonment as the ultimate source of mortality, particularly when calf mortality was due to another proximate cause (e.g., wolf predation). In our study, even occasional close proximity of neonates to their mothers did not necessarily mean they had been accepted and were being afforded the maternal investment necessary to promote their survival. Clearly, the challenge is compounded by the fact that some mothers were not radiocollared (Ballard et al. 1979; Carstensen Powell et al. 2005; Keech et al. 2011; Patterson et al. 2013). Our mean time to mortality for abandoned calves was 56 h but ranged from 43 to

86 h. Consequently, our ability to detect capture-induced abandonment of calves as it occurred required intense but noninvasive GPS monitoring for more than 3 days postcapture. This intensive monitoring also facilitated the rapid detection and investigative responses of mortalities, which minimized the risk of misidentifying the ultimate (e.g., abandonment) cause of mortality due to a different proximate cause (Severud et al., in press).

Potential predisposing factors.—There has been no shortage of speculation about specific factors contributing to the complexity of abandonment behavior, but almost 25 years after Livezey's (1990) review of capture-induced abandonment of ungulates, it continues at variable rates, inconsistencies among studies are common, sample sizes have been limited, and understanding abandonment remains a challenge (Bubenik 2007; Child 2007). Our analytical approach, focused on the most commonly considered predisposing factors among animal species (Trivers 1974; Livezey 1990; Clutton-Brock 1991; Klug and Bonsall 2007), yielded no indication of a clear influence on abandonment behavior of mothers in this study. Our comparisons of birth and capture dates of neonates abandoned and not abandoned were premised on consideration that a temporal pattern might be associated with differences in late winter-early spring weather conditions that might directly affect the viability of neonates (Verme 1962; Keech et al. 2000) and, consequently, the sensitivity of some mothers to capture disturbance. Little documentation addresses these direct relations to capture-induced abandonment by free-ranging mothers, and we observed no discernible patterns indicating an influence of birth or capture dates, linked with minimum or maximum ambient temperatures or precipitation, on maternal abandonment.

Variable capture-induced abandonment rates and associated bonding and handling times of previous studies indicate that these factors do not have strong predisposing effects on maternal abandonment behavior at the study cohort level. Yet Ballard et al. (1979) demonstrated that minimizing human contact may limit abandonment. At the individual level, these factors may critically interact with others, exerting a stronger influence (Livezey 1990; Keech et al. 2011; Patterson et al. 2013). However, findings from these studies can be difficult to interpret because much of the evidence is anecdotal and associated with a compelling degree of uncertainty, especially when capture-induced abandonment is not recognized and is underestimated.

Findings addressing potential effects of age of mothers on their tendency to abandon neonates when disturbed have been mixed. As in our study, age of the mother was not associated with capture-induced abandonment of white-tailed deer neonates in north-central Minnesota (Carstensen Powell et al. 2005). Nonetheless, anecdotal evidence from other studies of white-tailed deer has suggested primiparous mothers, typically yearlings, are more prone to abandon their young when disturbed (White et al. 1972; Beale and Smith 1973; Ozoga and Verme 1986).

Neonatal ungulates of small body size, indicative of nutritive failure, may be predisposed to maternal rejection, particularly when their mothers are in poor condition (Verme 1962; Langenau and Lerg 1976). However, we have little information about how body mass or other size metrics of moose neonates are related directly to their viability (Schwartz 2007). Despite recording wide ranges of body mass (12–20.5 kg) and hind foot length (42–49 cm) at capture in our study, mean development did not differ between abandoned and nonabandoned neonates. However, nutritive failure and diminished viability of neonates predisposing them to natural or capture-induced abandonment may be indicated at the individual level. In our study, 11 and 25% of the smallest individuals by body mass and hind foot length, respectively, were abandoned following capture. Schwartz and Hundertmark (1993) contended that hind foot (hind leg) length was a superior metric of prenatal growth in moose, whereas differences in body mass may be the poorest (Markgren 1969). At the individual level, numerous studies of ungulates have associated poor physical development and condition of ungulate neonates with maternal rejection, mortality shortly after birth, and with capture-induced and natural abandonment (Livezey 1990; Carstensen Powell et al. 2005; Patterson et al. 2013).

Rectal temperature has value as an indicator of hypothermia or hyperthermia, which can influence viability of ungulates on an individual basis (Bodie 1979; DelGiudice et al. 2001; Kreeger and Arnemo 2012). Despite a prolonged winter and cool spring, mean body temperatures at capture of moose neonates abandoned and not abandoned did not differ (38.7°C) and were well within the normal range of ungulates (DelGiudice et al. 2001; Kreeger and Arnemo 2012). Carstensen Powell et al. (2005) also observed no association of rectal temperature with abandonment by white-tailed deer.

In conclusion, the ability to monitor almost in real time the movement behavior of moose neonates and their mothers using GPS collar technology and a variety of computer-based techniques (Severud et al., in press) has facilitated a more in-depth characterization and understanding of human-induced abandonment and some of its complexities. Clearly other local factors (e.g., predators nearby), still beyond our view, also may influence apparent maternal behavioral responses to neonate capture and other human disturbance (Frid and Dill 2002). Still, this improved understanding and continued employment of GPS collar technology will enhance our recognition of the event as it occurs and will allow a more rapid response for neonate recovery or mortality investigation. Both accomplishments will improve data analyses by limiting the unknown introduction of serious biases and will facilitate gaining the necessary knowledge to further minimize the occurrence of human-induced abandonment. Further, these results likely have implications for the objective study of numerous species and the potential to illuminate what can be learned about natural abandonment.

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Appendix I

Effect size of group and time interval for explaining differences in the distance-to-capture site of moose mothers that abandoned at least 1 calf (Yes) and dams that did not abandon (No). Coefficient estimates and *SE*s were obtained by fitting a generalized estimating equations model; mother ID was specified to identify the different clusters, and an autoregressive model of order 1 was chosen to model within-mother correlation of distance values.

	Estimate	*SE*	Wald	Pr(>|W|)
Intercept (No, 1–6 h)[a]	600.81	166.89	12.96	0.0003
Abandoned (Yes)	20.74	253.98	0.01	0.9349
Time (7–12 h)	19.00	115.92	0.03	0.8698
Time (13–18 h)	−97.46	167.64	0.34	0.5610
Time (19–24 h)	−171.80	231.87	0.55	0.4587
Time (25–30 h)	−241.70	180.34	1.80	0.1801
Time (31–36 h)	−195.69	175.12	1.25	0.2638
Time (37–42 h)	−293.23	205.95	2.03	0.1545
Time (43–48 h)	−288.99	206.31	1.96	0.1613
Abandoned × Time (7–12 h)[b]	420.02	225.03	3.48	0.0620
Abandoned × Time (13–18 h)	1063.39	368.58	8.32	0.0039
Abandoned × Time (19–24 h)	1226.36	451.79	7.37	0.0066
Abandoned × Time (25–30 h)	1367.23	286.65	22.75	< 0.0001
Abandoned × Time (31–36 h)	1465.39	390.85	14.06	0.0002
Abandoned × Time (37–42 h)	1768.73	445.00	15.80	< 0.0001
Abandoned × Time (43–48 h)	1978.40	598.72	10.92	0.0010

[a] The intercept corresponds to the modeled distance-to-capture site of mothers that did not abandon their calf (or calves) during that first 1–6 h time interval.
[b] (×) denotes the modeled interaction between group (mothers that abandoned versus mothers that did not abandon) and time interval.

Appendix II

Effect size of group and time interval for explaining differences in the distance-to-capture site of moose mothers that abandoned both twins or a singleton (Yes_{All}), mothers that abandoned only 1 twin ($Yes_{1\ twin}$), and mothers that did not abandon (No). Coefficient estimates and *SE*s were obtained by fitting a mixed-effects model with mother ID as a random effect.

	Value	*SE*	*t* value	*P* value
Intercept (No)[a]	564.13	128.05	4.41	< 0.0001
Abandoned (Yes_{All})	−208.81	369.73	−0.56	0.5771
Abandoned ($Yes_{1\ twin}$)	427.77	326.54	1.31	0.2016
Time (7–12 h)	61.52	119.67	0.51	0.6078
Time (13–18 h)	−142.54	120.00	−1.19	0.2364
Time (19–24 h)	−123.42	120.67	−1.02	0.3077
Time (25–30 h)	−136.06	119.86	−1.14	0.2578
Time (31–36 h)	−208.28	119.83	−1.74	0.0839
Time (37–42 h)	−199.66	120.17	−1.66	0.0983
Time (43–48 h)	−197.33	119.04	−1.66	0.0991
Abandoned (Yes_{All}) × Time (7–12 h)[b]	530.45	344.06	1.54	0.1249
Abandoned ($Yes_{1\ twin}$) × Time (7–12 h)	309.75	305.75	1.01	0.3124
Abandoned (Yes_{All}) × Time (13–18 h)	1671.90	347.13	4.82	< 0.0001
Abandoned ($Yes_{1\ twin}$) × Time (13–18 h)	527.29	304.04	1.73	0.0846
Abandoned (Yes_{All}) × Time (19–24 h)	1778.16	344.40	5.16	< 0.0001
Abandoned ($Yes_{1\ twin}$) × Time (19–24 h)	505.06	308.10	1.64	0.1029
Abandoned (Yes_{All}) × Time (25–30 h)	1619.69	346.97	4.67	< 0.0001
Abandoned ($Yes_{1\ twin}$) × Time (25–30 h)	811.39	305.86	2.65	0.0087
Abandoned (Yes_{All}) × Time (31–36 h)	1689.33	347.14	4.87	< 0.0001
Abandoned ($Yes_{1\ twin}$) × Time (31–36 h)	880.67	303.98	2.90	0.0042
Abandoned (Yes_{All}) × Time (37–48 h)	2477.67	350.23	7.07	< 0.0001
Abandoned ($Yes_{1\ twin}$) × Time (37–48 h)	885.49	307.90	2.88	0.0045

[a] The intercept corresponds to the modeled distance-to-capture site of mothers that did not abandoned their calf (or calves) during that first 1–6 h time interval.
[b] (×) denotes the modeled interaction between group (mothers that abandoned, mothers that abandoned only 1 twin, and mothers that abandoned both twins or their singleton) and time interval.

Appendix III

Effect size of group and time interval for explaining differences in the distance-to-calf of moose mothers that did (Yes) and did not (No) abandon their calf (or calves). Coefficient estimates and *SE*s were obtained by fitting a generalized estimating equations model; mother ID was specified to identify different clusters, and an autoregressive model of order 1 was chosen to model within-dam correlation of distance values.

	Estimate	*SE*	Wald	Pr(>|*W*|)
Intercept (No)[a]	497.58	123.70	16.18	< 0.0001
Abandoned (Yes)	103.74	212.16	0.24	0.6249
Time (7–12 h)	−78.04	83.05	0.88	0.3474
Time (13–18 h)	−283.66	142.68	3.95	0.0468
Time (19–24 h)	−311.75	138.42	5.07	0.0243
Time (25–30 h)	−328.11	134.65	5.94	0.0148
Time (31–36 h)	−399.48	130.92	9.31	0.0023
Time (37–42 h)	−397.18	131.50	9.12	0.0025
Time (43–48 h)	−385.11	131.24	8.61	0.0033
Abandoned × Time (7–12 h)[b]	586.67	152.79	14.74	0.0001
Abandoned × Time (13–18 h)	1270.51	267.30	22.59	< 0.0001
Abandoned × Time (19–24 h)	1305.77	261.24	24.98	< 0.0001
Abandoned × Time (25–30 h)	1412.20	211.10	44.75	< 0.0001
Abandoned × Time (31–36 h)	1421.97	216.93	42.97	< 0.0001
Abandoned × Time (37–42 h)	1935.38	291.81	43.99	< 0.0001
Abandoned × Time (43–48 h)	2012.03	345.95	33.83	< 0.0001

[a] The intercept corresponds to the modeled distance-to-calf of mothers that did not abandon their calf (or calves) during that first 1–6-h time interval.
[b] (×) denotes the modeled interaction between group (dams that abandoned versus dams that did not abandon their calf [or calves]) and time interval.

Appendix IV

Effect size of group and time interval for explaining differences in the distance-to-capture site of moose calves that were (Yes) and were not (No) abandoned. Coefficient estimates and *SE*s were obtained by fitting a generalized estimating equations model; calf ID was specified to identify clusters, and an autoregressive model of order 1 was chosen to model within-calf correlation of distance values.

	Estimate	*SE*	Wald	Pr(>|*W*|)
Intercept (No)[a]	239.38	62.57	14.64	< 0.0001
Abandoned (Yes)	−73.23	84.70	0.75	0.3873
Time (7–12 h)	78.91	21.75	13.16	0.0003
Time (13–18 h)	136.91	32.81	17.41	< 0.0001
Time (19–24 h)	139.64	37.83	13.62	0.0002
Time (25–30 h)	164.48	39.00	17.78	< 0.0001
Time (31–36 h)	200.72	40.74	24.27	< 0.0001
Time (37–42 h)	200.35	40.93	23.96	< 0.0001
Time (43–48 h)	215.16	41.26	27.19	< 0.0001
Abandoned × Time (7–12 h)[b]	−77.16	33.24	5.39	0.0203
Abandoned × Time (13–18 h)	−142.80	45.87	9.69	0.0019
Abandoned × Time (19–24 h)	−178.91	44.15	16.42	0.0001
Abandoned × Time (25–30 h)	−255.83	72.24	12.54	0.0004
Abandoned × Time (31–36 h)	−287.13	67.87	17.90	< 0.0001
Abandoned × Time (37–42 h)	−284.22	74.10	14.71	< 0.0001
Abandoned × Time (43–48 h)	−218.86	52.32	17.50	< 0.0001

[a] The intercept corresponds to the modeled distance-to-capture site of calves that were not abandoned during that first 1–6-h time interval.
[b] (×) denotes the modeled interaction between group (calves that were abandoned versus calves that were not) and time interval.