SUMMER MOVEMENTS OF FEMALE MOOSE AT HIGH DENSITY

By

Kalin Ann Kellie

RECOMMENDED: _____

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Advisory Committee Chair

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Chair, Department of Biology and Wildlife

APPROVED: _____
Dean, College of Natural Science and Mathematics

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Dean of the Graduate School

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Date

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A

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Kalin A. Kellie, B. S.

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ABSTRACT

I examined factors influencing the summer movements of adult female moose (*Alces alces gigas*) at high density in interior Alaska, USA from 1996 to 2003. First, I tested how the distance moved from 4 to 0 days pre-partum was related to migration, change in cover use, reproductive maturity and individual behavior. Second, I evaluated whether long movements prior to parturition were related to predation on previous neonates. Third, I measured the scale of spatial fidelity exhibited by individuals to areas used in early spring (13 to 15 May) and areas used for parturition. Lastly, I compared summer movements of adult females during periods of low and high population density.

Net movement of females 4 to 0 days prior to parturition was related to migration and a change in cover use. Movement was not related to reproductive experience, individual behavior, or prior predation of neonates. Pre-partum movements were longest for moose moving from open to dense cover. Individuals displayed higher fidelity to areas used in early spring (13 to 15 May) than to areas used for parturition. This predictable use of fine-scale areas may facilitate effective management of forage quality in early spring.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ACKNOWLEDGMENTS

GENERAL INTRODUCTION

Spring Movement and Spatial Fidelity

Chapter 1 examines movements of parturient moose in early spring. During this period, females are influenced by factors such as predation risk (Berger 1991, Rachlow and Bowyer 1998, Bowyer et al. 1999, Barten et al. 2001), interference from conspecifics (Stringham 1974, Miquelle et al. 1992, Wass et al. 2003), and increased energy requirements to support late gestation, parturition, and neonate survival (Schwartz et al. 1987, Reese and Robbins 1994, Barboza and Bowyer 2000). Past research studies on the movement patterns of female moose in spring have suggested reasons for movement prior to parturition (Addison et al. 1993; Bowyer et al. 1999; Lawler et al. 2005), but few studies have included rigorous tests to discriminate among causative factors (Testa et al. 2000, Wass et al. 2003). During the few days surrounding parturition, females transition from a solitary role (or care of a yearling) to the vulnerable role of birthing and caring for a small neonate. Determining if particular life-history and habitat characteristics are linked to movements just before parturition will help identify factors important to females during this time of transition.

This research examined pre-partum movement patterns, factors that may affect movement distance, and the spatial fidelity of parturient moose in an interior Alaska population. Previous studies have reported that some female moose make unusually long movements just prior to parturition (Bowyer et al. 1999, Testa et al. 2000). First, I determined if individuals in my population followed a similar pattern of movement. Second, I examined the influence of three factors on the distance moved prior to

parturition: (1) remnant migration, (2) reproductive experience, and (3) change in use of cover. I predicted that longer movements immediately prior to parturition would be related to long migrations coupled with early parturition events, increased movement of more experienced individuals, and a change in cover use. I also evaluated the effect of past predation of neonates on pre-partum movements and predicted that the females in my population, where predation on neonates was low (Keech et al. 2000), would exhibit a lower percent of long-distance movements ($\geq$ 5 km) prior to parturition than females in populations where predation on neonates was high (Bowyer et al. 1999, Testa et al. 2000). Finally, I measured the scale of fidelity to areas used pre-partum and for parturition and evaluated the biological importance of spatial fidelity as a maternal strategy when females transition from late gestation to a role of neonate protection and care.

Movements of Female Moose at High Versus Low Density

Chapter 2 measures differences in summer movements between periods of low and high density with corresponding high and low twinning rates (Gasaway et al. 1992; Young and Boertje 2005; W. C. Gasaway, Alaska Department of Fish and Game, unpublished data; R. D. Boertje, Alaska Department of Fish and Game, personal communication). High-density moose populations can be a valuable resource to humans for consumptive and non-consumptive uses. When density becomes too high, however, long-term habitat degradation, coupled with severe weather, can result in a rapid population decline (Van Ballenberghe and Ballard 1998). High density can be curbed and stabilized through the harvest of females, but only in areas where access is

economical (Mercer and Manuel 1974). For example, subsistence hunters usually avoid costly transportation, which reduces the ability of managers to meet harvest objectives in remote areas. In addition, attempts to increase overall harvest of high-density populations can result in local overharvest in areas that are easy to access (Gasaway et al. 1983). Therefore spatially-regulated harvest using a quota system is desirable (Mercer and Manuel 1974, Young and Boertje 2005). Understanding the characteristics of female movements at high density can aid managers in development of spatially regulated harvest strategies.

In this chapter, two radiotracking studies separated by 20 years provided a unique opportunity to compare summer movements of adult females within a single population during periods of low (1976-1983) and high (1996-2003) density (Gasaway et al. 1992; Young and Boertje 2005; W. C. Gasaway, Alaska Department of Fish and Game, unpublished data; R. D. Boertje, Alaska Department of Fish and Game, personal communication). Between the first and second period, density increased 4-fold and the twinning rate declined to 1/4 of the rate observed at low density, indicating lower nutrition at high density (Blood 1974, Gasaway et al. 1992).

I examined the hypothesis that there is an inverse relationship between movement and density within moose populations. I used two indices of movement, K-function analysis (Ripley 1976) and minimum convex polygons (MCP, Mohr 1947), to compare the dispersion and extent of moose movement between the two periods. I predicted that movements would be reduced in scale at high density and MCP estimates would be smaller at high versus low density. To my knowledge, this is the second study to

examine the relationship between movement and density within a moose population and the first study to examine this relationship during summer.

SPRING MOVEMENTS AND SPATIAL FIDELITY OF MATERNAL MOOSE[1]

KALIN A. KELLIE[2,3], Institute of Arctic Biology, 311 Irving 1, P.O. Box 757000,

      University of Alaska, Fairbanks, AK 99775-7000, USA

RODNEY D. BOERTJE, Alaska Department of Fish and Game, 1300 College Road,

      Fairbanks, AK 99701, USA

PATRICIA DOAK, Institute of Arctic Biology, 311 Irving 1, P.O. Box 757000,

      University of Alaska, Fairbanks, AK 99775-7000, USA

ABSTRACT

Long-distance movements are made by some female ungulates immediately pre-partum.
We examined factors influencing these movements in female moose (*Alces alces gigas*)
in interior Alaska, USA. W tested how the distance moved from 4 to 0 days pre-partum
was related to individual behavior, remnant migration (the temporal overlap of migration
and calving), reproductive maturity, and change in cover use. In addition, we evaluated
the hypothesis that movements prior to parturition were related to predation on a female's
previous neonates. Finally, we measured the scale of spatial fidelity exhibited by
individuals to areas used in early spring and areas used for parturition. Movements prior
to parturition were longer when they included remnant migration, and both resident and
migratory female moose moved the longer distances when transitioning from open to

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[3] E-mail: kalin_kellie@fishgame.state.ak.us

dense cover. Individuals displayed higher fidelity to areas used in early spring than to areas used for parturition. We suggest that females exhibit higher fidelity to open habitats pre-partum, because these areas predictably yield high-quality forage in early spring. This predictable use of fine-scale areas may facilitate effective management of forage quality in early spring.

INTRODUCTION

Spring movements of parturient moose may be influenced by factors such as predation risk (Berger 1991, Rachlow and Bowyer 1998, Bowyer et al. 1999, Barten et al. 2001), interference from conspecifics (Stringham 1974, Miquelle et al. 1992, Wass et al. 2003), and increased energy requirements to support late gestation, parturition, and survival of neonates (Schwartz et al. 1987, Reese and Robbins 1994, Barboza and Bowyer 2000). Some studies have measured movement patterns of female moose in spring and suggested reasons for movement (Addison et al. 1993, Bowyer et al. 1999, Lawler et al. 2005), but few have included rigorous tests to discriminate among possible causative factors (Testa et al. 2000, Wass et al. 2003). During the days surrounding parturition, females transition from a relatively invulnerable role of solitary foraging to support late gestation to a more vulnerable role of birthing and caring for a neonate. Determining if particular life-history and habitat characteristics are linked to movements just before parturition will help

identify factors important to females during this time of transition.

Female ungulates sometimes move long distances 1 to 2 days prior to parturition (Bowyer et al. 1999, Testa et al. 2000, Lawler et al. 2005). Some moose swim to islands before parturition (Stephens and Peterson 1984, Wilton and Garner 1991). Parturient caribou (*Rangifer tarandus*) and Dall's sheep (*Ovis dalli*) have been observed moving to higher elevations and latitudes (Bergerud et al. 1984, Bergerud and Page 1987, Jakimchuck et al. 1987, Berger 1991), and caribou sometimes disperse along shorelines (Bergerud 1985). Rather than attraction to high-quality forage, these movements appear to reflect avoidance of areas where the risk of predation on neonates is high (Berger 1991, Rachlow and Bowyer 1998, Bowyer et al. 1999, Barten et al. 2001) and perhaps avoidance of intrusive conspecifics during initial bonding of females and neonates (Stringham 1974, Miquelle et al. 1992, Wass et al. 2003).

Patterns of movement prior to parturition can differ among individuals (Bowyer et al. 1999) and may be influenced by several factors. First, where green up precedes calving, migration to summer range may occur before parturition (Van Ballenberghe 1977, Ballard et al. 1991, Fancy et al. 1989). The unusually long movements made by some females just prior to parturition may reflect temporal overlap between the end of migration and the beginning of the calving season. That is, some females with earlier parturition dates may still be migrating, or may have just completed migration, during the final days prior to parturition. Second, previous reproductive experience may influence movement prior to parturition if older females learn to isolate and seclude themselves for parturition. Wass et al. (2003) observed that experienced (multiparous) farmed red deer

(*Cervus elaphus*) were more likely to pace fence lines prior to parturition than first-time breeders (primiparous). Fawn-rearing skills (as measured by neonate predation) of white-tailed deer (*Odocoileus virginianus*) improved with experience (Ozoga et al. 1986). Younger females also had difficulty establishing exclusive areas for parturition in a captive herd (Ozoga and Verme 1982). Third, at low elevations pre-partum moose often use open areas of aquatic vegetation and grasses in early spring (Phillips et al. 1973, Mytton and Keith 1981, MacCracken et al. 1993) but use dense cover for birth sites (Stringham 1974, Cederlund 1987, Langley and Pletscher 1994, MacCracken et al. 1997). Thus, females in exposed habitat just prior to parturition are likely to move longer distances in search of secure habitat than those already in dense cover. Finally, Testa et al. (2000) noted a positive relationship between distance moved prior to parturition and past predation on neonates. These authors suggested that parturient females were moving to avoid birth sites where they had encountered predators in past years.

Spatial fidelity of females has been measured relative to birth sites (Bowyer et al. 1999, Bertram and Vivion 2002, Testa 2004) but has not been evaluated during late gestation. The energetic cost of gestation increases foraging priorities (Schwartz et al. 1987), and solitary females may demonstrate fine-scale fidelity to foraging areas. Immediately after parturition, risks of predation and conspecific interference are elevated because of the presence of a neonate, and females may demonstrate fine-scale fidelity to areas of past neonate survival (Testa et al. 2000). Comparison of spatial fidelity to areas used in early spring, before parturition, versus immediately after parturition may provide clues to when parturient females are most spatially flexible.

Fidelity to birth sites can be further evaluated by comparing the scale of fidelity between populations with different levels of predation. Fidelity to birth sites is low where predation on neonates is high (MacCracken et al. 1997, Bowyer et al. 1998, Bertram and Vivion 2002, Testa 2004). Nonetheless, if neonate survival promotes the re-use of birth sites, spatial fidelity may increase where predation on neonates is low (Switzer 1997, Testa et al. 2000, Welch et al. 2000).

Our research examined pre-partum movement patterns, factors that may affect the distance an individual moved 4 to 0 days prior to parturition, and the spatial fidelity of parturient moose in an interior Alaska population. First, we determined if female moose in our population followed the pattern of long pre-partum movements observed in other populations. Second, we examined the influence of 3 factors on the distance moved prior to parturition: (1) remnant migration, movement related to the temporal overlap of the end of migration and the beginning of calving, (2) reproductive experience, and (3) change in use of cover. We also evaluated the effect of previous predation of neonates on pre-partum movements by comparing our population, where predation on neonates was low, with 2 populations where predation on neonates was higher (Bowyer et al. 1999, Keech et al. 2000, Testa et al. 2000). We predicted that our study population in the central Tanana Flats, Alaska, USA, would exhibit a lower percent of long-distance movements (≥ 5 km) prior to parturition compared to populations where neonate predation was high. Finally, we measured the scale of fidelity to areas used in early spring (before parturition) and areas used for parturition, evaluating the biological

importance of spatial fidelity as a maternal strategy when females transitioned from late gestation to neonate protection and care.

STUDY AREA

The central Tanana Flats is a 4,326 km^2 low-elevation (125-300 m) mosaic of mixed forest and freshwater fens (Racine and Walters 1994) centered 50 km S of Fairbanks, Alaska, USA (Fig. 1.1). The area includes the 2,640 km^2 Fort Wainwright military reservation where GIS mapping of vegetation was available. Winters from 1995-1996 to 2002-2003 were consistently cold and typical of interior Alaska, and were followed by cool, brief summers (November-March: $\bar{x}$ = -17.5 C$^{\circ}$, *SE* = 0.9; May-August: $\bar{x}$ = 13.7 C$^{\circ}$, *SE* = 0.3; Fairbanks International Airport weather station; National Weather Service). The area has a semi-arid continental climate. During the study period (1996-2003), average snow depths in winter were below the level (>70 cm) that hinders moose activity (Kelsall and Prescott 1971, Coady 1974, Sweanor and Sandegren 1989), except during 12 days in January 2000 (81.28 cm, Fairbanks International Airport weather station, National Weather Service).

Early successional habitat preferred by moose (Peek 1998, Bowyer et al. 2003) is created through summer wild fires (Viereck 1973), seasonal flooding, ice scouring, and changes in river flow (Yarie et al. 1998). These disturbances create a mosaic of mature coniferous forest, deciduous forest, shrub habitats, and open fens containing large quantities of preferred forage for moose. Detailed descriptions of vegetation are available elsewhere (LeResche et al. 1974, Gasaway et al. 1983, Racine and Walters 1994).

Date of green-up was measured as the day leaf-out was noted in a specific stand of paper birch (*Betula papyrifera*) near Fairbanks, Alaska, USA, by T. Fathauer (National Weather Service, Fairbanks, Alaska). This date corresponded closely to leaf-out of willow (*Salix* spp.) and other species of deciduous shrubs in the study area (pers. observation, K. Kellie). Shallow ponds usually melted several weeks prior to green-up and were always completely thawed during the sampling period (pers. observation, K. Kellie). The timing of parturition was similar to that of other interior populations at higher elevations where parturition often occurs prior to green-up (Van Ballenberghe et al. 1989, Bowyer et al. 1999). However, because of the lower elevation of the Tanana Flats, green- up overlapped or preceded parturition in all 8 years on our study area (Keech et al. 2000; R. D. Boertje, Alaska Department of Fish and Game, unpublished data; Fig. 1.2).

Moose in the Tanana Flats were partially migratory. Migrants moved from the foothills of the Alaska Range and from the low hills north of the Tanana River to the Tanana Flats, where they inter-mixed with nonmigratory moose in early spring (Gasaway et al. 1983). Parturition occurred in the Tanana Flats, and migrants returned to higher elevations for winter. Thus, summer densities (approximately 2.3 to 7.0 moose/km^2) were 2 to 4 times higher than densities reported for early winter (Gasaway et al. 1983). This migration pattern differs from the more common pattern of moose migration in North America where resident and migratory segments share a winter range and separate in summer (Hundertmark 1998).

Reproductive variables (i.e., twinning rates, age of first reproduction, and weight

of 10-month-old moose) measured annually during the study indicated that the population in the Tanana Flats was nutritionally stressed (Keech et al. 2000, Young and Boertje 2005). This was further supported by a survey of moose browse conducted during winter 1999-2000 which documented heavy use of preferred plant species (Seaton 2002). Wolves (*Canis lupus*), black bears (*Ursus americanus*) and grizzly bears (*U. arctos*) are present in the Tanana Flats, but mortality of young is relatively low (45% during first year of life) compared to other populations in interior Alaska (Keech et al. 2000, Testa 2004, Bertram and Vivion 2002).

METHODS

Moose Capture

Moose used in this study were collared by personnel of the Alaska Department of Fish and Game for on-going investigations of mortality, reproduction, dispersal, and habitat use (Keech et al. 2000, Seaton 2002, Young and Boertje 2005). We used data from females first captured as neonates ($n = 6$), 10-month-old moose ($n = 81$), or adults ≥ 3 years old ($n = 61$). Details on the capture of moose, including dosages of drugs, are described elsewhere (Keech 1999, Keech et al. 2000). Newborns were re-fitted with radio collars at 10 or 22 months of age. During March 1998-2000, we fitted moose 10-months-old with expandable radio collars from Advanced Telemetry Systems (ATS, Isanti, Minnesota, USA). A tooth was extracted if moose were first captured as adults, and ages were estimated by Matsons Laboratories (Milltown, Montana, USA) by counting cementum annuli (Gasaway et al. 1978).

Sampling Design

We began monitoring parturition of collared females at 36 months-of-age, because younger moose were not reproductively active in our study area (Keech et al. 2000). Thus, "adult" refers to a moose ≥ 3 years old. Each spring from 1996 to 2003, radiotracking began on 11-13 May, after most moose had completed spring migration (Gasaway et al. 1983). Adult females were located every 2 days with small, fixed-wing aircraft and the presence of a neonate was visually assessed. Because we observed females every 2 days, and females remain at the birth site with the neonate for a minimum 3 days post-partum (Altmann 1958), and usually much longer (Addison et al. 1990; Bowyer et al. 1999), we assume that the location where a female was first seen with a neonate accurately reflected the birth site. Once a female was observed with a neonate, we discontinued the 2-day visual observations of the individual for that year. Each year, some females were not observed with a calf, thus we concluded each field season when no new neonates were observed in a 4-day period (between 1 June and 16 June). Henceforth we refer to an observation of an individual in a particular year as a "moose-spring" observation.

We observed 30 to 79 parturient females each spring (439 moose-springs from 1996 to 2003) which ended with the observation of a young at heel. Visibility was excellent for most of the sampling period, but was sometimes compromised because of leaf-out when calving extended > 3 weeks beyond green-up (Fig. 1.2). For our analysis, we needed to visually verify the absence of a neonate > 2 days prior to the first sighting of a female with a neonate. Thus, we eliminated moose-spring observations that did not

meet this criterion ($n = 26$). We assessed reproductive history of all parturient females (i.e. multiparous or primiparous) using our records of parturition observations. If reproductive history was unknown because a female was first collared as an adult, the individual was not included in the analysis until either we observed its second parturition event or it reached 6 years of age. Females estimated to be $\geq$ 6-years-old at time of capture in March were assumed to be multiparous because all known-age females were multiparous by 6 years of age ($n = 79$).

Two moose gave birth in the foothills of the Alaska Range during spring 2003, although they had migrated to the Tanana Flats for parturition in previous springs. Thus, distance between their successive-year birth sites was unusually long (>50 km). These were the only 2 instances in 213 moose-spring observations recorded for migratory moose where individuals gave birth before migration (i.e., in the foothills). We considered these observations to be unusual and removed them from all analyses.

Data Analyses

Movements Prior to Parturition

There were 286 moose-spring observations available for measuring the distance moved $\leq$ 2 days prior to parturition. Fewer observations were available for earlier periods (3 to 10 days prior to parturition), because some moose gave birth shortly after 15 May. Distance between locations was calculated with the extension "Distance/Azimuth Tools v1.4b" (Jenness Enterprises, Flagstaff, Arizona, USA) for ArcView v3.2 (Environmental Systems Research Institute, Redlands, California, USA). We measured the net distance traveled by an individual in 2 days, and categorized distances in up to 5, 2-day periods

($\leq$ 2, 3-4, 5-6, 7-8, and 9-10 days) leading up to the first observation with a neonate. We

used a mixed-model analysis (PROC MIXED, SAS Institute 2000) to examine

differences in movement distance among 2-day periods as the parturition date approached

(sensu, Testa et al. 2000). Period * individual was included as a REPEATED statement

to model within-year covariance among observations from the same individual. Year

was included as a RANDOM effect with individual as the SUBJECT to define covariance

related to the use of individual in multiple years. We used the autoregressive covariance

structure (AR1) for both the repeated measure and random effect, because the probability

of correlation between observations is greater for observations that occurred closer

together in time. We transformed distances using $X^{0.25}$ to meet the assumption of a

normal distribution.

Finally we categorized pre-partum movement to examine the consistency of

individual movement, compare movement between populations, and compare movement

between migratory and resident moose. We adopted the criterion set by Bowyer et al.

(1999) to categorize long versus short distances moved: long movements were distances

$\geq$ 5 km traveled during a 2-day period. We used the $\geq$ 5 km criterion to compare

movement of individuals prior to parturition among 2-day periods within each year and

among years. To discuss the influence of migration on pre-partum movement, we

categorized females as migrants if the distance from their winter capture site (a single

location) to the birth site (a different location each year) was $\geq$ 20 km.

Estimation of Cover Type

Because we were interested in the relationship between concealment cover and

movement prior to parturition, we assigned cover classes to locations recorded 4 days

prior to parturition and at the birth site. Locations were plotted in ArcView 3.2

(Environmental Systems Research Institute, Redlands, California, USA). We used a GIS

layer of vegetation recommended for use at the 1:50,000 scale. This layer was developed

by Alaska Biological Research, Inc. (ABR, Inc, Fairbanks, Alaska, USA) for the U.S.

Army on Fort Wainwright (Jorgenson et al. 1999). They delineated stands of continuous

vegetation and assigned vegetation types using Soil Conservation Service vegetation

maps (Alaska Department of Natural Resources, Fairbanks, Alaska, USA) corrected with

true-color aerial photographs taken in 1995 at the 1:24,000 scale. Accuracy of the

vegetation classification was verified on the ground at 240 sites by Jorganson et al

(1999). Vegetation types for polygons were based on the Level IV Alaska Vegetation

Classification (Viereck et al. 1992). Spring locations of our collared moose encompassed

24 different vegetation types.

　　　　To analyze the relationship between movements of moose prior to parturition and

change in cover use, we categorized vegetation types into 3 cover classes: (1) dense

cover, (2) moderate cover, and (3) open habitat, based on cover relative to the height of a

moose (approximately 1.5 to 2.8 m). Viereck et al. (1992) used tree canopy closure ($\geq$ 3

m from the ground) to describe cover for forest classes. They used shrub canopy cover

(0.2 to 3 m from the ground) to describe cover for shrub classes. Forest in our study area

consisted largely of spruce (*Picea* spp.), and the density of foliage increased below the

crown height. Thus, because canopy cover was not reported between 1.5 and 3 m for

forest classes, we assumed that forest classes with > 25% canopy cover $\geq$ 3 m from the

ground were dense cover at moose height, and canopy cover 10 - 25% $\geq$ 3 m from the ground were moderate cover moose height (i.e., 1.5 to 2.8 m, Viereck et al. 1992). We categorized shrub classes with > 75% canopy cover 1.3 to 3 m above the ground as dense cover, 25 -75% canopy cover 1.3 to 3 m above the ground as moderate cover, and < 25% canopy cover 1.3 to 3 m above the ground as open. All herbaceous classes had a canopy height < 1.5 m from the ground, and were categorized as open.

Thus, dense cover, where a moose was less likely to be detected when feeding or resting, consisted of mature forest or closed shrub communities with a canopy dominated by *Picea mariana*, *P. glauca*, *Larix laricina*, *Alnus crispa*, and ground cover dominated by *Vaccinium* spp., *Ledum* spp., *Sphagnum* spp., *Betula nana*, and *Eriophorum* spp. The moderate cover category, where a moose might be visible when feeding, included tall and medium shrub communities with a canopy dominated by *Picea mariana, P. glauca, Larix laricina, Betula papyrifera, Salix* spp., and *Alnus crispa*. Finally, the open habitats, where a moose would be most exposed because of low vegetation, were fens and low shrub communities dominated by *Salix* spp., *Carex* spp., *Eriophorum* spp., *Equisetum* spp., *Menyanthes trifoliate,* and young *Betula papyrifera* (Jorgenson et al. 1999). A similar classification for lowland areas was used by Berg and Phillips (1974).

Factors Affecting Movement Prior to Parturition

We employed a mixed-model ANCOVA (PROC MIXED, SAS Institute 2002) to examine how the distance moved immediately prior to parturition was affected by remnant migration, reproductive experience, and change in cover type. We used the distance moved 4 to 0 days prior to parturition as our response variable. Habitat data

were only available for the Fort Wainwright lands within our study area; thus, our model

of factors affecting movement was limited to the 199 moose-spring observations in that

area (Jorgenson et al. 1999; Fig. 1.1).

The influence of remnant migration, movement related to the temporal overlap of

the end of migration and the beginning of calving, was represented by a continuous

variable. For each parturition event, we divided net migration distance (distance between

capture location and birth site) by the timing relative to the beginning of parturition (i.e.,

earlier parturition events received lower values). Thus long-distance migrants giving

birth earlier in the season had larger values of remnant migration than those giving birth

late in the season. Additionally, long-distance migrants had larger values of remnant

migration than short-distance migrants and residents. We used a meristic, ranked

variable to examine the influence of reproductive experience: (1) inexperienced

(primiparous), (2) somewhat experienced (multiparous ≤ 6 years old), (3) moderately

experienced (7-9 years old), and (4) highly experienced (≥ 10 years old).

To address the hypothesis that movement prior to parturition was related to a

change in vegetative or concealment cover we used a categorical variable. There were 9

possible transitions of cover type (dense, moderate and open) when moving from cover

used 4 days prior to parturition (T_4) to cover used at the birth site (T_0). We included a

REPEATED statement for year with individual as the SUBJECT, specifying the

autoregressive covariance structure (AR1), to create a covariate for the use of individuals

in multiple years. We used a RANDOM statement to estimate the covariance for each

year separately and correct for possible differences in environmental conditions among

years. All distance measurements were transformed using $X^{0.25}$ to meet the assumption of a normal distribution. We used the CONTRAST statement within PROC MIXED to contrast the mean distance for each T_4-T_0 cover combination with the mean for the remaining 8 combinations. We verified that there was no change in the spatial availability of cover classes during the period of movement by comparing location distribution during 4 versus 0 days prior to parturition. We used the program BLOSSOM (USGS, Fort Collins, Colorado, USA) to perform a multi-response permutation procedure (MRPP) comparing the distribution of locations 4 versus 0 days prior to parturition (Cade and Richards 1999).

We evaluated the hypothesis that long movements 2 to 0 days prior to parturition are more frequent in populations experiencing high predation on neonates. We used the ≥ 5 km definition of "large" pre-partum movement for this discussion (Bowyer et al. 1999). We compared the percent of moose that moved ≥ 5 km pre-partum in our study population, where neonate predation was low (Keech et al. 2000), with the Denali National Park (Bowyer et al. 1999) and Nelchina Basin populations (raw data for Nelchina Basin provided by W. Testa, pers. comm.), where neonate predation was high (Ballard et al. 1991, Bowyer et al. 1999, Keech et al. 2000, Testa et al. 2000).

Spatial Fidelity

We examined spatial fidelity to areas used in early spring, before parturition, and to areas used for parturition. We defined fidelity for each individual as the distance between successive-year locations. Fidelity to areas used for parturition was defined as the distance between successive birth sites. Fidelity to areas used in early spring (before

parturition) was defined by the distance between successive-year locations recorded during 13-15 May. We chose these dates because sampling began at this time each year and locations were available for all individuals. We did not include individuals in springs when they gave birth before 16 May. Samples included observation of a female during 13-15 May and at the birth site in 2 successive years, yielding 48 moose and 99 samples for evaluation of spatial fidelity. We used PROC MIXED (SAS Institute 2000) to perform a pair-wise t-test comparing fidelity to areas used in early spring versus areas used for parturition. We included individual as a REPEATED statement, specifying the auto-regressive covariance structure (AR1), to model possible covariance from using the same individual in multiple years. We transformed distances ($X^{0.25}$) to meet assumptions of a normal distribution and equal variance.

We also report maximum spatial fidelity to illustrate the ability of females to return to a fine-scale area. Maximum spatial fidelity in spring was defined as the closest distance between an individual's locations in consecutive springs (13 May to parturition date). We calculated the distance between every year 1: year 2 pair of spring locations for each individual with the extension "Distance by ID" (Jenness Enterprises, Flagstaff, Arizona, USA) for ArcView v3.2 (Environmental Systems Research Institute, Redlands, California, USA). Measurements of areas used pre-partum and for parturition used a single location for each year, but the number of locations used to calculate maximum fidelity varied widely (4 to 24 locations per moose per spring). Therefore, we do not statistically compare maximum spatial fidelity with fidelity to areas used in early spring and areas used for parturition because of differences in sampling design.

RESULTS

Movement Prior to Parturition

The distance traveled by a female moose differed among the 5, 2-day periods leading to parturition ($F = 5.45$; 4, 576 df; $P < 0.001$; Table 1.1). Distance traveled ≤ 2 and 3-4 days prior to parturition were each longer than the mean distance traveled in all periods ($t = 2.45$, $P = 0.014$ and $t = 3.28$, $P = 0.001$, respectively), whereas distances traveled during 5-6, 7-8 and 9-10 days prior to parturition did not differ from the mean ($P > 0.50$). There was little correlation between distances moved by an individual in successive periods ($Z = 0.79$, $P = 0.431$). In 106 (37 %) of 286 moose-spring observations, females moved ≥ 5 km either ≤ 2 or 3-4 days prior to parturition. Where movement was recorded both ≤ 2 days and 3-4 days prior to parturition, females moved ≥ 5 km during both periods in only 13 (6 %) of the 217 moose-spring observations. These 13 movements were made by different individuals. In 33 observations, females moved long distances ≤ 2, but not 3-4 days prior to parturition, and in 28 observations females displayed the opposite pattern.

The distance moved between 4 and 0 days prior to parturition ranged from 0.1 to 21.9 km (median = 2.9 km, $\beta_0 = 1.191$, SE = 0.081). There was no difference in the distribution of locations 4 versus 0 days prior to parturition at the landscape scale ($P = 0.535$). Thus, our assumption that the availability of cover was similar between 4 and 0 days prior to parturition was supported. As expected, remnant migratory movements at the beginning of the calving season were related to longer movements prior to parturition ($n = 199$; 1, 174 df; $\beta_2 = 0.251$; SE = 0.112; $F = 5.05$; $P = 0.026$). Surprisingly, many

females with short-migrations and resident females also made long-distance movements prior to parturition. Twenty-three percent of the 89 females with short migrations (< 20 km) moved ≥ 5 km ≤ 2 days prior to parturition, while 33% of the 198 females with long migrations (≥ 20 km) moved ≥ 5 km ≤ 2 days prior to parturition.

The effect of changing cover type explains additional variation in the distance moved prior to parturition ($n = 199$; 8, 183 df; $F = 2.83$; $P = 0.003$; Table 1.2). Specifically, distances moved from open habitats to dense cover were much longer than the mean distance for all observations ($n = 31$, 187 df, $t = 3.48$, $P < 0.001$) and were also longer than the mean distance traveled between all other transitions of cover classes ($\beta_3 = 0.265$; $SE = 0.076$; Table 1.2). Four days prior to parturition, 41, 23 and 36 % of females were in open, moderate and dense cover, respectively. When observed at the birth site 4 days later, 24, 28, and 48 % of females were in stands categorized as open, moderate and dense cover, respectively. Forty-two percent of the time females remained in the same cover type between 4 and 0 days prior to parturition. Twenty percent of the time females moved to a vegetation type with decreased cover: 9 % to moderate cover and 11 % to open habitat. Finally, 38 % of the time females moved to a vegetation type with increased cover: 13 % to moderate cover and 25 % to dense cover (Table 1.2).

Individuals did not maintain a consistent pattern of movement from year to year. Ninety-two of 290 individuals observed for 1 year moved ≥ 5 km immediately prior to parturition. Only 19 of 87 moose observed for 2 consecutive years moved ≥ 5 km in both years, and only 2 of 52 moose observed in 3 consecutive years moved ≥ 5 km in all three years. Observations of an individual were not related among years in the model testing

differences in movement among the 2-day periods leading up to parturition ($Z = 0.77$, $P = 0.220$). Likewise, there was no relationship among observations of an individual in different years in the model of factors affecting movement prior to parturition ($Z = 0.50$, $P = 0.617$).

Spatial Fidelity

Spatial fidelity to areas used in early spring (13 to 15 May) was higher and less variable than fidelity to areas used for parturition (i.e. birth sites; $n = 99$; $t = 25.54$; 50.6 df; $P < 0.001$). Distances between early spring locations from successive years ranged from 0.1 to 19.9 km (median 2.0 km), whereas distances between successive birth sites in successive years ranged from 0.1 to 56.5 km (median 3.8 km). When all spring locations were considered for an individual (4 to 24 per individual), females were located within 0 to 5.1 km of their closest location from the previous spring (maximum fidelity median = 0.4 km). Birth sites were never the closest pair of successive-year locations.

DISCUSSION

Movement Prior to Parturition

Female moose in the Tanana Flats moved significantly longer distances ≤ 2 days and 3-4 days prior to parturition than in earlier periods (Table 1.1). In most instances, moose only moved long distances in 1 of the 2-day periods immediately prior to parturition. In the few instances where a female moved ≥ 5 km in both 2-day periods, it is likely that she was still moving to the birth site when observed, causing the distance to be split between the 2 different time periods (i.e., ≤ 2 days, 3-4 days).

Our finding of long movements ≤ 2 days prior to parturition is consistent with the behavior described for populations with higher levels of neonate predation (Ballard et al. 1981, Bowyer et al. 1999, Testa et al. 2000). Nevertheless, long movements 3-4 days prior to parturition were not detected in the Denali and Nelchina studies (Bowyer et al. 1999, Testa et al. 2000). We cannot quantitatively distinguish among 3 possible explanations for this disparity. First, some females in our population may have long delays between movement and parturition. We do not know of an adaptive advantage nor can we propose any advantage to females arriving at the birth site 2 days earlier in the Tanana Flats versus in other populations. Second, we know that on rare occasions we failed to detect a neonate until the second post-partum observation. Nevertheless, we believe it is unlikely that failure to detect neonates caused a substantial number of movements to be assigned to the wrong period. Neonates gain weight and mobility at a rapid pace (Altmann 1958, Stringham 1974, Keech et al. 2000), allowing us to distinguish between neonates < 2-days-old versus >2 days-old. Third, our sampling resolution may be responsible for this outcome. Some observations may have been recorded after movement to the birth site, but a few hours before parturition. When this occurred, movement to the birth site was categorized into the 3-4 day period, and most of the final 2-day period was spent at the birth site. Thus, the distance measured between those observations would have included little or no pre-partum movement.

This study linked movements prior to parturition to both remnant migratory movements and shifts in cover use. Our hypothesis that movement prior to parturition increased with reproductive experience was not supported, although a positive

relationship between these 2 factors has been reported for white-tailed deer (*Odocoileus virginianus*, Ozoga and Verme 1986) and elk (*Cervus* elaphus, Vore and Schmidt 2001). Perhaps it is more efficient for movement prior to parturition to evolve as an instinctive reaction to environmental cues that occur at all levels of experience rather than as a learned behavior that develops only after the loss of $\geq$ 1 neonate (Clutton-Brock and Guinness 1974).

Remnant migration clearly contributed to some long movements 4 to 0 days prior to parturition, especially during the first few days of the calving season. Nevertheless, a similar proportion (33 % versus 23 %) of both long-distance ($\geq$ 20 km) and short-distance migrants (< 20 km) moved long distances ($\geq$ 5 km) 2 days prior to parturition. Thus, migration alone does not explain long pre-partum movements. However, migration may have a larger effect on movement prior to parturition in populations experiencing greater temporal overlap between migration and calving (Fig. 1.2).

The mean distance moved 4 to 0 days pre-partum was longer for shifts from stands of open habitat during pre-calving to dense cover for parturition (Table 1.1). Further, although the availability of cover types was similar between 4 and 0 days prior to parturition, there was an increase in the use of dense cover between those periods (36 % to 48 %). The use of dense cover for calving has been well documented for moose (Peterson 1955, Markgren 1969, Langley and Pletscher 1994, Stringham 1974, Cederlund 1987), but in previous studies relatively little was known about habitat used in early spring before transitioning to the birth site. Stands of vegetation classified as dense cover contained fewer preferred forage species than moderate cover or open habitat (Viereck et

al. 1992; Jorgansen et al. 1999), and shifts from open to closed habitats may result in lower nutrition (Edwards 1983, but see Bowyer et al. 1999).

Our results support the hypothesis that movement prior to parturition reflects a tradeoff of priorities as the calving date approaches (Edwards 1983, Berger 1991, Testa et al. 2000). The advantage of using stands with increased cover may be related to isolation and reduced visibility rather than improved nutrition (Markgren 1969, Edwards 1983, Addison et al. 1990, Langley and Pletscher 1994, Leptich and Gilbert 1986; but see Bowyer et al. 1999). Movement from open to closed cover likely reduces visual detection of the mother-young pair. In early spring, bears (*Ursus* spp.) are often present in open, lowland habitats (Unsworth et al. 1989). Black bears (*Ursus americana*) rarely prey on adult moose (Ballard et al. 1990, Gasaway et al. 1992), but their predation on neonates is well documented for interior Alaska (Osborne et al. 1991, Ballard et al. 1990, Keech et al. 2000, Bertram and Vivion 2002). Females with neonates may avoid open areas to decrease encounters with these and other predators (Bleich 1999, Kunkel and Pletscher 2000, White and Berger 2001).

Females also may move from open to closed areas to avoid other moose. Moose density in spring is extremely high in the Tanana Flats (approximately 2.3 to 7.0 moose/km^2). Moose aggregate in open aquatic lowlands in early spring before leaf out (LeResche 1972, Phillips et al. 1973, Berg and Phillips 1974, Peek et al. 1974, MacCracken et al. 1997). Aggregations in prime foraging habitat might increase altercations with conspecifics and endanger neonates. This may motivate females to avoid these areas at parturition (Molvar and Bowyer 1994). When captive white-tailed

deer and elk were confined at high densities during parturition, neonate mortality

increased because of injury and interference from other pre-partum females (Ozoga et al.

1982, Wass et al. 2003). Even at low density, large groups of moose were observed

feeding on exposed, south-facing slopes in early spring, and larger group size was

correlated with increased aggressive behavior (Molvar and Bowyer 1994).

Our results do not support the hypothesis that movement prior to parturition is a

reaction to previous predation on neonates (Testa et al. 2000). Predation on neonates was

higher in Denali (ca. 80 % mortality by 16 June, Bowyer et al. 1999) and Nelchina (73 %

mortality by 31 July, Testa 2004) than in the Tanana Flats (ca. 20 % mortality by 31 July,

Keech et al. 2000). We expected the Tanana Flats population to exhibit a lower

percentage of long movements pre-partum, because fewer females had experienced

previous predation on a neonate. Surprisingly, the percent of moose moving ≥ 5 km just

prior to parturition was similar between the Tanana Flats (37 %, $n = 217$), Denali

National Park (20%, $n = 20$; Bowyer et al. 1999), and the Nelchina Basin (41 %, $n = 157$,

W. Testa, pers.comm). These results make it unlikely that pre-partum movement is a

result of direct avoidance of predators or avoidance of the sites where previous predation

on neonates occurred. Nonetheless, indirect avoidance of predators, such as a tendency

to avoid use of exposed habitats for parturition (Bleich 1999, White and Berger 2001),

was supported by our model of movement prior to parturition. Also, it is possible that

avoidance of conspecifics is driving pre-partum movement observed the central Tanana

Flats, whereas avoidance of predators results in a similar movement pattern observed in

Denali National Park and the Nelchina Basin. We were unable to evaluate that possibility

with these data.

Spatial Fidelity

Individuals did not display consistent patterns of movement 4 to 0 days prior to parturition in successive years. We suggest that movement of moose pre-partum is likely related to life-history characteristics or environmental conditions that vary between years, such as the length of gestation (Schwartz and Hundertmark 1993) or the perceived risks and benefits of surrounding vegetative cover for parturition (Edwards 1983, Addison et al. 1990, Berger 1991).

Individuals exhibited low fidelity to areas used for parturition compared to areas used in early spring. The coarse scale of spatial fidelity to areas for parturition was similar to fidelity measured in other interior Alaska populations with higher predation (MacCracken et al. 1997, Bowyer et al. 1999, Testa et al. 2000, Bertram and Vivion 2002). Thus, fine-scale spatial fidelity for parturition may not be advantageous at any level of predation. If predators can recall areas where neonates were previously detected, predictable use of areas for parturition may decrease neonate survival (MacCracken et al. 1997). Selecting random locations for a birth site may decrease encounters with predators (Bowyer et al. 1999). In addition, fine-scale fidelity to birth sites may not be advantageous if forage in areas used for parturition suffers lasting damage from heavy browsing and bark stripping post-partum (Miquelle and van Ballenburghe 1989, MacCracken et al. 1997, Bowyer et al. 1999).

Higher fidelity to pre-partum areas indicates that individuals are able to return to the same fine-scale area (i.e., within a median 0.4 km) in successive years. Apparently,

females are capable of higher fidelity than they exhibit toward areas used for parturition. Though not quantified, moose reportedly re-use areas at a fine scale during other times of the year, both within the lifetime of an individual (LeResche 1972, Berg 1971, Mytton and Keith 1981, Andersen 1991a) and within populations over time (Edwards and Ritcey 1956). Some studies have documented areas of aggregation and routes of migration used consistently over several years (Sandegren and Sweanor 1988, Mauer 1998) probably because of habitual behavior of individuals (Pulliainen 1974). In Norway, the presence of centuries-old moose traps along active migration corridors indicates that moose populations can maintain fidelity to areas through several generations, probably because young learn movement patterns from their mothers (Andersen 1991b).

Areas used in early spring (before parturition) may offer dependable high-quality forage during a time when energy demands are high (Gasaway and Coady 1974, Regelin et al. 1985, Schwartz et al. 1984) and consequences of undernutrition are severe (Hight 1966, Keech et al. 2000). Spring aggregation of moose has been linked to green-up and the acquisition of emergent forage (LeResche 1972, LeResche 1974, Sandegren et al. 1985, Hauge and Keith 1981), and green-up often overlaps with parturition at high latitudes. If chronology of green-up is spatially predictable in subsequent springs, it may be advantageous to re-use areas where green-up first occurs. For example, MacCracken et al. (1997) reported that each year moose aggregated in ponds, which thawed and began growing new aquatic vegetation about 1 month before new leaves appeared. Similarly, Molvar and Bowyer (1994) described use of open, south-facing slopes by moose in early May. These slopes were clear of snow while deep snow remained ($\leq$ 1.5 m) in forested

habitats.

Future studies examining the energetic tradeoff associated with shift in cover use should directly measure habitat selected pre- and post- parturition and record the duration of use. We were unable to directly address the quality and quantity of forage available, and relied upon coarse cover descriptions for analysis. Nonetheless, we believe that these preliminary results are informative and suggest that future data collection begin in early April to capture the entire sequence of habitat use in spring.

Conclusions

Biologists have long recognized that some female moose increase their movements prior to parturition, apparently to isolate themselves from conspecifics and elude potential predators. We examined movement patterns, habitat use and site fidelity of parturient females before and after they transitioned to a maternal role. We discarded reproductive experience as a factor influencing movement prior to parturition. We also suggest that movement prior to parturition is not the result of prior encounters with predators during calving but may still relate indirectly to the risk of predation. The first parturition events of the year may overlap with the end of migration for long-distance migrants. The connection between long movements prior to parturition and a transition from open to closed cover provides quantification for the hypothesis that females move prior to parturition to change habitat use.

MANAGEMENT IMPLICATIONS

By evaluating habitat use and spatial fidelity before and after parturition, we may be better prepared to enhance spring habitat. At the landscape level, areas used pre-

partum and for parturition can overlap (Fig. 1.1), yet at the stand level we find differences in use patterns pre- and post-partum. In spring, moose rebound from a negative energy balance by increasing intake rates and ingesting higher-quality forage (Schwartz and Renecker 1998). Habitat improvement or conservation efforts may effectively increase forage quality in stands used predictably in early spring, before parturition (Phillips et al. 1973, Mytton and Keith 1981, MacCracken et al. 1993, Rea and Gillingham 2001). Alternatively, improving forage quality in stands used for parturition may not be effective because areas used for parturition apparently are less related to nutritional priorities and more spatially flexible. Thus, attempts to improve nutrition in habitats used for parturition would provide unpredictable benefits while requiring large-scale manipulation and perhaps increased expense. For example, females may discontinue use of manipulated areas for parturition if other important characteristics, such as concealment from predators, shade from solar radiation, and isolation from conspecifics, are altered.

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TABLE 1.1. — Distance moved by parturient moose during 5 successive 2-day periods prior to parturition in the Tanana Flats, Alaska, USA from 1996 to 2003. Sample size references the number of moose-spring observations. Statistics were conducted on transformed means ($X^{0.25}$), while medians are presented here for descriptive purposes.

Days to parturition	n	Distance Moved Median (km)	Range (km)
≤ 2	286	5.002	0.056 – 37.224
3 – 4	217	3.065	0.021 – 32.576
5 – 6	213	2.277	0.010 – 22.982
7 – 8	169	2.250	0.024 – 25.246
9 – 10	123	1.946	0.062 – 21.226

TABLE 1.2. — Distances moved by parturient female moose in the Tanana Flats, Alaska, USA, from cover type used 4 days prior to parturition (T_4) to cover type used at the birth site (T_0). Degrees of freedom (df), F-statistics and P-values are reported from contrasts of the mean distance of each cover combination against the mean for the remaining 8 combinations. Cover categories are dense (D), moderate (M), and open (O). Statistics were conducted on transformed means ($X^{0.25}$) while medians are presented here for descriptive purposes.

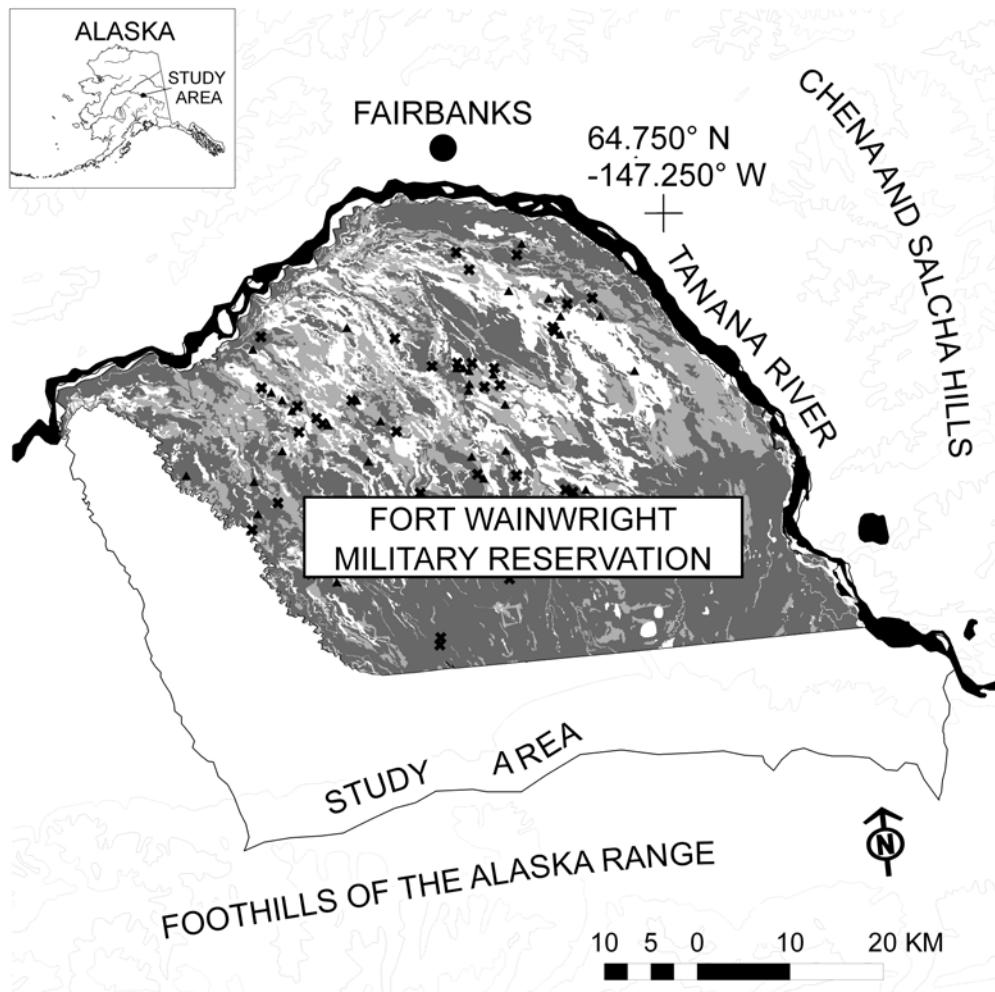| Cover Class | | | Median | | | |
T_4	T_0	n	(km)	df	F	P
D	D	45	2.64	182	1.57	0.211
D	M	17	2.24	186	1.30	0.256
D	O	10	3.78	188	0.91	0.342
M	D	20	2.97	179	1.11	0.294
M	M	14	4.59	185	2.99	0.085
M	O	12	2.94	184	0.00	0.952
O	D	31	6.25	188	12.23	< 0.001
O	M	25	2.42	176	0.48	0.489
O	O	25	2.20	185	5.43	0.021

FIGURE 1.1.— The Tanana Flats, Alaska, USA where female moose were radiotracked each spring from 1996 to 2003. Cover types are depicted on Fort Wainwright Military Reservation: white = open cover, light gray = moderate cover, dark gray = dense cover. We illustrate birth sites (✗) and locations 4 days prior to parturition (▲) from spring 2003 as an example.
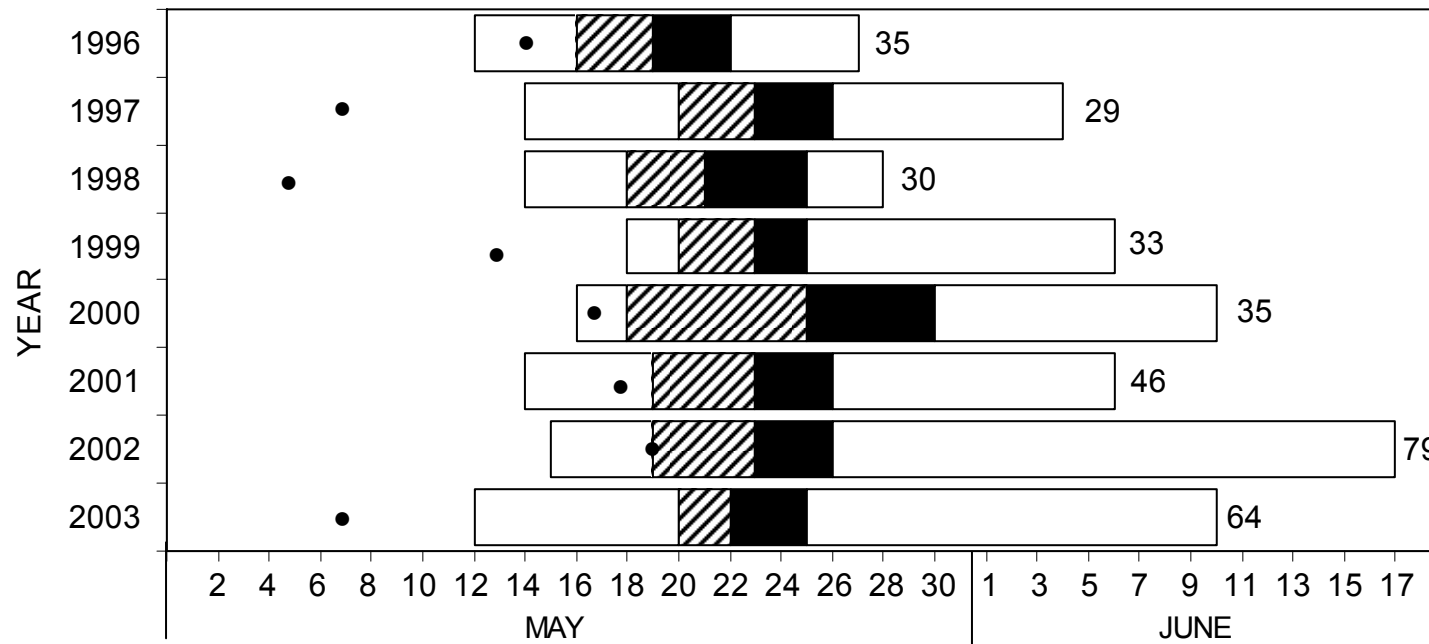
FIGURE 1.2.— Timing and synchrony of calving in the Tanana Flats. White bars indicate first and last 25% calving, hatched bars indicate 25 through 50% calving and black bars indicate 50 through 75% calving. Estimates of calving may be slightly biased late (1-2 days maximum) because we may have initially missed seeing a calf from the air. Green-up dates are denoted with a black circle (●). Sample size (no. of parturient females) is listed to the right of each bar.

Data summarized from Keech et al. 2000 and unpublished data from R. D. Boertje, Alaska Department of Fish and Game.

Restricted movements of Alaskan moose at high versus low population density[1]

Kalin A. Kellie[2], Institute of Arctic Biology, 311 Irving 1, P.O. Box 757000, University of Alaska, Fairbanks, AK 99775-7000, USA, kalin_kellie@fishgame.state.ak.us

Rodney D. Boertje, Alaska Department of Fish and Game, 1300 College Road, Fairbanks, AK 99701, USA, rod_boertje@fishgame.state.ak.us

William C. Gasaway[3], Alaska Department of Fish and Game, 1300 College Road, Fairbanks, AK 99701, USA

Stephen DuBois, Alaska Department of Fish and Game, P.O. Box 209, Delta Junction, AK 99737, USA, steve_dubois@fishgame.state.ak.us

Patricia Doak, Institute of Arctic Biology, 311 Irving 1, P.O. Box 757000, University of Alaska, Fairbanks, AK 99775-7000, USA, ffpd@uaf.edu

Abstract

Understanding characteristics of female movements at high versus low density can aid managers in developing movement-based harvest and management strategies. We radiotracked adult female moose in summer (*Alces alces*) during periods of low population density (n = 12; 1976-1983) and high population density (n = 12; 1996-2003)

in interior Alaska, USA. We used these data to compare the scale and pattern of movement at the 2 densities. A reduction in twinning rates between the 2 periods (39 % to 10 %) indicated nutrition of females declined as density increased. At high density, females restricted summer movements when intraspecific competition for resources was likely high. Ripley's K-function analysis indicated that summer locations were more clustered at high density ($P = 0.001$) and movement was reduced ($F = 9.32$; $P = 0.006$). To our knowledge, this is the first study to examine the relationship between summer movements and density within a moose population.

Introduction

High-density moose populations can be a valuable resource for consumptive and non-consumptive uses. When density becomes too high, however, long-term habitat degradation can result in a rapid population decline (Van Ballenberghe and Ballard 1998). Density and the coincident changes in habitat quality also may impact movement patterns. Direct intraspecific aggression and indirect competition for resources could lead to increased or decreased movement as females balance the energy expenditure of movement with the consequent changes in nutritional intake.

Populations with high and increasing density can be stabilized through harvest of females, and understanding the characteristics of female movements at high density can aid managers in development of spatially explicit strategies for harvest. Population

management through harvest is likely to be successful only in areas where access is economical (Mercer and Manuel 1974). For example, subsistence hunters usually avoid costly transportation to remote areas, which reduces the ability of managers to meet harvest objectives in remote areas. In addition, because movement may decline at high density, attempts to increase overall harvest at high densities can result in local overharvest in highly accessible areas (Gasaway et al. 1983). Therefore, a spatially regulated harvest with a quota system is desirable for stabilizing high-density populations (Mercer and Manuel 1974, Young and Boertje 2005).

Wildlife studies examining movement patterns at multiple densities within the same population are rare. Like many wild species, ungulate populations are difficult to experimentally manipulate, and the relationship between movement and density is usually evaluated with between-population comparisons (e.g., Oehler et al. 2003). Although these comparisons provide useful information, they cannot correct for underlying differences in resource distribution (VanHorne 1983), and they may not reflect the within-population response of movement to changes in intraspecific competition (Johnson 2002).

Results vary among ungulate studies which compared within-population movements at different densities. Two long-term studies of Roe deer (*Capreolus capreolus*) in Europe were compared to demonstrate that home range size decreased at high density (Kjellander et al. 2004). Marshall and Whittington (1969) reported that movements of white-tailed deer (*Odocoileus virginianus*) decreased at high density, whereas another white-tailed deer study reported the opposite response (Kilpatrick et al.

2001). Mechanisms that drive the relationship between density and movement are not known but likely stem from an increase in either direct intra-specific aggression or indirect intra-specific competition for resources. We are aware of only 1 moose study which examined within-population change in winter home range during 6 years of increasing density (Sweanor and Sandegren 1989). These authors reported a decrease in the home-range size of moose as population density increased, but this was not significant. Perhaps the study period needed to be longer to encompass the delayed effects of increasing density on intraspecific competition (Blood 1973, McCullough 1979).

In this paper, 2 radiotracking studies separated by 20 years provided a unique opportunity to compare summer movements of adult female moose within a single population during periods of low (1976-1983) and high density (1996-2003). Density was 4 times higher in the later period (Gasaway et al. 1992, Young and Boertje 2005) and twinning rates indicated that females during the second period were on a lower nutritional plane (i.e., 1/4 the twinning rate; Blood 1973; Gasaway et al. 1992; W. Gasaway, Alaska Department of Fish and Game, unpublished data; R. Boertje, Alaska Department of Fish and Game, pers.comm.). This study examines the hypothesis that an inverse relationship exists between movement and density within moose populations. We used 2 indices of movement, K-function analysis and minimum convex polygons (MCP), to compare the dispersion and extent of moose locations between the 2 periods (Mohr 1947, Ripley 1976). Based on the observations of Sweanor and Sandegren (1989), we predicted that

movements would be reduced in scale at high density, and that MCP estimates would be smaller at high versus low density.

Study Area

Located immediately south of Fairbanks, Alaska, USA, the central Tanana Flats are centered at 64 30'N, 147 30'W. The flats are a low-elevation (167 m) mosaic of poorly drained fens, shrub, and mixed forest. Vegetation and population indices for this moose population have been summarized for a 13,044 km^2 study area encompassing the central Tanana Flats (Gasaway et al. 1983, Boertje et al. 1996). The study area is within the taiga ecosystem of interior Alaska, USA. Summers were cool and short relative to moose populations at lower latitudes (May to Aug; 1976-1983: $\bar{x}$ = 14.0 Cº, SE = 0.294; 1996-2003: 1976-1983: $\bar{x}$ = 13.7 Cº, SE = 0.267; Fairbanks International Airport weather station, National Weather Service). Renewal of succession in this area is accomplished primarily through wild fire (Viereck 1973), and major fires occurred in 1980 and 2001 (Alaska Department of Natural Resources, unpublished data).

After a population crash in the late 1960s, moose in the central Tanana Flats were at low but increasing density (0.28 to 0.63 moose/ km^2 in early winter) during the first sampling period (1976-1983). Population density increased rapidly during 1978-1985 and was high (1.15-1.76 moose/ km^2 in early winter) during the second period (1996-2003) and increasing at a slow rate (Young and Boertje 2005, R. D. Boertje, Alaska Department of Fish and Game, personal communication). Twinning rates (cows with twins/cows with neonates) of radiocollared cows (>2-years-old, ca. 39%) during the first period (1976-1983) indicated a high level of nutrition (Gasaway et al. 1992; W. C.

Gasaway, Alaska Department of Fish and Game, unpublished data). Twinning rates of radiocollared cows (>2-years-old, ca. 10 %) during the second period (1996-2003) were 1/4 as high as those recorded during the first period and typical of a low plane of nutrition (Gasaway et al. 1992, R. D. Boertje, Alaska Department of Fish and Game, unpublished data). A recent survey of winter browse conditions also indicated that removal of preferred browse species was high (Seaton 2002).

Summer densities were typically 2 to 4 times higher than densities reported for early winter (ca. 0.56 – 2.52 moose/ km^2 in period 1; ca. 2.3 – 7.04 moose/km^2 in period 2; Gasaway et al. 1992; R. D. Boertje, Alaska Department of Fish and Game, unpublished data). In early spring, migrants moved to the Tanana Flats from higher elevations to the north and south (Gasaway et al. 1983). These migrants returned to higher elevations from mid-summer to late autumn where they remained until early spring. Resident moose remained in the Tanana Flats throughout the year (Gasaway et al. 1983).

Methods

Data Collection

Moose were radio collared during 1976–1983 and 1996–2003, primarily to study productivity, survival, and dispersal (Gasaway et al. 1980, 1983, 1985, 1992; Keech et al. 1999, 2000; Seaton 2002, Young and Boertje 2005). All individuals used in this paper were adult females ($\bar{x}$ = 6.3 years old, *SE* = 0.5). We primarily used PA-18 Piper Super Cub aircraft to radiotrack moose. Moose were located as frequently as 1 location/day, and sometimes as infrequently as 1 location/summer. Individuals were radiotracked from

2 to 6 consecutive years. Moose locations obtained during the low-density period were recorded on fine-scale 1:63,360 United States Geological Survey topographic maps by experienced observers and later digitized using ArcView 3.2 (Environmental Systems Research Institute, Redlands, California, USA). Locations obtained during the high-density period were recorded using a Global Positioning System. Some inestimable error is associated with both methods of recording locations, and was higher when visual confirmation could not be obtained. Mapping locations on paper during the first study probably did not substantially increase location error because locations were mapped using fine-scale maps by experienced observers who were familiar with the study area.

Statistical Analysis

All individuals included in this study were adult female moose that resided in the central Tanana Flats throughout the year. Uniform sampling of moose locations was difficult because timing and frequency of data collection differed among years and between study periods. To compare movement among individuals, we standardized sampling by choosing 12, 5-day intervals (2 to 10 days apart) where summer locations of most moose were recorded at least once (Harris et al. 1990, Kenward 2001). Our analyses were limited to the summer, defined as 15 May- 31 August. Because data were collected infrequently, we maximized the number of moose available for analysis by pooling across years. This assumed that movement patterns were consistent among years, which is supported by research demonstrating that adult female moose typically exhibit high spatial fidelity, even when nutrition is poor (Albright and Keith 1987; Andersen 1991a, 1991b; Histøl and Hjeljord 1993, Kellie et al. in prep.). We had 11 to

12 locations per individual for movement analysis using both K-function and MCP

methods ($n = 12$ during high and low density periods).

We used Ripley's K-function analysis (Ripley 1976), modified for replicated

sampling (Diggle et al. 1991, Diggle 2003), to examine differences in dispersion of

moose locations. K-function analysis is useful for evaluating dispersion because it

compares the dispersion of locations over a range of distances (Cressie 1993, Diggle et al.

1991). We used MAPTOOLS, version 0.4-8 to import point shapefiles, and then centered

point patterns for all individuals on the coordinates: 0,0.

We used SPLANCS (Rowlingson and Diggle 1993), within the R-Project

statistical package (version 2.0, R Development Core Team, 2004) to calculate K-

functions. Within each individual's location pattern, the point density was calculated at

multiple spatial scales. This range of point density estimates was achieved by (1)

counting the number of neighboring locations that occurred within a circle of radius h

centered on each location (Fig. 2.1), (2) averaging among all locations for that h, and (3)

repeating the process in circles where h was expanded in 30-m increments until reaching

the maximum radius of 4.5 km. As suggested by Cressie (1993), we chose a maximum

analysis radius that was approximately 1/3 the extent of most point distributions. Thus a

1 x 150 matrix (K_{ij}), or K-function, of average location densities for distance h was

calculated for each individual moose (j) within each period (i; Fig. 2.1).

Locations along the periphery of point distributions may have fewer neighbors

than those near the center. Thus, an outer extent must be specified to correct for that bias

so that areas of analysis can be weighted by the percent of these areas that extend beyond

the boundary (Ripley 1976, Rowlingson and Diggle 1993). For this edge correction, we used a bounding box that encompassed all location patterns.

A mean K-function, weighted by the location contribution of each K_{ij} (11 or 12 locations/ individual), was determined for each period (K_i) and a similarly weighted mean for all K_{ij} across the 2 periods (K). The difference between dispersion of moose locations between periods (D) was determined by summing the integrated difference between each K_i and K (Fig. 2.2). We used bootstrap methods to evaluate the probability of D resulting from random processes. We randomly sorted all K_{ij}s into 2 groups, obtained group K-functions and integrated the difference between the two groups (D^*). This process was repeated 999 times, and the rank of D in the distribution of 999 D^* iterations was used to obtain a P-value.

We used the MCP method as an index of the minimum movement demonstrated by individuals (Mohr 1947) to compare 2-dimentional movement patterns between periods. Because sample sizes were small, we use MCP estimates solely as an index of moose movement rather than an estimate of home range size (sensu Lowry et al. 2001, McCorquodale 2003). The MCP method was chosen because it provides more consistent estimates of area than other common indices of area when sample sizes are low (Harris et al. 1990, Belant and Follmann 2002, Girard et al. 2002). Thus, we assume that our MCP estimates represent a similar proportion of the total area used by different individuals. Kenward (2001) suggested that the number of locations needed to estimate actual home range increases with the size of the home range. Thus, assuming that our MCPs represent a constant percentage of individual movement might tend to underestimate larger

movements relative to shorter movements. This type of bias, however, is likely to reduce the power of our test, rather than cause a directional bias in comparisons. Nevertheless, we included the number of years over which a female was sampled as a covariate to correct for possible effects of across-year sampling of locations on minimum convex polygons (MCPs). We tested for differences between the 2 periods using ANCOVA (PROC GLM, SAS Institute, Inc. 2000) with a log transformation of MCP size to meet assumptions of normality and equal variance.

Results

Location density (K_j) was lower at all spatial scales (0 to 4.5 km) for females sampled during low population density (1976-1983) versus high density (1996-2003; Fig. 2.2). That is, summer locations for individuals were less clustered during the low-density period (D = 312.22, P = 0.001, Fig. 2.2). We recognize that this D statistic does not include within-individual variation, and the actual P value may be slightly higher.

The relative area of female movements, as measured by MCP, was significantly larger during the earlier period (n = 12, 25% = 35.9 km^2, median = 48.5 km^2, 75% = 116.6 km^2) than during the later period (n =12, 25% = 9.1, km^2, median = 16.1 km^2, 75% = 30.2 km^2, F = 9.32, df =1, P = 0.006; Fig. 2.3). We did not detect an effect of the number of years of radiotracking on MCP size (t = 0.02, P = 0.892) in the model relating population density to the extent of movement. This reinforced the hypothesis that females are spatially conservative in their use of summer range through time.

Discussion

Our results support our working hypothesis that an inverse relationship existed between density and movement (Sweanor and Sandegren 1989, Hundertmark 1998). K-function analysis of locations indicated more clustered distribution of locations during the second, high density period; thus, female movements were apparently more restricted at high population density (Fig. 2.2). When density increased 3-fold, and twinning rates declined (1/4 as high in period 2 versus period 1; Gasaway et al. 1983, Boertje et al. 1996), MCP areas contracted to 1/3 of the size measured at low density (Fig. 2.3). These results suggest that movements of female moose are restricted at higher densities and presumably increased competition.

Our assumption of conservative movement among years was supported by the negligible effect of years sampled on MCP size. These results concur with previous authors (Albright and Keith 1987; Andersen 1991a, 1991b; Histøl and Hjeljord 1993), who observed that female moose are highly philopatric to their range over time. Thus it is unlikely that our results were confounded by pooling across years for individual moose.

As is common with large, wide-ranging animals, we had to rely on observational results rather than performing controlled manipulations of density. In any such study, observed patterns may be due to other uncontrolled factors. In specific, differences in movement between the 2 periods may have been related to factors such as change in predation, weather or habitat. Nevertheless, the pattern we report agrees with other

studies of movement for free-ranging moose (Cederlund et al. 1989, Sweanor and Sandegren 1989, Sæther and Andersen 1990).

Restricted movements of female moose at high density may be a strategy to conserve energy. Between-population comparisons of daily activity in winter indicate that individuals move less when availability of forage declines (Cederlund et al. 1989, Sæther and Andersen 1990). Over 5-day periods in winter, moose also moved shorter distances in a low-nutrition population when compared to a high-nutrition population (Sæther and Andersen 1990).

In moose, increasing density eventually results in intense intraspecific competition for resources, reduced body condition, and reduced productivity (Blood 1973, McCullough 1979, Gasaway et al. 1992, Boer 1992). How these physiological changes are connected to restricted movement are less well studied. We did not directly test the effects of intraspecific competition on movement, but at high density, when nutrition was lower (i.e. lower twinning rates), locations were more clustered (Fig. 2.2).

We suggest that when population density approaches carrying capacity, opportunities for selective feeding may decline. Movement patterns may contract because of intraspecific competition for forage and consequent damage to plant growth (Bryant et al. 1983) is elevated throughout the landscape. Thus the energetic cost of expanded movement would be greater than the negligible benefit of increasing the area used for foraging. Moose density in the central Tanana Flats is highest in summer because moose migrate into the area from the surrounding hills (Gasaway et al. 1983). Thus, density was extremely high during the second period. If intraspecific competition

is high, preferred browse species may be heavily used even during summer, resulting in low quality and less preferred re-growth of forage following defoliation (Miquelle 1983). Studies describing detailed movements at several different densities are needed to confirm the inverse relationship between intraspecific competition and movement (Hundertmark 1998, Bowyer et al. 2003).

When individuals exhibit restricted movement, management may be most successful if localized harvest strategies are implemented. Porter et al. (2004) noted that localized harvest strategies are appropriate when animal movement meets 3 criteria: 1) high spatial fidelity, 2) low natal dispersal, and 3) a limited scale of movement. Analysis of female movements in white-tailed deer populations indicated a spatial separation between matrilineal groups (Tierson et al. 1985, Mathews and Porter 1993, Aycrigg and Porter 1997). Females within the groups associated during all seasons, even if individuals migrated between seasonal ranges (Mathews and Porter 1993). A localized harvest strategy based on matrilineal grouping led to the development of a new, successful technique for management of white-tailed deer (McNulty et al. 1997, Henderson et al. 2000, Oyer and Porter 2004).

Two of the suggested criteria for implementing localized harvest have been measured for female moose in several populations. First, fidelity of female moose to their range is apparently high, both in winter and summer (LeResche 1972, Berg 1971, Albright and Keith 1987, Histøl and Hjeljord 1993, Mytton and Keith 1981, Kellie et al. in prep.). This high spatial fidelity is consistent even when their range is severely degraded from overbrowsing and nutrition is compromised (Sweanor and Sandegren

1989; Andersen 1991a, 1991b; Kellie et al. in prep.). Second, the dispersal of young

female moose appears to be low at all levels of density and nutrition (Gasaway et al.1985,

Cederlund et al. 1987, Sweanor and Sandegren 1989, Cederlund and Sand 1992,

McLaren et al. 2000, Hjeljord 2001). We addressed the third parameter of movement:

the scale of female movements. Our data indicated that female moose restrict their

movement at high density. Thus, female moose may be suitable for localized

management when density is high. Matrilineal groups described for white-tailed deer

have not been studied in moose, but the similarity of female movement patterns between

these cervidae indicates the possibility of matrilineal spatial organization in moose.

Density is high or low only in relation to the carrying capacity of the habitat.

Application of movement parameters described here should be based on similarity of

nutritional indices rather than comparison of density thresholds. For example, the

population density at which movement patterns contract will likely depend on the

productivity of the habitat.

Management Implications

To our knowledge, this is the second study to examine the relationship between

movement and density within a moose population, and the first study to examine this

relationship during summer. Although more study is needed, the restricted movement

demonstrated by female moose at high density may allow managers to fine-tune harvest

strategies, habitat manipulations, and monitoring techniques. Porter et al. (2004)

developed localized management of female white-tailed deer for urban and suburban

areas, but the same methodology could be applied to populations in more remote areas

where access is limited. Focusing harvest objectives on moose adjacent to access routes could allow prioritization of agency funds and personnel (i.e., radiotracking studies, habitat manipulation, surveys). Priority could be given to portions of the population where harvest can be used effectively to control density. Finally, early-winter census data could be directly linked with the harvested portion of the population, even if the areas are spatially distinct because of migration.

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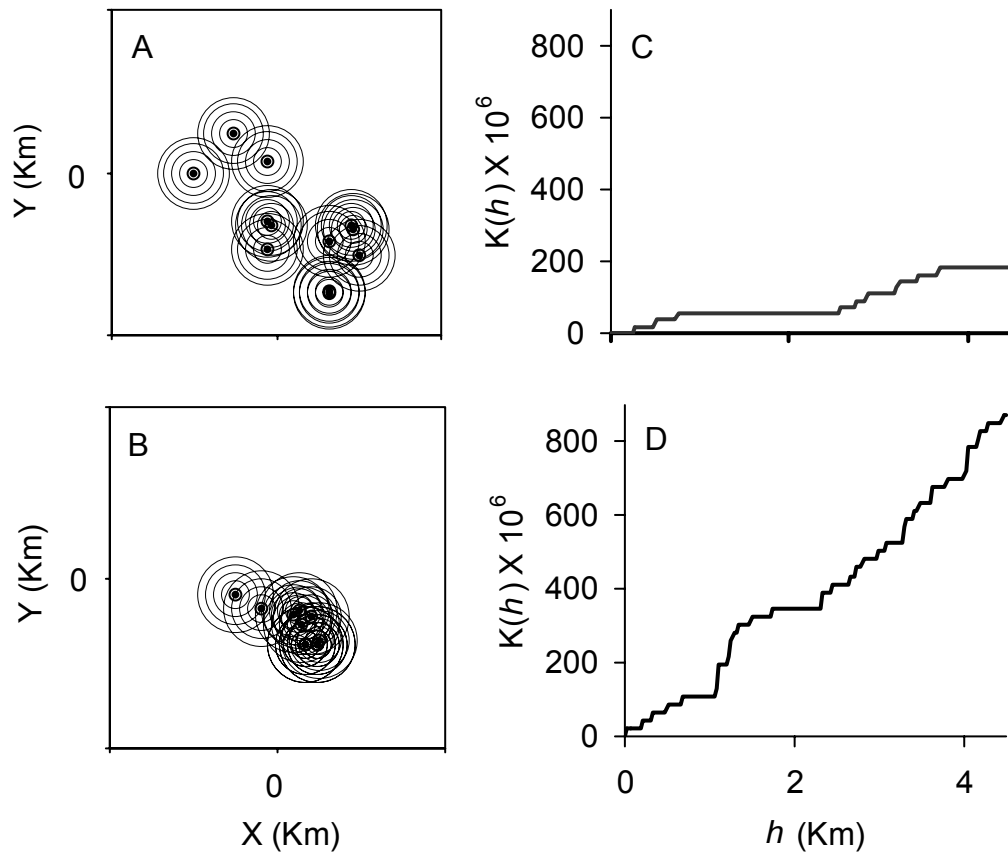
FIGURE 2.1.— Two examples of location patterns centered on (0,0) for individual adult female moose at low (A) and high (B) population density in the central Tanana Flats, Alaska, USA. Boxes around location patterns represent the boundary box used for edge correction in the analysis. Circles around locations represent areas of increasing radius (*h*) used to estimate location densities. These circles of increasing area were calculated for each location and averaged among all locations at each radius *h*, resulting in the K-functions illustrated for low (C) and high (D) population density.
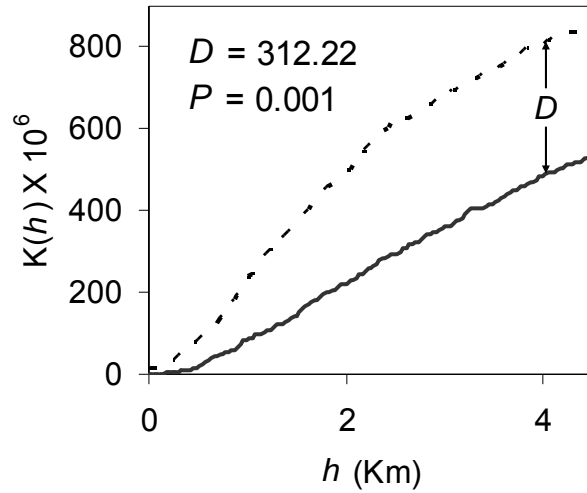
FIGURE 2.2.— Weighted mean K-functions, $K_j(h)$, at a range of distances (h) for locations obtained from female moose in the Central Tanana Flats, Alaska during summer, when population density was low (1976-1983; solid), and when population density was high (1996-2003; dotted). D is the area between the two K-functions. Higher values of K(h) indicate greater clumping at that distance (h).
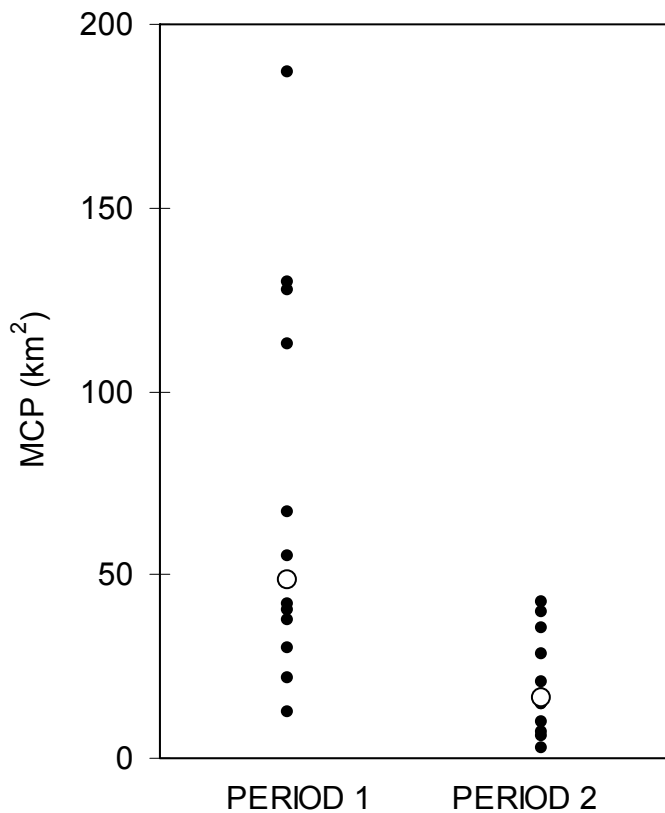
FIGURE 2.3.— Distribution of summer MCP calculations for female moose in the central Tanana Flats portion of Game Management Unit 20A, interior Alaska. MCPs were estimated during a period of low density from 1976-1983 (PERIOD 1), and a period of high density from 1996-2003 (PERIOD 2). Median values are large open circles.

GENERAL CONCLUSIONS

This study demonstrated that moose in the Tanana flats engaged in longer-than-normal movements just prior to parturition. These movements were linked to both remnant migratory movements and shifts in cover use. Remnant migration clearly contributed to some of the long pre-partum movements. The influence of migration on earlier parturition events explained the long distances measured ≤ 2 and 3-4 days prior to parturition during the first days of calving. Nevertheless, a similar proportion (33 % versus 23 %) of both long-distance (≥ 20 km) and short-distance migrants (< 20 km) moved long distances (≥ 5 km) prior to parturition. Thus, migration alone does not explain long pre-partum movements. However, migration may have a larger effect on movement prior to parturition in populations experiencing greater temporal overlap between migration and calving.

The mean distance moved pre-partum was longer for shifts from stands of open habitat during pre-calving to dense cover for parturition (Table 1.1). Further, the availability of cover types was similar between 4 and 0 days prior to parturition, yet there was an increase in the use of dense cover between those periods (36 % to 48 %). The use of dense cover for calving has been well documented for moose (Peterson 1955, Markgren 1969, Stringham 1974, Cederlund 1987, Langley and Pletscher 1994), but in previous studies relatively little was known about habitat used before arrival at the birth site. Stands of vegetation classified as dense cover contained fewer preferred forage species than moderate cover or open habitat (Viereck et al. 1992; Jorgansen et al. 1999),

and shifts from open to closed habitats may result in lower nutrition (Edwards 1983, but see Bowyer et al. 1999).

Our hypothesis that movement prior to parturition increased with reproductive experience was not supported, although a positive relationship between age and distance moved has been reported for white-tailed deer (*Odocoileus virginianus*, Ozoga and Verme 1986) and elk (*Cervus* elaphus, Vore and Schmidt 2001). Perhaps it is more efficient for movement prior to parturition to evolve as an instinctive reaction to environmental cues that occur at all levels of experience rather than as a learned behavior that develops only after the loss of ≥ 1 neonate (Clutton-Brock and Guinness 1974).

Individuals exhibited low fidelity to areas used for parturition compared to areas used pre-partum. The coarse scale of spatial fidelity to areas for parturition was similar to fidelity measured in other interior Alaska populations with higher predation (MacCracken et al. 1997, Bowyer et al. 1999, Testa et al. 2000, Bertram and Vivion 2002). Thus, fine-scale spatial fidelity at parturition may be disadvantageous at any level of predation. If predators can recall areas where neonates were previously detected, predictable use of areas for parturition may decrease neonate survival (MacCracken et al. 1997). Selecting unpredictable locations for a birth site may decrease encounters with predators (Bowyer et al. 1999). In addition, forage in areas used for parturition could suffer lasting damage from heavy browsing and bark stripping post-partum (Miquelle and van Ballenburghe 1989, MacCracken et al. 1997, Bowyer et al. 1999), which may reduce the subsequent benefits of that area.

Biologists have long recognized that some female moose increase their

movements prior to parturition, apparently to isolate themselves from conspecifics and elude potential predators. We examined movement patterns, habitat use and site fidelity of parturient females before and after they transitioned to a maternal role. We discarded reproductive experience as a factor influencing movement prior to parturition. We also suggest that movement prior to parturition is not the result of prior encounters with predators during calving but may still relate indirectly to the risk of predation. The first parturition events of the year may overlap with the end of migration for long-distance migrants. The connection between long movements prior to parturition and a transition from open to closed cover provides quantification for the hypothesis that females move prior to parturition to change habitat use.

Our results support the hypothesis that an inverse relationship exists between density and movement (Sweanor and Sandegren 1989, Hundertmark 1998). K-function analysis of locations indicated more clustered distribution of locations during the second, high density period; thus, female movements were apparently more restricted at high population density (Fig. 2.2). When density increased 3-fold, and twinning rates declined (1/4 as high in period 2 versus period 1; Gasaway et al. 1983, Boertje et al. 1996), MCPs contracted to 1/3 of the size measured at low density (Fig. 2.3). These results suggest that movements of female moose are restricted with increasing density and competition.

Our assumption of consistent use of summer range among years was supported by the negligible effect of years sampled on MCP size. These results concur with previous studies (Albright and Keith 1987; Andersen 1991a, 1991b; Histøl and Hjeljord 1993),

which also demonstrated that female moose are highly philopatric to their range over time. Thus it is unlikely that our results were confounded by pooling across years.

We suggest that when population density approaches carrying capacity, opportunities for selective feeding may decline. Movement patterns may contract because intraspecific competition for forage is similar across the landscape. Likewise, the damage to plant quality and growth resulting from increased competition may be widespread (Bryant et al. 1983). Thus, the energetic cost of expanded movement may outweigh the benefit of increasing the area used for foraging. Moose density in the central Tanana Flats is highest in summer because moose migrate into the area from the surrounding hills (Gasaway et al. 1983). Thus, density was extremely high during the second period. If intraspecific competition is high, preferred browse species may be heavily used even during summer, resulting in low quality and less preferred re-growth of forage following defoliation (Miquelle 1983). Studies describing detailed movements at several different densities are needed to confirm the inverse relationship between intraspecific competition and movement (Hundertmark 1998, Bowyer et al. 2003).

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