Exploring the role of parental proximity in the maternal–neonate bond and parental investment in moose (Alces alces) through postcapture movement dynamics

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\textbf{Abstract}
Disturbance can induce some dams to abandon their neonates, whereas others continue parental investment. Understanding the variability of the dam–neonate bond and parental investment of large, mobile species, reclusive during calving, such as moose (Alces alces), can be challenging. Advances in global positioning system (GPS) collar technology and analytical approaches allowed us to better understand the role that dam–neonate proximity plays in maintaining the maternal–neonate bond and parental investment. In 2013 and 2014, we used movement behavior of 50 free-ranging GPS-collared dams and their 74 GPS-collared neonates during 96 hr postcapture/release of neonates to examine home range (HR) sizes, overlap of their HRs, reunions (≤26 m), and dynamic interactions of their movements. Mean area of 95% kernel density estimator (KDE) HRs of neonates (23.5 ha) not abandoned by their dams was more than 2 times that of abandoned neonates (10.4 ha). Mean HR area of dams continuing to invest in their neonates (104 ha) was smaller than that (897 ha) of abandoning dams. Mean overlap of core (50% KDE) and 95% KDE HRs of dam–neonate pairs when investment continued was 38.7% and 42%, whereas corresponding overlap of HRs associated with abandonment was 0.1% and 2.7%. Mean proportion of pairwise hourly location-fixes indicative of reunions of dams investing in their neonates was 0.37 and occurred at a mean interval of 2.7 hr. A stronger ($p \leq .05$) interaction of mean hourly distances moved ($d_{ij}$) between dams investing in their neonates was associated with closer proximity compared with dams abandoning neonates. Our collective data indicate that the spatial proximity of dams investing in their neonates, and their stronger bond, nurtured neonate vitality in a way that reinforced continued investment. In contrast, the abandoning behavior of more distant dams had a diminishing influence on viability of their neonates via nutritional deprivation and limited reciprocal stimulation.

\textbf{KEYWORDS}
abandonment, Alces alces, maternal–neonate bond, moose, neonates, parental investment
1 INTRODUCTION

Even though parental investment has been one of the most thoroughly studied topics in life-history evolution, across species there remains a great deal to understand about investment instinct and behavior relative to the maternal–neonate bond and offspring survival during this sensitive time (Altmann, 1963; Bubenik, 1982, 2007; DelGiudice et al., 2018; Geist, 1982; Klug & Bonsall, 2007). The maternal–neonate relationship is highly complex and involves numerous physical, physiological, hormonal, olfactory, and behavioral interactions, changes, and cues, beginning in prepartum females and continuing long after parturition (Leuthold, 1977; Lévy et al., 1996; Nowak et al., 2000; Poindron & Lévy, 1990; Poindron et al., 1993; Vince, 1993). Birth and care of offspring demand major energetic, metabolic, and behavioral investments by ungulate dams for the survival of their own young, and thus, their own reproductive fitness (Clutton-Brock, 1991; Keech et al., 2000; Klug & Bonsall, 2007; Trivers, 1972). Both are closely linked to population performance and dynamics (Caswell, 2001; Gaillard et al., 1998; Heppell et al., 2000; Lenaz et al., 2010; Raithel et al., 2007).

The welfare of offspring relies not only on the dam’s ability to provide a healthy internal preparturition environment, but on her proficiency at affording the neonate an ecologically appropriate and safe external environment following birth (Keech et al., 2000, 2011; Ralls et al., 1986; Severud, DelGiudice, et al., 2019; Severud et al., 2015; Severud, Obermoller, et al., 2019). Spatial proximity to its neonates is likely critical to the dam’s success (DelGiudice et al., 2015, 2018). The ever-changing natural environment poses many challenges to the dam’s ability to provide for the basic needs (food, water, cover) of its offspring, whether related to habitat, or natural and anthropogenic disturbances associated with weather, fire, predation, or humans. Indeed, research is increasingly demonstrating the notion that human disturbance stimuli are analogous to predator risk for prey species, because responses to both “…divert time and energy from other fitness-enhancing activities…” including feeding and parental care (Gutzwiller et al., 1994; Lima, 1998; Lima & Dill, 1990; Steidl & Anthony, 2000). Specifically, studies have shown that variability of perceived risk (e.g., attack and capture probabilities) induces similar responses by prey; the greater the perceived risk, the stronger the response (Abrams, 1993; Frid & Dill, 2002; Hugie & Dill, 1994). Disturbance stimuli associated with humans approaching on foot may be indistinguishable by prey from true predatory stimuli (Frid & Dill, 2002). Behavioral responses by dams to such challenges may be quite variable, ranging from steadfast commitment to their young, including aggressive defense of them, to immediate or ultimate abandonment (Alexander et al., 1984; DelGiudice et al., 2015, 2018; Keech et al., 2011; Livezey, 1990; Ralls et al., 1986).

In a world of intensifying wildlife management, enhancing our understanding of influences of human disturbance is increasingly critical. Just as neonates are not passive recipients of maternal care, the strength of the maternal–neonate bond is not determined solely by the dam’s behavior. Rather, interactive behavior between neonates and their dams helps to insure successful rearing through this most vulnerable period. Stringham (1974) reported that for semicapitive moose (Alces alces), a period of “intensive reciprocal stimulation” begins between a calf and its dam immediately after birth. Studies of captive and semicapitive moose indicated that the persistence of a short visual and vocal distance between the dams and their neonates is important to the interactive formation and strengthening of the maternal–neonate bond (Bogomolova et al., 1992; Bubenik, 2007; Cederlund, 1987; Stringham, 1974). Furthermore, evidence from studies of domestic ruminants indicates that early activity and associated energy levels of neonates, olfactory and visual cues, vocalizations, and licking of fluids from neonates by dams all contribute to the maternal–neonate bond and to the establishment and maintenance of maternal investment behavior (Hersher et al., 1963; Nowak et al., 2000). Moreover, neonate behavioral effects on dams can be as profound as nipple localization and suckling stimulation increasing her prolactin concentrations, a hormone important to lactation (Nowak et al., 2000).

Proximity of cervid dams to their neonates is important to establishing and maintaining their bond and to neonate survival, but periodic separation is a natural part of this relationship and is essential to the mother’s survival (Bubenik, 2007; Carstensen Powell et al., 2005; DelGiudice et al., 2018; Ralls et al., 1986; Severud, DelGiudice, et al., 2019). For moose, elk (Cervus elaphus), caribou (Rangifer tarandus), and northern deer (Odocoileus spp.), parturition immediately follows the nutritional bottleneck of winter. Consequently, maternal investment must include acquiring sufficient nutrition to support energy-costly lactation and to begin recovery of the dam’s body condition, which is important to defending themselves and their newborns (Poole et al., 2007; Robbins, 1993; Smith, 1987). Because the birthing season typically begins just prior to spring green-up, and condition of individual dams and habitat quality naturally vary, separation distance and time apart can also be quite variable (Severud, DelGiudice, et al., 2019). Furthermore, disturbances, whether natural (e.g., predation) or from anthropogenic sources (e.g., neonate capture/release), may also influence aspects of these separations, and presumably, negatively impact the interactive reciprocal stimulation between dams and neonates, ultimately compromising the bond (DelGiudice et al., 2015, 2018; Johnsen, 2013). Enhancing our understanding of variability of the dam–neonate bond and maternal investment of large, mobile species, such as moose, that generally inhabit rugged forested terrain and are reclusive during calving can be particularly challenging.

Recent advancements in global positioning system (GPS) collar technology and novel analytical approaches allowed us to GPS-collar free-ranging, moose neonates of GPS-collared dams and monitor synchronous hourly movements for a parent study focused on calf survival, cause-specific mortality, and impacts on projections of a population that had recently and rapidly declined (DelGiudice, 2012; Severud, DelGiudice, et al., 2019; Severud et al., 2015; Severud, Obermoller, et al., 2019). This first-time-ever opportunity to intensely monitor free-ranging dams and their neonates had facilitated an unprecedented ability to track capture-induced abandonment as it occurred in near real time, and
consider new approaches to neonate capture and handling that would minimize this human-induced disturbance of the maternal instinct (DelGiudice et al., 2015, 2018; Severud et al., 2016). Up to this point, most of the reported accounts of this highly variable postdisturbance abandonment behavior in wild ungulates, free-ranging and in captivity, were anecdotal, and perhaps often misclassified (Livezey, 1990; Patterson et al., 2013).

Herein, we expanded our examination of the movement behavior of 50 free-ranging GPS-collared moose dams and their 74 GPS-collared neonates during 48–96 hr following disturbance by our neonate capture operations to better understand the potential role proximity between them plays in maintenance and variability of the maternal–neonate bond and maternal investment.

We predicted that:

1. The 96-hr postcapture HR of the abandoned neonates would be smaller than those of neonates not abandoned, whereas HRs of the dams continuing investment would be smaller than those of abandoning dams.
2. Overlap of HRs of dams continuing to invest and their neonates would be greater than that of abandoning dams and their young.
3. Reunions to within 26 m would occur more frequently between dams investing in their young compared with dams ultimately abandoning their neonates.
4. Reunions would occur more frequently as time elapsed postcapture of neonates.
5. Dams in closer proximity to their neonates and continuing to invest in them would have greater influence on their movements than dams rejecting and ultimately abandoning their young.

1.1 | Study area

We captured moose neonates on a 6,068-km² study area located between 47°06′N and 47°58′N latitude and 90°04′W and 92°17′W longitude in the Northern Superior Upland region of northeastern Minnesota (Minnesota Department of Natural Resources [MNDNR], 2015). Topography is undulant, and rugged cliffs and rocky outcrops are prevalent. Elevations range from 200 m to 650 m above sea level (Severud, DelGiudice, et al., 2019; Severud, Obermiller, et al., 2019). This area is characterized by bogs, swamps, lakes, and streams; stands of lowland 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 paper birch (Betula papyrifera) are commonly intermixed with conifers.

Overall, moose density was 0.86/km², but ranged from 0.32 to 2.66/km² (Giudice, 2016). Because of a steady moose decline in northwestern Minnesota, followed by a precipitous decrease in the northeastern population, state and tribal harvests did not occur during our study (DelGiudice, 2012). Gray wolves (Canis lupus) and black bears (Ursus americanus) commonly prey on moose and can have particularly marked impacts on calves (Fritts & Mech, 1981; Lenarz et al., 2009; Patterson et al., 2013; Severud et al., 2015; Severud, Obermiller, et al., 2019). Wolf and bear densities have been estimated at 3 and 23 per 100 km², respectively (Erb et al., 2015; Garshelis & Noyce, 2011; D. L. Garshelis, MNDNR, unpublished data). White-tailed deer (O. virginianus) are managed at prefawning densities of ≤4/km² and are the principal prey of wolves (DelGiudice et al., 2002; MNDNR, 2011; Nelson & Mech, 1986). Wolves and bears are also major predators of fawns throughout summer (Carstensen et al., 2009; Kunkel & Mech, 1994). Mean daily minimum and maximum temperatures during April to July, ranged from −5.2°C to 13.3°C and 3.3°C to 24.6°C in 2013, and from −16.6°C to 21.1°C and −6.7°C to 33.3°C in 2014, at Ely, Minnesota (Midwestern Regional Climate Center, 2015).

2 | METHODS

2.1 | Adult capture and monitoring

On 1st May 2013 and 2014, we began computer-monitoring hourly location-fixes of 73 and 70 adult (>1.5 years) female moose, respectively. The animals had been captured by aerial darting with carfentanil, thiafentanil, and xylazine during late January–early February 2013 (73) or early February 2014 (18), as part of a companion survival and cause-specific mortality study; immobilizations were reversed with naltrexone and tolazoline (Butler et al., 2013; Carstensen et al., 2014, 2017). Handling included fitting the moose with Iridium GPS collars (Vectronic Aerospace GmbH, Berlin, Germany). Fifty of the 73 and 14 of the additional 18 adult females captured in 2013 and 2014, respectively, were determined to be pregnant by serum progesterone concentrations ≥2.0 ng/ml (Butler et al., 2013; Murray et al., 2006; Testa & Adams, 1998; M. Carstensen, MNDNR, unpublished data). A last incisor (I4) was extracted from most adults for aging by counting cementum annuli in the laboratory (Seergeant & Pimlott, 1959).

Each year, adult hourly location-fixes were transmitted 4 times daily to our base station, which permitted monitoring their movements in near real time (Severud et al., 2015). Our primary monitoring objective was to identify when and where pregnant females made a “calving movement,” a variable, atypical long distance movement (e.g., 0.4–22.7 km over a mean 14.4 hr; Severud et al., 2015) ending with localization of spatially clustered location-fixes for 1–15 days (DelGiudice et al., 2018; DeMars et al., 2013; McGraw et al., 2014; Poole et al., 2007; Severud et al., 2015).

We employed a 3-pronged monitoring approach, which included a base station computer receiving daily-transmitted location-fixes, a web-mapping service, and automated reports (see details in Severud et al., 2015). This approach provided 24/7 access to raw and processed (distances between locations) location-fix data, views of location data overlaid on Google Earth (Google, Mountain View, California, USA) imagery, and automated reports, updated every 12 hr, and including plotted mean hourly distances moved for up to 10 days.
2.2 | Neonate capture and handling

During both years, we assumed parturition occurred within 12 hr of a dam beginning localization and then allowed a minimum of 24 additional hours for bonding (Severud et al., 2015). Mean allowable bonding times were 40.6 hr (±3.1 [SE]) and 50.4 hr (±3.7) during 2013 and 2014 (DelGiudice et al., 2015, 2018; Severud et al., 2015). In 2013, ground captures were helicopter-assisted (Quicksilver Air, Inc., Fairbanks, Alaska), locating the calving site from overhead with dam GPS coordinates we provided, landing some distance away to allow 1-2 handlers to disembark, guiding them in from overhead via 2-way communication, and then landing again out of sight. The calf-handling protocol included fixing ear tags; collecting blood samples from the jugular vein; recording body mass, other morphological characteristics, and rectal temperature; fitting a 420-g GPS collar (GPS PLUS VERTEX Survey-1 GLOBALSTAR with expandable belt; Vectronic Aerospace GmbH, Berlin, Germany); and examination for injuries or abnormalities. These collars were programmed to collect hourly fixes in sync with those of their dams (Obermoller et al., 2018; Severud et al., 2015). Calf location-fixes were transmitted to our based station 8 times per day (every third successful fix). All fixes were also stored on-board.

We had planned to limit time for capturing calves when dealing with aggressive dams (e.g., piloerection, foot stomping, roaring, or charging) to 10 min and designed the handling protocol to be 5–6 min to limit separation from the dam (DelGiudice et al., 2015; Keech et al., 2011). Capture-related data are summarized in Table 1. There were no differences in birth- or captured- related characteristics, and rectal temperature; fitting a 420-g GPS collar (GPS PLUS VERTEX Survey-1 GLOBALSTAR with expandable belt; Vectronic Aerospace GmbH, Berlin, Germany); and examination for injuries or abnormalities. These collars were programmed to collect hourly fixes in sync with those of their dams (Obermoller et al., 2018; Severud et al., 2015). Calf location-fixes were transmitted to our based station 8 times per day (every third successful fix). All fixes were also stored on-board.

We divided our 2014 neonate capture season (no helicopter assistance) into 2 phases as summarized in Table 1. During phase 1, our team of 3-4 biologists approached the calving site (cluster of dam’s location-fixes) on foot at a modest pace, until we were within 50 m, at which point we ran, captured, and handled all neonates according to the same protocol used in 2013, including the handling of twins (DelGiudice et al., 2018). However, after the first dam we approached abandoned her twins subsequent to their release, we excluded blood sampling in an attempt to be less invasive (DelGiudice & Severud, 2016). However, abandonment continued intermittently, and as in 2013, there was no informative temporal pattern of the behavior to use as guidance for modifications (DelGiudice et al., 2018; Severud et al., 2016).

We ceased operations to reconsider our capture approach and handling protocol. Other than highly variable, anecdotal accounts, the literature offered little understanding of capture-induced abandonment behavior in ungulates. However, studies of behavioral responses of ungulate prey to predators and human hunters (Abrams, 1993; Frid & Dill, 2002; Hugie & Dill, 1994) and one comparison of moose neonate capture techniques in Alaska (Ballard et al., 1979), proved to be of notable value. Consequently, we resumed captures on 21 May (start of phase 2) with a reduced capture team of 2 biologists, a more rapid approach time, and a protocol that limited handling to fitting the GPS collar, sexing each neonate, and visually scanning for injuries and abnormalities. Additional preparation details were reported in DelGiudice et al. (2018). During this phase, mean handling time was only 0.7 min and capture-induced abandonment was limited to just 1 of 10 dams abandoning twins. Noteworthy, this dam did not abandon twin neonates after we captured and handled them in 2013, 5 weeks earlier than in 2014.

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).

### Table 1

Summary of capture, handling, and abandonment information for moose (*Alces alces*) neonates, May–June 2013 and 2014, northeastern Minnesota

| Year | Capture dates | No. of neonates | No. of neonates abandoned | No. of abandoning dams of total | Mean handling time (range) min |
|------|---------------|----------------|--------------------------|-------------------------------|-------------------------------|
| 2013 | 8-17 May      | 49 (25 f, 24 m) | 9 (6 f, 3 m)              | 7 of 31                       | 9.1 (3.0–18.0)                |
| 2014 | Phase I       | 12 (6 f, 6 m)   | 7 (4 f, 3 m)              | 5 of 9                        | 7.5 (4.0–10.4)                |
|      | Phase II      | 13 (5 f, 8 m)   | 2 (2 f)                  | 1 of 10                       | 0.7 (0.2–2.2)                 |

aAdditional details available in DelGiudice et al. (2015), DelGiudice et al. (2013).
bMean birth dates were 11 May (5-16 May) and 19 May (May-17 June) during 2013 and 2014 (Severud et al., 2015; Severud, Obermoller, et al., 2019).
cOverall twinning rates were 58.1% and 32.0% in 2013 and 2014.
(Severud, Obermoller, et al., 2019; V. St-Louis, MNDNR, unpublished data). We subsequently calculated the spatial overlap between a dam’s HR and its neonate’s HR by quantifying the area of overlap between them, and dividing by the area of the neonate’s and dam’s HRs combined, as if merged (i.e., the area of overlap or intersection between the 2 HRs was counted only once). Two perfectly overlapping HRs would be assigned 100%, whereas 2 nonoverlapping HRs would be assigned 0%.

Mean location-fix accuracy of our adult collars was 3.7 m (±0.3) and 7.0 m (±0.3) in the open and under ≥80% canopy closure, respectively, and correspondingly, was 24.9 m (±2.7) and 40.3 m (±1.3) for our calf collars (Severud et al., 2015; Severud, Obermoller, et al., 2019). We calculated the Euclidean distance between each dam and its neonate(s) hourly (up to 96 hr postcapture) to understand how spatial proximity changes over time when investment continues versus when rejection and abandonment occur. Details of simulations (10,000) for accounting for measurement error of collars in calculating the distance between GPS-collared neonates and dams are described by Severud, Obermoller, et al. (2019). Mean measurement error associated with these distances was 25.6 m (95% confidence intervals [CI] = 25.0–26.2 m) and was similar among canopy classes. Based on this finding, we used a 26-m threshold to identify times when a dam was in close proximity to its neonate (hereafter a reunion event), then calculated the average time span between the reunion events for dams investing in their neonates versus for dams abandoning their neonates. We also calculated and averaged the proportions of reunion events across all hourly time stamps of each dam–neonate pair.

To measure the geometric similarity between the trajectories of a neonate and its dam, we used the dynamic interactions (DI) method introduced by Long and Nelson (2013). The DI method is a path-based approach for measuring the cohesiveness of corresponding movement vectors and is based on 2 geometric properties of a movement vector: displacement (di) and direction (θ) of the moving object between different time segments (Long & Nelson, 2013). The method defines a localized index (di) and a global dynamic interaction index (di). The localized index is calculated by a simple multiplication of displacement and direction components in time t through Equations (1)–(3) (Long & Nelson, 2013):

\[
di_d = f_d(d_i^t, d_i^b) = \begin{cases} 
1, & d_i^t + d_i^b = 0 \\
1 - \frac{d_i^t - d_i^b}{d_i^t + d_i^b}, & d_i^t + d_i^b > 0 
\end{cases} 
\quad (1)
\]

\[
di_b = g_b(\theta_i^a, \theta_i^b) = \begin{cases} 
0, & \text{either } \theta_i^a \text{ or } \theta_i^b \text{ is undefined} \\
1, & \text{both } \theta_i^a \text{ and } \theta_i^b \text{ are undefined} \\
\cos(\theta_i^a - \theta_i^b), & \text{otherwise} 
\end{cases} 
\quad (2)
\]

\[
di = di_d \times di_b 
\quad (3)
\]

where \(di_d\) and \(di_b\) are displacement and direction components, respectively, and measure cohesiveness in displacement and direction separately for corresponding segments in time t for individuals a (e.g., dam) and b (e.g., neonate). The term \(di_d\) ranges from 0 to 1, from no interaction (0) to maximum interaction (1), respectively. However, the \(di_b\) index varies between −1 for an opposing pair of directions to 1 for an aligning pair of movement vectors in the same direction (Long & Nelson, 2013). The global index \(di\) represents the average of localized indices throughout an entire trajectory of n points and n–1 movement vectors (Equation 4). The \(di\) statistic ranges from −1 (avoidance) to 1 (identical movement behavior).

\[
di = \frac{1}{n-1} \sum_{i=1}^{n-1} (di_d \times di_b) 
\quad (4)
\]

We quantified the aforementioned similarity indices for each dam–neonate pair and calculated summary statistics for nonabandoning (continued investment) and rejection/abandoning groups.

The three approaches that we present are complementary, because the DI approach does not take into account the spatial proximity between a dam and its neonate; examining HR overlap and reunion statistics provided a more complete picture of the movement patterns and relative space use of dam–neonate pairs.

We compared mean 50% and 95% KDE HR areas, HR spatial overlap, proportion of reunions, and the 3 movement similarity matrices of the nonabandoning and abandoning groups using 95% CIs calculated around the means (mean ±1.96*SE) to assess significant differences. Because of the tight connection between CIs and p-values, this is equivalent to inferring statistical significance at the .05 level (Murtaugh, 2014). Because previous work showed that the general movement patterns did not differ across years, we pooled the 2 years for these analyses (DelGiudice et al., 2015, 2018).

### 3 RESULTS

Mean 95% KDE HR area of neonates not abandoned by their dams (23.5, range = 1.7–107.4 ha) was about 2 times that of abandoned neonates (10.3, range = 0.8–57.7 ha) with slightly overlapping 95% CIs (Figure 1), whereas the mean HR of dams not abandoning their neonates (104, range = 0.5–1,588 ha) was significantly (p ≤ .05) smaller than that of abandoning dams (897, range = 7.3–2,171 ha; Figure 1). Mean HR size of nonabandoning dams was 4.4 times the HR of their neonates, whereas mean HR area of abandoning dams was 87 times the HR of their offspring (Figure 1). Mean core HR of neonates not abandoned was 4.0 ha (range = 0.2–36.2 ha) compared with 1.8 ha (range = 0.02–10.2 ha) for abandoned neonates, whereas mean core HR of dams not abandoning their offspring was 18.4 ha (range = 0.02–267 ha) versus 201 ha (range = 1.4–511 ha) for abandoning dams (Figure 1). Mean overlap of core and 95% KDE HRs of dams continuing to invest in their neonates was 38.7% (range = 0.0%–94%) and 42% (range = 0.2%–98%), but corresponding overlap of HRs
associated with abandonment was only 0.1% (range = 0.0%–0.7%) and 2.7% (range = 0.0%–20.6%, Figure 2).

The mean proportion of hourly location-fixes indicative of dam–neonate reunions (≤26 m apart) during the 96 hr postdisturbance was significantly (p ≤ .05) higher for those dams accepting and continuing to invest in their neonates (0.37, range = 0.02–0.59) than for dams in the process of abandoning their offspring (0.01, range = 0.0–0.05; Figure 3). When the maternal–neonate bond remained intact, the mean proportion of hourly reunions was highest (0.42) during the first 24 hr postdisturbance, but did not change significantly (p > .05) throughout the 96-hr monitoring interval (Figure 3). The mean interval between these reunions was 2.7 hr (95% CL = 2.5–3.0, range = 1.8–6.9 hr). For the dams that abandoned their neonates, there was only one reunion interval for a dam–neonate pair that allowed measurement (7.5 hr), which occurred within the first 24 hr.

We measured overall di, and its two components, di_θ and di_d, separately for each dam–neonate pair. In analyzing the movement data of our dams and neonates, there were no significant differences in di_θ during the first or second 24-hr intervals postdisturbance, or during the second 48 hr of monitoring, and mean values were relatively close to 0, indicating no similarities or strongly opposing hourly movements relative to direction (Figure 4). Because di is derived from the product of di_θ and di_d, the low and nonsignificant di_θ findings were enough to
account for the similarly low di values and absence of a difference between the 2 groups (nonabandoned vs. abandoned). However, there were more notable similarities (behavioral interactions) reflected by mean di values of dams investing in their neonates and dams abandoning their young during the 96 hr postdisturbance (0.46 vs. 0.41, Figure 4). Mean displacement values during the first and second 24 hr postdisturbance were 18.0% and 15.8% greater (p ≤ .05), respectively, for dams that remained closer and continued to invest in their neonates, indicating a stronger correlation in distance moved by the dams and their neonates, but this difference was not apparent during the second 48 hr. The di of the abandoning dam–neonate pairs was more variable during this latter portion of the monitoring period as the sampling size decreased by almost 50% (Figure 4). Mean di values were stable within both groups throughout the 96 hr of monitoring.

4 | DISCUSSION

Linear movements of free-ranging moose dams and their neonates can be quite variable, but on average, the movements of dams that remained in close proximity to their neonates and continued parental investment after human disturbance have been
readily distinguishable from those of dams that rejected and ultimately abandoned their offspring (DelGiudice et al., 2015, 2018). These divergences in their movement dynamics, and consequently in the dam's parental investment, were mirrored by marked differences between neonates benefiting from that investment versus those abandoned. Findings from additional multidimensional metrics presented herein broaden and deepen our understanding of dam and neonate movement behavior, and how they maintain the spatial proximity that apparently is important to reinforcing their bond and supporting parental investment. This is highlighted particularly by the greater mean HR size of the seemingly more vital neonates that were not rejected, twice that of abandoned neonates, and average greater overlap of both their core and 95% KDE HRs with those of their dams. Nevertheless, interestingly, how the 95% KDE HRs of dams and their neonates overlap on the landscape, whether investment continues or not following disturbance, can vary markedly within either group. Figure 5 provides examples of 2 pairs from each group, to offer insight as to how dams and neonates with the stronger bond may move and use their environment compared with dams and neonates where the bond has functionally broken down.

We previously reported that despite the disturbance of our capture operations, most GPS-collared dams remained on average <500 m from the capture sites and stayed even closer to their newborns, a mean 256 m (2013) and 102 m (2014), during the 2–4 days postcapture (DelGiudice et al., 2015, 2018). Furthermore, the proximity maintained between these dams and their neonates was in part due to the steadily increasing distance their neonates put between themselves and their respective capture sites, moving in the direction of their dams (DelGiudice et al., 2018). This is consistent with their more interactive and similar movement behavior and apparent reciprocal stimulation that appears to nurture and strengthen the maternal–neonate bond and encourage investment by dams (Bogomolova et al., 1992; Bubenik, 2007; Cederlund, 1987; Stringham, 1974). Our present findings suggest that dams that continued to invest in their neonates during this critical interval following parturition, and more importantly, the capture disturbance, were able to at least meet their immediately heightened nutritional needs associated with lactation (Robbins, 1993), within variable, but relatively small HR areas around their neonates (Figure 5). This would appear critical to the “parent–offspring conflict” discussed by Trivers (1985), where the dam is selected to balance the benefits of continued investment in the neonate's rapid increase in nutritional requirements and survival, with the costs of investment in her own condition and future reproductive success.

In marked contrast, the smaller HRs of the rejected neonates, which had remained close to the disturbance sites, typically showed little to no overlap with the much more expansive 50% and 95% KDE HRs (Figures 1 and 5) of their frequently more distant and far-ranging dams (DelGiudice et al., 2015, 2018). This appeared to reflect less vigor in offspring in the process of being rejected and the markedly diminished willingness of their dams to accept or invest in them, both negatively impacting their bond (Langenau & Lerg, 1976). Previous reports showed maternal deer reduced their daily movement rates immediately postparturition and remained close (means of 130–140 m) to their neonates (Carstensen Powell et al., 2005; Hawkins & Klimstra, 1970; Ozoga et al., 1982; Peterson et al., 2018); however, to the best of our knowledge, there are no other reported data documenting HR size of moose or other cervid newborns, or the degree to which they share the HR of their dams (Figures 1, 2, and 5). This is where the ability to GPS-collar newborns and their dams (Severud et al., 2015), and record synchronous hourly location-fixes, provided an invaluable advantage for our unique, more in-depth examination.

The value of close proximity to strengthening and sustaining the maternal–neonate bond was indicated further by the high frequency
of reunions to within 26 m of nonabandoning dams and their neonates. Importantly, our synchronous hourly location-fixes likely provided a minimum number of reunions; the actual frequency of reunions during the 96-hr monitoring interval may be higher and more variable. Bogomolova et al. (1992) noted that captive moose dams remained within 50 m of their neonates for 7–8 days and contended that a strong maternal–neonate bond required constant contact. Our estimates of HR overlap of dams and neonates and hourly distances between them, provide useful context for contact and close proximity, relative to bonding for free-ranging moose. Still, it is likely that functionally, these metrics may be quite variable because of the mixed influence that olfactory, visual, and auditory cues, and numerous other factors have on this bond and parental investment (Nowak et al., 2000; Stringham, 1974). Indeed, the quality of these interactions, which may in part be related to the distance separating dams and their neonates, and time apart notably influence neonate survival (Estes & Estes, 1979). Based on location-fixes of these dam–neonate pairs, we estimated a mean reunion interval of about every 2.7 hr, although as indicated by our hourly data, this interval can be quite variable. Although we cannot confirm that calves were nursing during these reunions, we are confident it was highly likely. Periodic nursing bouts not only provide nutrition vital to the calf’s survival, but the associated suckling activity, sustained energy level, supported vitality, and associated aforementioned cues are all intricate contributors to reinforcing and sustaining the maternal–neonate bond and assuring parental investment (Langenau & Lerg, 1976; Lickliter, 1985; Nowak et al., 2000; Stringham, 1974). In captive and semicaptive moose, frequency and duration of nursing bouts for moose neonates have been variable and change as the neonates age and begin foraging on solid foods, which occurs within 2–3 weeks (Bubenik, 2007; Schwartz, 1992). Stringham (1974) emphasized the absence of a strict nursing schedule, but observed about 1 nursing bout per hour during the first week of life and 1 bout every 3 hr by week 9, but these were semicaptive moose. Similarly, in captivity, deer neonates were observed to nurse at least hourly, and frequently up to 3 bouts per hour, whereas free-ranging does may seek out and attend their neonates from 2 to 10 times per day (Robbins, 1993; White et al., 1972). Noteworthy, the mean high
frequency of reunions in our nonabandoning pairs was reasonably stable throughout the 96 hr.

We previously reported that abandoning dams had returned to within a mean of 256 m from their neonates 3 and 8 times during the first 24 hr (12.5% of 24 location-fixes) and 48 hr (16.7% of location-fixes) postcapture (DelGiudice et al., 2018). However, our additional analyses herein indicate that the weak maternal–neonate bond was reflected more clearly by a near absence of reunions to within 26 m during the 4 days postcapture. Certainly, reunions within 26 m are much more indicative of potential opportunities for nursing and other nurturing behavior, whereas the absence of such reunions can be detrimental to the neonate’s welfare and the bond with its dam in a number of ways. Opposite to the reinforcing influence of a dam remaining in close proximity to its offspring, the absence of maternal care associated with prolonged distant separations, without periodic reunions, can exacerbate negative impacts of other stressors on the newborn’s behavior, which can have short- and long-term effects on the dam–neonate bond (Henry et al., 2009). The moose calf’s metabolic rate is greatest during the first 2 weeks of life, and its associated energy requirement can be increased by not only cold weather and precipitation, but by the stress of the dam’s absence (Henry et al., 2009; Robbins, 1993). These neonates require a sizable volume of highly digestible milk during their first week (estimated 3–4 L/24 hr) to meet their high energy requirements (Gasaway & Coady, 1974; Reese & Robbins, 1994; Robbins, 1993). The progressive nutritional deprivation of neonates in the process of being rejected steadily reduces their energy levels and vitality, as does the absence of nurturing (e.g., licking) from the dam (Hersher et al., 1963), which in turn, importantly may reinforce the dam’s instinctive response to reject (Langenau & Lerg, 1976; Lent, 1974; Nowak et al., 2000; Stringham, 1974; Verme, 1962).

The most notable finding from our examination of dynamic interaction of movement data was the stable (mean $d_{id} = 0.45–0.48$), relevant correlation of mean hourly distances moved ($d_{id}$) during the 96-hr monitoring period overall, and particularly during the first and second 24-hr intervals for those dams and neonates that remained in close proximity. This is perhaps indicative of a self-reinforcing and stronger maternal–neonate bond. Maximum $d_{id}$ values documented were 0.85, 0.65, and 0.56 during the first and second 24-hr and

**FIGURE 6** Examples of local analysis of dynamic interaction of movements (distance, $d_{i}$; direction, $d_{i\theta}$; $d_{id} = d_{i} \times d_{i\theta}$) of moose (Alces alces) dams and their neonates during 96 hr postcapture/release of neonates when maternal investment continued (nonabandoning) versus when rejection (abandonment) occurred, mid-May–mid-June 2013 and 2014, northeastern Minnesota. Dam–neonate pair IDs also correspond to those in Figure 5.
second 48-hr intervals, respectively. Corresponding maximum values for rejecting dam–neonate pairs were 0.55, 0.58, and 0.56, respectively. The much higher interaction with their neonates by the group of investing dams during the first 24 hr postdisturbance compared with the second 24 hr and second 48 hr (Figure 4) may reflect a degree of recovery from capture and handling-induced stress subsequent to the first 24 hr. We did not expect to calculate a mean di of the abandoning dams and their neonates as high as 0.41 (96 hr), given the often markedly greater distance between them compared with dams that consistently invested in their offspring. It may be that all of the mean di values are somewhat low, attributable to the hourly synchronous location-fixes rather than more frequent sampling (S. Dodge, Department of Geography, University of California-Santa Barbara, personal communication). Additional research should explore whether more frequent location-fixes would be more sensitive to the dynamic interaction of movements of moose dams and their offspring. Figure 6 provides examples comparing the stronger movement interactions of individual dam–neonate pairs, as indicated by di, di, and di, associated with persistent maternal–neonate bonds versus when neonates were rejected and ultimately abandoned by their dams. These are the same pairs used to reflect the differences in HR overlap in Figure 5 and clearly illustrate the variable, but more frequent influence that dams maintaining close proximity can have on the movements of their offspring (note the greater frequency of values between 0.5 and 1.0).

5 | CONCLUSIONS

The location-fix and movement data collected during our study supported all of our predictions but one. The value of close proximity of dams to their neonates for nurturing and maintaining a strong bond and parental investment, particularly following disturbance, is reflected by our calculations of core and 95% KDE HR size, percent overlap of dam and neonate HRs, frequency of dam–neonate reunions, and mean temporal intervals between reunions. Furthermore, we believe that the interactive movements and reciprocal stimulation facilitated by this proximity, as characterized, contributed to nurturing neonate vitality that likely positively reinforced or encouraged dams to continue investment, promoting a positive feedback loop. In contrast, the collective data associated with rejection strongly indicate that the absence of close proximity and limited reciprocal stimulation (including nursing), fed a negative feedback loop, so that as neonate vitality diminished (lower movement rates), the dam’s decision to reject and abandon was reinforced. We have an enhanced understanding of a functional meaning of close proximity between dams and neonates relative to successfully maintaining a strong maternal–neonate bond, which has implications for survival. We believe our approach, metrics, and findings may have applicability relative to other disturbances, depending on their specific dynamics. Clearly, the strength of the maternal–neonate bond of moose and other cervids can be further assessed and better understood (e.g., parent–offspring conflict) following any variety of disturbances by more frequent, synchronous sampling of location-fixes and using metrics reflective of dam–neonate proximity.

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CONFLICT OF INTEREST

None declared.

AUTHOR CONTRIBUTION

Glenn D. DelGiudice: Conceptualization (lead); Data curation (lead); Formal analysis (equal); Funding acquisition (lead); Investigation (equal); Methodology (equal); Project administration (lead); Resources (lead); Software (supporting); Validation (equal); Visualization (equal); Writing—original draft (lead); Writing—review & editing (lead). Mohsen AhmadiKhani: Conceptualization (supporting); Data curation (supporting); Formal analysis (equal); Investigation (equal); Methodology (equal); Resources (supporting); Software (equal); Writing—review & editing (supporting). Véronique St-Louis: Conceptualization (supporting); Data curation (supporting); Formal analysis (equal); Investigation (equal); Methodology (equal); Resources (supporting); Software (equal); Writing—review & editing (equal). William J. Severud: Conceptualization (equal); Data curation (equal); Formal analysis (supporting); Funding acquisition (supporting); Investigation (equal); Methodology (equal); Project administration (lead); Writing—review & editing (equal). Tyler R. Obermoller: Conceptualization (equal); Data curation (equal); Investigation (equal); Methodology (equal); Project administration (equal); Writing—review & editing (equal).

DATA AVAILABILITY STATEMENT

Data are available at the Data Repository for the University of Minnesota (DRUM), https://doi.org/10.13020/rkp-6h68.

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