

VARIATION IN FINE-SCALE MOVEMENTS OF MOOSE IN THE UPPER KOYUKUK RIVER DRAINAGE, NORTHCENTRAL ALASKA

Kyle Joly¹, Timothy Craig^{2,4}, Mathew S. Sorum¹, Jennifer S. McMillan³, and Michael A. Spindler²

¹National Park Service, Gates of the Arctic National Park and Preserve, 4175 Geist Road, Fairbanks, Alaska 99709; ²US Fish and Wildlife Service, Kanuti National Wildlife Refuge, 101 12th Avenue, Fairbanks, Alaska 99701; ³Bureau of Land Management, Central Yukon Field Office, 1150 University Avenue, Fairbanks, Alaska 99709; ⁴Retired

ABSTRACT: Fine-scale movements form the foundation of local habitat selection by animals. In northern interior Alaska, the Dalton Highway Corridor Management Area and other parts of Game Management Unit 24 are accessible to moose hunters from the Dalton Highway. Concern that these areas may be a population sink for moose (*Alces alces*) inhabiting the Gates of the Arctic National Park and Preserve and the Kanuti National Wildlife Refuge prompted this study of movements. We found that migratory bulls and cows traveled about the same distance over the course of a year as non-migratory moose. Although counterintuitive, this may reflect the selective foraging behavior of a low density (~0.1 moose/km²) moose population in habitat with abundant forage. Maximum movement rates by bulls occurred at the onset of rut at the end of the hunting season. This spike in movement may have given local residents the impression that local moose were migratory and vulnerable to hunting from non-residents. Movement rates were lowest in winter for both bulls and cows, and declined with increasing winter severity, but not temperature specifically. Reduced movement rates by cows during the calving season were not readily evident and annual fidelity to calving sites was minimal.

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Although moose (*Alces alces*) migrate long distances in northern interior Alaska (Mauer 1998), prior to this study little was known about migratory patterns in the upper Koyukuk River drainage where land and moose management is complicated by a mosaic of lands administered by the State of Alaska, National Park Service, US Fish and Wildlife Service, Bureau of Land Management, and private entities (Fig. 1). Public wildlife advisory groups were concerned that moose harvested within and around the Dalton Highway Corridor Management Area (DHCMA) were influencing (lowering) moose density in the Gates of the Arctic National Park and Preserve (GAAR) and Kanuti National Wildlife Refuge (KNWR).

However, migration of moose between these conservation units and the DHCMA is limited and likely not a management concern (Joly et al. 2015).

Analysis of fine-scale movements by moose is useful to better understand their local ecology and behavior that is integral for implementing informed management strategies. Just as moose exhibit variation in large-scale migratory movements (Mauer 1998, Joly et al. 2015), fine-scale movement patterns vary individually, by gender, and in response to local physiographic variables. Movement in other boreal regions occurs relative to an individual's need for cover, forage, and reproduction (Leblond et al. 2010). Improved comprehension of factors

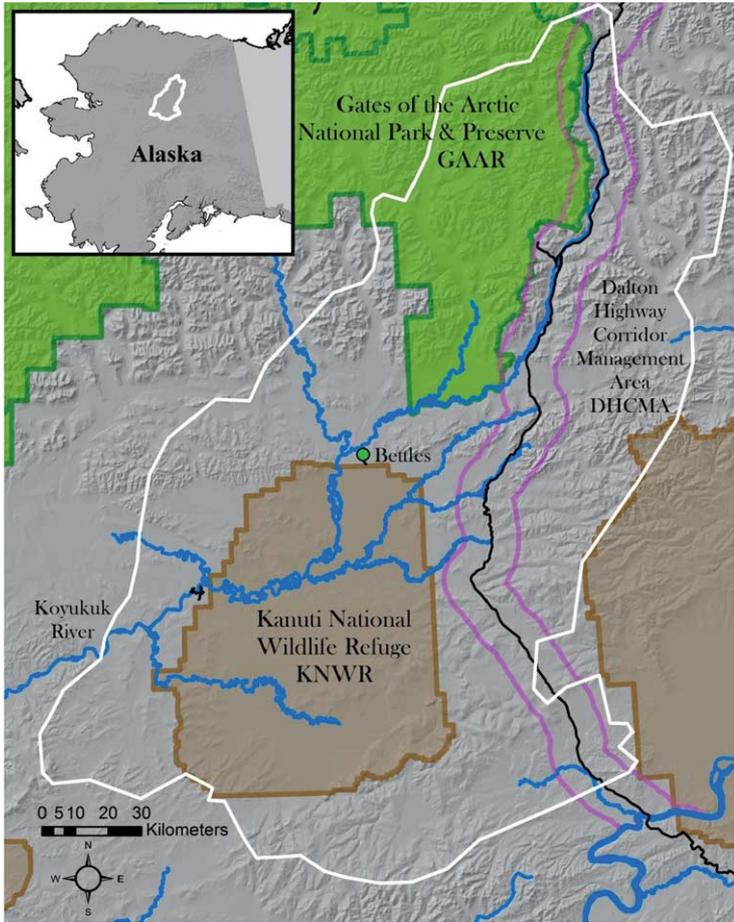


Fig. 1. The upper Koyukuk River study area (white polygon) in northcentral Alaska which encompassed moose locations derived from GPS telemetry data from 2008–2013.

influencing fine-scale movements in a heterogeneous landscape is critical to understanding moose behavior and their distribution across the landscape.

In this study, we examined fine-scale movement data collected as part of a larger project that assessed moose movements between GAAR and KNWR, and the DHCMA. Our goals were to better understand the fine-scale movements of moose in the upper Koyukuk River drainage relative to migratory status, sex, season, physiography, temperature, and winter severity. We hypothesized that migratory moose traveling to and from wintering areas would travel

farther annually than non-migratory moose, and that harsher winter conditions would reduce movement rate.

METHODS

Study Area

The study was in the upper Koyukuk River drainage that encompasses the southern slopes of the central Brooks Range, including the southeastern portion of GAAR, all of KNWR, and other state, federal (including portions of the DHCMA), and native lands (Fig. 1). Moose density in the upper Koyukuk is very low (~ 0.1 moose/km²; Lawler et al. 2006), and the physiography

and habitat types are diverse. In the north, rugged mountains (up to 2000 m in elevation) divided by narrow river valleys dominate the landscape. Habitats range from alpine tundra to shrubs, boreal forest, and muskegs with declining elevation. Alders (*Alnus* spp.), willows (*Salix* spp.), and dwarf birch (*Betula glandulosa*) dominate shrub habitats. Black spruce (*Picea mariana*) is the most prevalent tree species, with white spruce (*Picea glauca*), poplar (*Populus balsamifera*), and numerous shrub species common in riparian areas. Birch stands (*Betula papyrifera*) occur on south-facing slopes at moderate elevations and are common in recently burned areas. The landscape becomes progressively flatter (elevations typically <500 m) to the south with more muskegs, streams, and lakes interspersed within boreal forest and broad riparian zones. The regional climate is strongly continental, with long, extremely cold (<-45° C) winters, and brief hot (>30° C) summers. Snow depth exceeds 90 cm many winters, with >60 cm in most.

Moose Relocation Data and GIS Analyses

Adult moose were darted using a mixture of carfentanil citrate and xylazine from Robison R-44 helicopters, and instrumented with a GPS radio-collar. Moose captured north and east of Bettles, Alaska (Fig. 1) were designated as ‘northern moose’ and those in and around KNWR as ‘southern moose’. Radio-collars deployed in March 2008 collected 1 GPS location/day, and thereafter all collected 3 locations/day. About half of the radio-collars were instrumented with temperature sensors.

Movements of northern and southern moose were contrasted due to the substantial differences in terrain and habitat. Migratory status of individual moose was ascertained from net-squared displacement analyses (Bunnefeld et al. 2011) as described by Joly et al. (2015). Average movement rates and

distance traveled were calculated based on successive locations; results are reported as mean rates and distances with their associated standard error (SE). Differences in mean movement rates by sex, season, and migratory status were not statistically assessed because of the varied annual sample size and differential location rates.

We analyzed the data on a weekly basis and across 6 designated seasons: Spring, 26 March – 27 May; Calving, 28 May – 23 June; Summer, 24 June – 26 August; Hunting, 27 August – 23 September; Fall/Rut, 24 September – 25 November; Winter, 26 November – 25 March. We did not determine exact calving sites in this remote landscape due to budgetary restrictions preventing survey flights. Instead, we assessed an individual cow’s annual fidelity to a calving area by calculating the distance between locations nearest to the expected calving date (i.e., June 1). For example, for each cow we measured the distance between its location on 1 June 2010 with those on 1 June 2008, 2009, and 2011, assuming 2010 was the most central location.

Movement was related to terrain ruggedness (Sappington et al. 2007) and temperature using regression analysis; $P < 0.05$ was the critical significance level. Likewise, we assessed whether moose exhibited elevational migrations to presumably take advantage of potential temperature inversions on extremely cold days (<-20° C). We compared DEM-assigned elevations from each location to the temperature at the nearest weather station in Bettles, Alaska (<<http://www.ncdc.noaa.gov/>>, accessed July 2014). Winter severity was classified in 3 categories from the total number of days with snow and depth of snow as recorded in Bettles: mild (<135 days with ≥ 30 cm snow and <7 days with ≥ 60 cm snow), moderate (>170 days with >30 cm snow, >50 days with >60 cm, or <14 days with >90 cm snow), or severe (>170 days with ≥ 30 cm of snow,

>100 days with ≥ 60 cm, or >30 days with ≥ 90 cm snow).

RESULTS

A total of 37 adult moose (26 cows, 11 bulls) were captured and instrumented with GPS radio-collars. Eighteen northern cows were marked: 5 in March 2008, 9 in October–November 2008, 2 in November 2009, and 2 in April 2011. Eight southern cows and 11 northern bulls were marked in April 2011. The 37 GPS units collected a total of 71,675 locations.

Cows with 1 location/day had ~10% lower total annual movement (492.2 ± 71.4 km) than cows with 3 locations/day (544.5 ± 34.6 km); this was expected given the more intensive sampling regime that captures tortuous movements (July 2005). Cows (534.6 ± 30.7 km) and bulls (523.6 ± 43.0 km) traveled similar distances over the course of a year. Southern cow moose (616.3 ± 75.9 km) walked ~17% further than northern cow moose in a year (493.7 ± 21.6 km). Non-migratory ($n = 5$; $528.5 \pm$

68.0 km) and migratory ($n = 9$; 525.9 ± 50.7 km) cows had similar annual movement distances. Likewise, annual movement distances were similar between non-migratory ($n = 4$; 543.4 ± 78.8 km) and migratory bulls ($n = 4$; 528.2 ± 78.8 km).

Bull and cow movement rates were not substantially different in fall, winter, and spring and both moved the least during winter (Fig. 2). Movement rates of bulls were ~45% higher than cows during the calving and hunting seasons; conversely, cows moved more than bulls during summer (Fig. 2). Movement rates of migratory cows were ~20% less than non-migratory cows in summer (87 ± 10 versus 107 ± 12 m/h) and ~25% less in fall (50 ± 9 versus 65 ± 10 m/h). Southern cow moose had ~40–65% higher movement rates in spring, fall, and winter (77 ± 6 , 69 ± 8 , 60 ± 7 m/h, respectively) than northern cow moose (56 ± 4 , 49 ± 5 , 36 ± 5 m/h, respectively).

Weekly movement rates were most pronounced by both sexes during calving, continued through summer by cows, and

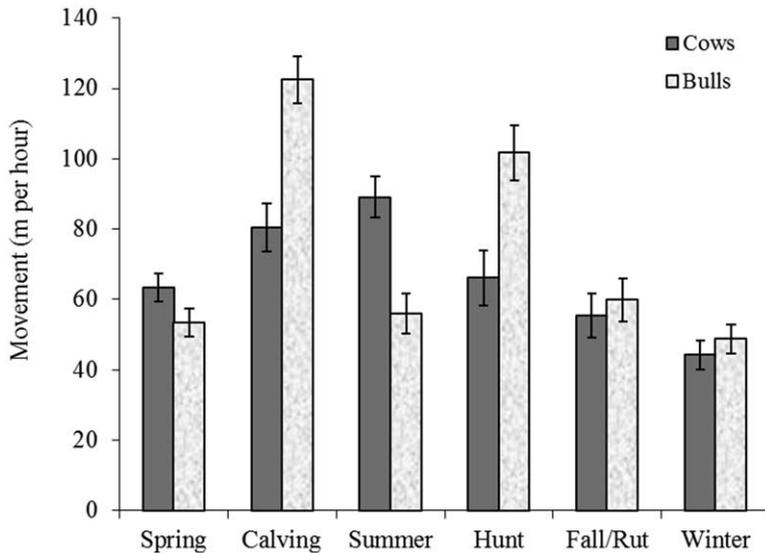


Fig. 2. Mean seasonal movement rates (meters per hour) and standard errors (SE) of GPS radio-collared bull (light bars) and cow (dark bars) moose in the upper Koyukuk River drainages, northcentral, Alaska, 2008–2013.

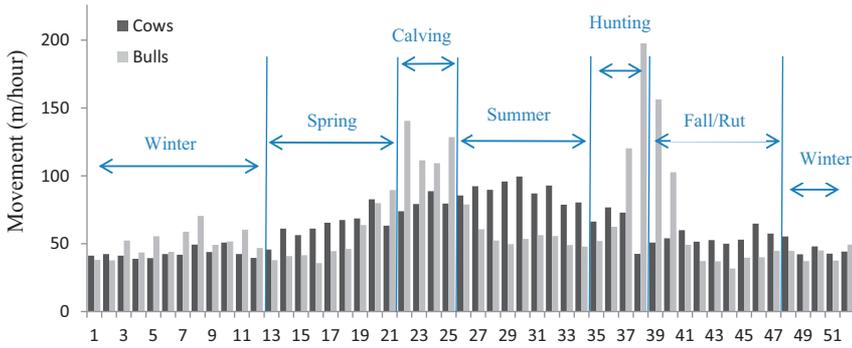


Fig. 3. Weekly movement rates (m/h) of GPS radio-collared bull (light bars) and cow (dark bars) moose in the upper Koyukuk River drainages, northcentral, Alaska, 2008–2013. Week 1 is 1–7 January, and subsequent seasons are delineated accordingly.

increased again by bulls during the rut (Fig. 3). Locations of individual cows during calving were, on average, $\sim 8,400$ m horizontal distance from previous calving sites ($n = 21$ cows with 59 potential calving events, range = 227–43,654 m). Only 3 (8%) potential calving sites were < 1 km from the next nearest location for all potential calving events.

Winter movement rates of cows were $\sim 20\%$ longer in mild (39 ± 2 m/h) versus moderate and severe winters (32 ± 2 and 33 ± 3 m/h, respectively). Although GPS radio-collars were not deployed on bulls during the only severe winter (2008–2009), their movement rates were $\sim 10\%$ higher in mild (40 ± 5 m/h) than moderate winters (36 ± 5 m/h). We found no evidence that moose utilized higher elevations for thermal advantage during temperature inversions in extreme cold weather. Movement rates were significantly, and negatively associated with fine-scale (180 m) terrain ruggedness for 50% of moose ($n = 32$); conversely, 2 southern cow moose had significant positive associations. Cows used the highest elevations during fall (576 ± 2 m) and the lowest in spring (413 ± 2 m). Bulls were also at lowest elevations during spring (334 ± 4 m), but at highest elevations in summer (528 ± 4 m).

Use of low elevations in spring may reflect earlier green-up.

The relationship between movement rate and temperature was strongest in spring when 80% of moose had significant positive associations between movement rates and collar temperature ($n = 15$); no moose had a negative association. An obvious pattern was not observed in other seasons; $> 33\%$ of movement rates were negatively associated with temperature (i.e., greater movement rates at colder temperatures) and 13% had positive associations. Lastly, we found that moose repeatedly crossed the Dalton Highway, the Trans-Alaska Pipeline System, and its associated maintenance road.

DISCUSSION

Fine-scale movements of moose provide critical behavioral and ecological information and are the foundation of large-scale movements such as migration. Migration can reduce predation and the energy required to avoid predation, and hence increase productivity (Avgar et al. 2013, White et al. 2014); however, migration can impose costs as well. For example, increased exposure to predation can occur along the course of the migration route or at its terminus (Middleton et al. 2013), and longer migrations require higher energy output (Fancy and White

1987). Counterintuitively, we found that non-migratory moose moved similar distances in a year as migratory moose, despite having smaller home ranges and not traveling between summer and winter ranges (Joly et al. 2015). Although high habitat quality typically results in smaller home ranges and lower movement rates (Hundertmark 1997, Dussault et al. 2005), it is not clear why migratory moose would not travel farther than non-migratory moose. We offer 3 possible explanations related to foraging, terrain ruggedness, and predation.

Moose are highly selective browsers (Risenhoover 1987, Hundertmark 1997) and browse utilization rates in our study area are among the lowest in Alaska (Paragi et al. 2008). Where forage quantity and quality are high relative to moose density, such as in our study area, only a small proportion of forage biomass is consumed (Hundertmark 1997). Under these conditions, moose may move rapidly between stands of readily available, small diameter forage with high digestibility (Vivas and Saether 1987). These moose adopt an intake maximization strategy rather than an energy conservation strategy, which would not be surprising during productive seasons. In contrast, Dussault et al. (2005) found lower movement rates in high quality habitats in eastern Canada.

Terrain ruggedness may influence moose movement as the majority of northern moose inhabiting much more mountainous, rugged terrain had lower movement rates. In the less rugged southern portion there was no clear association between movement rates and ruggedness. Moose may move less in rugged terrain simply because of the increased energetic expense and difficulty to do so. Moreover, the actual overland distance travelled by moose may be underestimated for northern moose since movement calculations typically do not account for vertical movement required to navigate rough terrain; vertical movement within elevated

terrain results in shorter calculated distances than travel in flat terrain (Dettki and Ericsson 2008).

Lastly, higher predation pressure could cause increased movement for our moose with small home ranges (see Ballard et al. 1980). The Dalton Highway provides access and facilitates hunting and trapping within the DHCMA, and combined with disturbance from human activities in the area, is generally thought to have reduced the abundance of wolves (*Canis lupus*) and bears (*Ursus arctos* and *U. americanus*) in the DHCMA. Unfortunately, only limited information is available about predator populations in this region. Nonetheless, in GAAR where hunting and trapping regulations are restrictive, cows moved less than cows in KNWR where limited, but more hunting and trapping occurs – weakening the predator abundance explanation.

Bulls and cows traveled similar distances over the course of a year and their movement rates were similar in the fall/rut and winter seasons (Fig. 2). Movement rates for both bulls and cows were lowest during winter as documented elsewhere (Fig. 2 and 3; Hundertmark 1997, Dussault et al. 2005). Winter movement rates of bulls and cows were higher during mild winters and more restricted in harsher winters as deep snow impacts movement, distribution, and home range size (van Ballenberghe 1977, Miquelle et al. 1992, Ball et al. 2001). Our limited data suggest that bulls may be less sensitive to winter severity than cows, possibly because their larger size facilitates movement through deep snow and they use larger foraging areas. We did not find that lower winter temperatures reduced movement rates or led to elevational migrations. Indeed, we found slightly higher movement rates at extreme low temperatures and that moose mostly used lower elevations during winter.

Bull and cow movement rates varied during other seasons; for example, bull

movement rates were substantially higher during the hunting season (Fig. 2). This abrupt and marked movement likely related to the concern of public hunting advisory groups that moose might be migrating out of the conservation units (GAAR and KNWR) into areas where hunting regulations were more liberal. Related analyses (Joly et al. 2015) indicate that such concerns are mostly unwarranted.

Bulls and cows also had different movement rates during calving. It is intuitive that cow movement would be less than that of bulls when cows tend calves. Our data suggest that cow movement rates do not drop substantially during calving, rather, that bull movement rates increase measurably during early summer. In fact, cow movement rates were higher during calving than earlier in spring; however, we could not parse individual cows by their reproductive status.

We found that analyzing weekly movement rates was insightful in that these movements identify temporal patterns that are otherwise masked in seasonal timeframes. For instance, increased movement rates of bulls between mid-September and early October corresponded to the hunting season and onset of rut, but were masked by seasonal averages (Fig. 3). Further, the weekly analysis revealed a spike in cow movement prior to peak calving, which may be an anti-predatory behavior. Cows often make substantial shifts (>5 km) just prior to parturition (Bowyer et al. 1999, Testa et al. 2000, McGraw et al. 2014), and successive calving locations were located an average >8 km apart: <10% of potential calving sites were located within 1 km of previous potential calving locations and none within 225 m. These data are consistent with other studies (e.g., Chekchak et al. 1998, Testa et al. 2000, McGraw et al. 2014) that found little annual fidelity to calving sites.

This study is the first of its kind in this region and was an offshoot of a larger investigation about migratory movements. Our analysis of fine-scale movements surprisingly revealed that 1) migratory and non-migratory moose traveled similar distances in a year, 2) terrain ruggedness was related to movement distance, and 3) that bulls increased movement more than cows in spring. We also found that bulls did not seek higher elevation during extreme cold, bulls more than doubled their movement during the rut, and that cows had little annual fidelity to calving sites. Further study of fine-scale movements should contribute meaningfully to improved understanding of behavioral adaptations and micro-habitat selection by moose.

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