MOVEMENTS OF FEMALE MOOSE IN RELATION TO BIRTH AND DEATH OF CALVES

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ABSTRACT: We followed the daily movements of 24-59 parturient moose every spring from 1994-1997 in southcentral Alaska, an area with heavy predation of calves. We tested the hypotheses that: (1) selection of a parturition site involves movements not typical of normal home range use; (2) movements during the neonatal period increase risk to calves; and (3) females are more likely to return to an area for parturition if their previous calf escaped predation. Movements of moose increased significantly in the 2 days prior to parturition, were greatly reduced for at least the next 9 days and did not approach pre-parturition levels until calves were about 26 days old. Daily movements by females that eventually lost a calf (> 48 hours after day observed) were greater than those by females that successfully reared their calf or calves through the first 45 days of life ($P = 0.049$). Distances between parturition sites in successive years were greater among females that lost their calves the first year (4.9 vs 2.6 km, $P = 0.02$), regardless of the age at which the calf died.

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The selection of birth sites by moose (*Alces alces*) usually is considered in the context of providing nutritious forage for adult females during lactation and safety from predators (Stringham, 1974, Leptich and Gilbert 1986, Berger 1991, Wilton and Garner 1991, Bergerud 1992). The resulting behavior is a balance between these two needs among choices that cannot optimize both (Edwards 1983, Berger 1991, Bowyer *et al.* 1999). The pattern of movements around the time of parturition may reflect the animal's changing ecological priorities. Unusual movements leading up to the selection of the birth site, for example, may be viewed as an indicator of shifting habitat requirements by moose as the priorities of gestation change to those of parturition and lactation. Similarly, when predation on the calf occurs, movement *per se* may play a role in predation, either as a response to the presence of the predator (Franzmann and Peterson 1978, Ballard *et al.* 1980), or in a manner that affects calf vulnerability, such as leaving scent trails (Bowyer *et al.* 1999).

Fidelity to a site for reproduction is not uncommon in nesting species (e.g., Greenwood and Harvey 1982, Beletsky and Orians 1991), but examples from Cervidae are few (e.g., white-tailed deer, *Odocoileus virginianus*; Nixon *et al.* 1992). Fidelity of moose to a birthing site between years has been suggested, but is not well established (Addison *et al.* 1990, Bowyer *et al.* 1999, Welch *et al.* 2000). If birth sites are chosen to avoid predation of calves, then previous reproductive success at a site might predispose a female to return to the vicinity of "safe" birth sites. When a calf is lost to predation, the birth site that year may be avoided, especially if the predation occurred nearby while the calf was young.

Our objectives were to characterize the daily movements of adult female moose in relation to birth and death of their calf or calves, and test several hypotheses about movements within and between years. We tested the hypotheses that: (H1) birthing site selection is an active process involving movements not typical of normal home range use; (H2) movements during the neonatal period increase risk to calves; and (H3) birth site selection is affected by previous reproductive success near that site. We could not directly determine the causes of calf mortality, but predation, mostly by brown bears (*Ursus arctos*), has accounted for > 80% of neonate mortality in this area (Ballard *et al.* 1981, Ballard *et al.* 1991). The temporal pattern of calf mortality and its magnitude, as well as the density of predators during this study was consistent with those earlier accounts (Testa 1998, Testa *et al.* 1998, Testa *et al.* 2000). Wolf and bear numbers have either increased or remained the same, while productivity was similar to that reported by Ballard *et al.* (1991) and winter snow depths were mild to moderate (Testa 1998). Continuing heavy predation on calves therefore was assumed.

STUDY AREA

Moose were studied in the Nelchina Study Area (NSA), an area of approximately 4,200 km^2 near the abandoned townsite of Nelchina (62°15'N, 147°15'W) in southcentral Alaska. Climate and vegetation in the region were described by Skoog (1968). The Chugach and Talkeetna mountain ranges insulate the area from coastal influences on precipitation and temperatures. Annual temperatures range from -50 to +32°C, and precipitation typically ranges from 22-42 cm, most of this falling as snow (Skoog 1968). The study area included subalpine heath and woody shrubs such as resin birch (*Betula glandulosa*), alder (*Alnus fruticosa*), and willow (primarily *Salix pulchra*, *S. alexensis*, *S. glauca*) in foothills of the Talkeetna Mountains in the west, progressing to a boreal forest of mixed birch (*Betula papyrifera*), aspen-poplar (*Populus tremuloides* and *P. balsamifera*), and spruce (*Picea glauca* and *P. mariana*) in hills and lowlands to roughly 800 m elevation. Bogs of sphagnum, sedges and low shrubs, with scattered *P. mariana* were extensive in lower areas, predominantly the western portion of the study area from 800 - 620 m elevation. Moose were at moderate density (0.6-0.8/km^2) and subject to high rates of predation, primarily by brown bears, on calves in early summer (Ballard *et al.* 1991, Testa *et al.* 2000).

METHODS

Adult female moose were captured in March, November and December 1994, and November 1995 and equipped with VHF radiocollars. Except for 13 moose that were captured by helicopter net-gun on 16-17 November 1994, all moose were darted from a helicopter with a mixture of carfentanil citrate and xylazine hydrochloride (Schmitt and Dalton 1987).

Daily radiotracking flights, weather permitting, were made of adult moose from mid-May to mid-June 1994-1997, to detect and monitor survival of new calves. Such flights continued at 1-3 day intervals from mid-June to the end of June, and every 3-4 days during July. Sighting probability of calves in the relatively open habitat of our study area was 0.97, so that death was assigned to the day on which a calf disappeared and did not thereafter reappear (Testa *et al.* 2000). Locations of each moose were determined with a Global Positioning System (GPS) receiver in the airplane as it passed directly over the moose. The precision of locations was estimated by obtaining similar data from 2 fixed positions in the study area. No corrections were made for selective availability of GPS satellites; expected precision of locations obtained from an airplane while radiotracking was roughly ± 120 m (Carrel *et al.* 1997). Daily movements were calculated as the distance from the previous day's location. Distance from birthing site also was calculated for each location. If a female's birthing site was known in successive years, the distance between those sites was calculated. No attempt was made to visit birthing sites on foot, or to subjectively categorize habitats of birthing sites.

Distances between successive daily locations for each radiocollared female were analyzed with respect to date of parturition (-9 to +45 days) and date of a calf's presumed death (disappearance). Due to the repeated measures for each moose, movements were analyzed using SAS PROC MIXED (Littel *et al.* 1996) for mixed, repeated measures linear models. The random effects of individual moose were modeled first, with periods (days) as fixed effects in models predicting either distance moved, or the natural log of distance moved per day. A variety of error structures (Unstructured, Variance Component, Compound Symmetry, 1st Order Time Series, Heterogeneous Compound Symmetry, Heterogeneous 1st Order Time Series) were used to model the data, and the best model was chosen by using the average of Akaike's and Schwarz's information criteria (Littel *et al.* 1996). This analysis was first applied to daily distances moved from 9 days prior to 1 day after the first observation of a female with a calf to address the hypothesis (H1) that movements immediately preceding births are unusual. We tested the hypothesis that daily movements may increase the risk of calf mortality by including age of calf, year, and fate of calf (survived, died > 48 hours after observation, or died in the next 24 hour interval) in the repeated measures model. Because the hypothesis being tested relates to predation, cases where the death of a calf was known not to involve predation (3 females) were excluded. Finally, we modeled distances between successive birth sites with respect to whether at least 1 of the female's offspring survived in the first summer.

RESULTS

Two hundred locations were obtained for 2 fixed sites in the study area. Mean deviation from the average position was 57 m (SD = 50 m) and 95% of the positions were < 136 m from the average position. A total of 171 birth sites of 12-58 female moose per year were found from 1994-1997. Median distance between successive birth sites of 9-41 female moose per year was 4.7 km (n = 97, range 0.03-34.0 km).

The median of daily movements from 8-2 days prior to parturition was just 0.9 km, but increased on the day prior to detection of a calf (i.e., in the interval from 48-24 hours prior to birth) to 2.2 km (Fig. 1). The best mixed model of movements prior to and just after parturition employed a 1st Order Time Series error structure for ln (distance), repeated measures blocking on moose (P = 0.0001), and fixed effects for day (F = 65.50; 10, 999 df; P = 0.0001) (Table 1). The greatest differences were seen between daily movements 9-2 days prior to the first sighting of the calf and

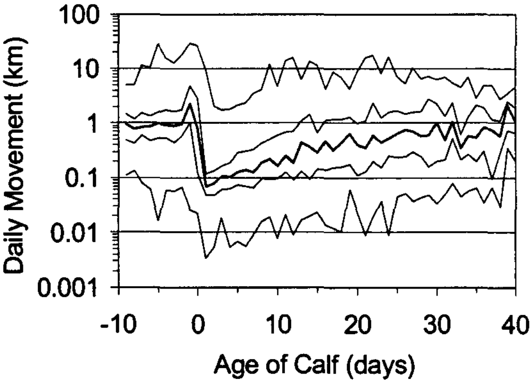

Fig. 1. Median (bold line) and quartiles of distances moved ($\log_{10}$ scale) from previous day by female moose in relation to their parturition date (day 0). Distances are shown only for moose that had not lost a calf.

Table 1. Estimates of daily movements (km) by female moose as a function of days prior to calving (detection of the calf = day 0) from a mixed repeated measures model (SAS PROC MIXED). The standard errors are asymmetric due to exponential transformation from logarithms used in the model.

Day	Distance (km)	SE	df	*t*	$P>\|t\|$
-9	0.864825	0.765-0.977	1240	-1.19	0.2355
-8	0.732052	0.647-0.829	1251	-2.51	0.0121
-7	0.878191	0.780-0.989	1249	-1.09	0.2740
-6	0.791732	0.706-0.888	1248	-2.04	0.0416
-5	0.879123	0.787-0.982	1249	-1.16	0.2452
-4	0.852207	0.768-0.946	1250	-1.54	0.1240
-3	0.844929	0.764-0.935	1250	-1.67	0.0958
-2	0.942616	0.854-1.041	1248	-0.60	0.5499
-1	2.142179	1.941-2.364	1249	7.74	0.0001
0	0.650476	0.591-0.716	1249	-4.50	0.0001
1	0.090839	0.083-0.100	1240	-25.92	0.0001

those movements on days -1 ($F = 76.28$; 1, 1254 df; $P = 0.0001$), 0 ($F = 6.28$; 1, 1269 df; $P = 0.0001$), and +1 ($F = 487.12$; 1, 1249 df; $P = 0.0001$). Distances from the eventual birth site were variable, but the median distance for all moose was close to 4 km (Fig. 2) until 2 days before parturition. The median distance to the birth site 2 days prior to parturition (Fig. 2) and the sum of the median daily movements in that 2-day interval (Fig. 1) were nearly the same, indicating that the final movement to the birth site was highly directional.

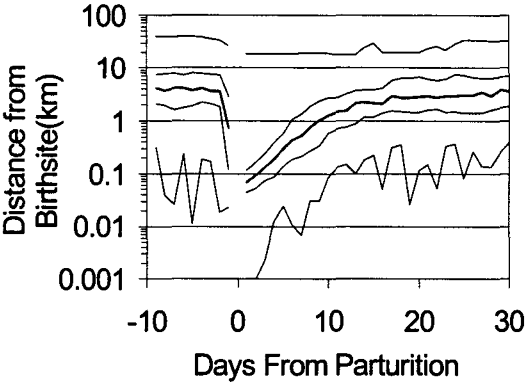

Fig. 2. Median (bold) and quartiles of distances that female moose were found from the birth site of their calf in relation to parturition date. Distances are shown only for moose that had not lost a calf.

Apparent movements after parturition were close to those expected from measurement errors for GPS coordinates (< 120 m), but increased steadily and were more variable than observed prior to parturition (Fig. 1). Median movements by females with calves did not exceed those prior to parturition until calves were nearly a month old (Fig. 1). The distance from the birth site, however, approached the pre-parturition distance asymptotically by about 17 days after parturition (Fig. 2), indicating that dispersion of parturient moose within the adult's home range was probably close to that before parturition by that time.

Daily movements by females eventually losing a calf (> 48 hrs prior to calf disappearance) exceeded those of females with calves of the same age that survived by 12% ($F = 3.89$; 1, 1825 df; $P = 0.049$). Daily movements just prior to the disappearance of the calf (24-48 hours prior to disappearance) were intermediate in value, though not significantly different from either of the other 2 categories.

The locations of birth sites in successive years were closer together (predicted value from PROC MIXED = 2.6 km) if at least 1 calf survived to the end of July the first year ($F = 5.58$; 1, 72 df; $P = 0.0208$) than if no calf survived (4.9 km). Only 2 of 97 successive pairs of birth sites were less than the expected error of GPS locations, 120 m apart, indicating low fidelity of moose to particular birth sites. Among females that lost their calf (or both calves if twins), there was no relationship between distance between successive birth sites and the age of calf when it died ($F = 0.87$; 31, 65 df; $P = 0.66$).

DISCUSSION

While not previously quantified to the extent here, movements by adult female moose to secluded areas for parturition often have been reported (Peterson 1955, Markgren 1969, Stringham 1974, Addison *et al.* 1993, Langley and Pletscher 1994). Sites favored by moose for parturition tended to feature good concealing vegetation (Stringham 1974, Leptich and Gilbert 1986, Langley and Pletscher 1994) or good visibility of the surrounding landscape, (Wilton and Garner 1991, Bowyer *et al.* 1999), although the presence of forage also has been cited as advantageous (Altmann 1963, Stringham 1974, Bowyer *et al.* 1999). Use by parturient moose of small islands, where encounters with predators are less likely or water may aid in defense from predation, also has been noted (Peterson 1955, Bailey and Bangs 1980, Stephens and Peterson 1984, Addison *et al.* 1993). Most arguments for selection of parturition sites by moose and many other ungulates hinge on tradeoffs between nutritional needs of the mother during lactation, and the need to reduce the risk of predation (Bergerud *et al.* 1984, Bergerud 1985, Berger 1991, Bergerud 1992, Schwede *et al.* 1993, Bowyer *et al.* 1998, Rachlow and Bowyer 1998, Bowyer *et al.* 1999). The highly directional movements we observed in moose immediately prior to parturition (Figs. 1 and 2) suggest a distinct shift in maternal priorities. Unless the nutritional needs of gestation are markedly different from those of lactation, the movement to a parturition site by moose in this study was most likely due to advantages of the new site in protecting calves from predation. With some exceptions, most movements of moose immediately after parturition were well within the expected precision of our GPS receivers, consistent with the sedentary behavior often reported for moose at that time (Stringham 1974, Ballard *et al.* 1980, Bubenik 1998, Hundertmark 1998).

In relation to the death of calves, the daily movements by radiocollared females whose calves died > 48 hours after the observation were 12% larger than those of females with surviving calves. In the period just prior to the calf's disappearance, however, the movements tended to be smaller than movements on previous days, but still slightly greater than those of females with surviving calves. Over 70% of mortality on moose calves was attributed to brown bears in our study area, but some losses to wolves (*Canis lupus*) and black bears (*Ursus americanus*) also occur (Ballard *et al.* 1981, Ballard *et al.* 1990). On the Kenai Peninsula, Alaska, black bears caused moose with calves to move significant distances over 1 - 2 days prior to killing the calf, whereas kills made by a wolf and by brown bears occurred within 1.6 km of the calf's capture site (Franzmann and Peterson 1978). Ballard *et al.* (1980) found that movements by moose with calves were positively correlated with the density of brown bears, and that these movements could sometimes be associated with the presence of a bear in the immediate vicinity. The larger movements > 48 hours prior to the calf's death may reflect either the active evasion of predators in an area as suggested by these authors, or a greater risk of detection created by movements *per se.* The weak trend toward smaller movements that we observed by moose just prior to losing their calf may represent an "end game" strategy of hiding from nearby predators.

Fidelity of moose to particular birth sites was low, and moose in this study dispersed their subsequent birthing site 88% further from the previous site in response to the loss of their calf or calves regardless of the age of the calf at death. This was similar to the results of Welch *et al.* (2000), but without the effects of logging that were the focus of that study. "Spacing out" of birthing sites is an oft-cited strategy of ungulates seeking to avoid predation (Edwards 1983, Bergerud *et al.* 1984, Berger 1991, Bergerud 1992). As an extension of this, Bowyer *et al.* (1999) suggested that moose might select their birth sites randomly in suitable habitat in order to minimize the predator's ability to use previous knowledge to aid in detection of calves. Our results indicate that such behavior also may have a temporal component in the individual's strategy of spacing out birth sites. The success (or failure) of a reproductive attempt by a moose may serve as an index to predator abundance that prompts increased spacing of the birth sites between seasons, regardless of the age and location of the calf when killed.

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