

MOOSE MOVEMENT PATTERNS 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: Understanding movement patterns of moose (*Alces alces*) is critical to understanding their ecology and sound management. Our study was prompted by concern that the Dalton Highway Corridor Management Area (DHCMA), where the Dalton Highway facilitates access for non-local hunting, may be a population sink for moose that also reside in more remote and protected areas like Gates of the Arctic National Park and Preserve (GAAR) and Kanuti National Wildlife Refuge (KNWR). We did not detect substantial migrations between DHCMA and GAAR or KNWR. However, we estimated that 14–60% of moose in our study area were migratory depending on sex, location within our study area, and methodology utilized to differentiate migratory behavior. A quarter of the animals displayed mixed-migratory strategies where migration is exhibited by a single individual in some years but not others. The percentage of moose that were migratory in our study population, and the distances they migrated, were lower than reported from studies elsewhere in interior Alaska. We hypothesize this may be related to their very low density (~0.1 moose/km²) and/or higher terrain ruggedness in part of the study area. Winter severity did not appear to impact migration, but home range sizes were smaller in severe winters.

ALCES VOL. 51: 87–96 (2015)

Key words: Alaska, *Alces alces*, conservation, migration, moose, strategy, winter severity

Moose (*Alces alces*) across their circum-polar range often exhibit migratory patterns (e.g., van Ballenberghe 1977, Ball et al. 2001, White et al. 2014), but migration is not a ubiquitous trait among all populations (Mueller et al. 2011) and they are not widely perceived as migratory by the general public. Migration is thought to increase fitness because animals gain access to better quality or quantity of forage, experience a reduction in predation, or possibly reduced exposure to parasites or disease (van Ballenberghe 1977, Avgar et al. 2013). Variability in migration among individuals may be the norm where habitat conditions sustain resident populations but fitness varies spatially (Fryxell and Holt 2013).

Movements of moose in the upper Koyukuk River drainage (Fig. 1) are not well understood. On the lower Koyukuk River, an area where moose density is comparatively high (5/km²), 83% of adult moose and 58% of cow-calf pairs were migratory, and movement between summer and winter ranges averaged 42 and 31 km, respectively (Osborne and Spindler 1993). In the Arctic National Wildlife Refuge and neighboring Canada, northeast of our study area and where moose density is much lower (~0.4/km²; Caikoski 2010) than in the lower Koyukuk study area, 88% of moose were classified as migratory (Mauer 1998). There, the mean maximum migration distance was 123 km (i.e., the mean longest migration

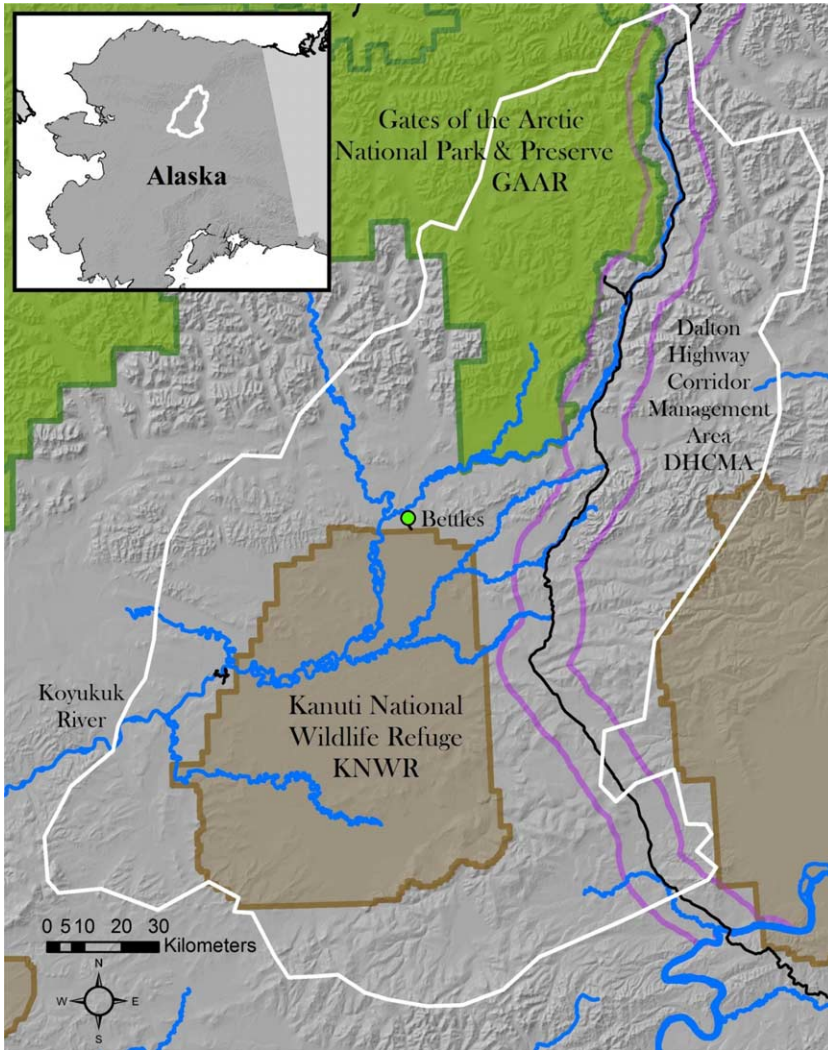


Fig. 1. The Upper Koyukuk River study area (white polygon) in northcentral Alaska, encompassing moose locations derived from GPS and VHF telemetry data from 2008–2013.

distance by individual moose). Moose density is even lower in the upper Koyukuk section of our study area (~0.1/km²; Lawler et al. 2006).

Land and wildlife management in our study area falls within a complicated patchwork of authorities and includes lands administered by the State of Alaska, National Park Service, US Fish and Wildlife Service, Bureau of Land Management, and private

entities. Public wildlife advisory groups interested in hunting opportunities and management in the upper Koyukuk River drainage were concerned that harvest was high within and near the Dalton Highway Corridor Management Area (DHCMA) which contains the only road in northern Interior Alaska (Fig. 1). Harvest opportunity was open to all Alaskan residents in the DHCMA, whereas only local residents

harvest moose within Gates of the Arctic National Park and Preserve (GAAR) and much of the Kanuti National Wildlife Refuge (KNWR). Subsistence hunters in the upper Koyukuk were concerned that moose were migrating long distances, as in the eastern Brooks Range (Mauer 1998), from their exclusively subsistence hunting areas into general harvest areas, causing a local decline in density and hunting opportunity. The possibility that hunter effort and success in one portion of the region was negatively affecting another area where distinct user groups hunted was an important management concern. Therefore, our goal was to better understand the migratory patterns of moose in the upper Koyukuk River drainage, and we were specifically interested to identify if moose moved between lands with different management goals and hunting regimes.

METHODS

Study area

Our study area falls within the upper Koyukuk River drainage in north-central Alaska (Fig. 1), and encompassed the southern flanks of the central Brooks Range, including the southeastern portion of GAAR, all of KNWR, and other state, federal, private, and native lands. It included portions of the DHCMA which contains an all-weather highway and had special hunting restrictions. The terrain and vegetation communities are diverse. Rugged mountains to 2000 m in elevation with narrowly-confined glacial river valleys are covered with a mix of alpine, shrub, and boreal forest habitat types in the northern portion. Shrub habitats were dominated by alders (*Alnus* spp.), willows (*Salix* spp.), and dwarf birch (*Betula glandulosa*). Black spruce (*Picea mariana*) is the most prevalent tree species, with white spruce (*Picea glauca*) and poplar (*Populus balsamifera*) common in riparian areas, and birch stands (*Betula papyrifera*) occur on south-facing slopes and in areas that burned.

Extensive tracts of tussock (*Eriophorum* spp.) tundra occur in wetter, flatter 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 (dropping below -45° C) winters, and brief, but hot (temperatures >30° C) summers. Forest fires are common during summer months, and snow depth exceeds 90 cm many winters with 60 cm during most.

Moose relocation data and GIS analyses

The project ran between March 2008 and April 2013. Adult moose were darted using a mixture of carfentanil citrate and xylazine from Robison R-44 helicopters. Moose were instrumented with either a GPS collar equipped with a VHF beacon or a standard VHF 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’. GPS collars deployed in March 2008 collected 1 GPS location/day, thereafter, all collected 3 locations/day. An attempt to relocate moose visually from small aircraft using the VHF beacons occurred ~monthly from March 2008 to April 2013. These efforts were much more consistent for the southern moose due to budgetary restraints, weather, and logistics. Movements of northern and southern moose were compared due to differences in terrain, habitats, and sampling effort.

Migratory status was assessed using 2 different methods using individual moose as the sample unit for both techniques. First, for both GPS- and VHF-collared moose, we calculated distances between summer (i.e., the closest relocation July 1) and winter (i.e., the closest relocation to January 15) locations to assess migratory status and distance moved. Moose that consistently

demonstrated separation between summer and winter locations were categorized as migratory (i.e., winter locations were not located sympatrically with summer locations or vice versa), whereas those without consistent separation between ranges were categorized as non-migratory. Distance between summer and winter ranges was not a determinate. Moose that had separation in some years but not others, or did not have a discernible pattern, were categorized as having a mixed-migratory strategy. Distances between winter and summer locations were averaged for moose that had multiple years of data. While somewhat subjective, this methodology mimics other studies (e.g., Osborne and Spindler 1993, Mauer 1998) that were conducted adjacent to ours, thereby allowing more direct comparison.

Second, net squared displacement (NSD) of GPS-collared moose was used to determine migratory status on an annual basis (see Bunnefeld et al. 2011). The NSD measures straight line distances between a starting location and all successive relocations within the entire annual movement path. The first position was set to July 1 when moose are in their summer range, and we excluded all individuals sampled <330 days. Moose displaying “home range” movement patterns according to Bunnefeld’s nomenclature were categorized as non-migratory, “migration” as migratory, and “mixed migratory” and “dispersal” as mixed migratory (no moose dispersed from the study area). Moose that did not consistently have the same movement status among years were considered mixed migratory. The shape of movement patterns, not NSD distance, was the determinate of migratory status (Bunnefeld et al. 2011). There were insufficient VHF data to quantify migration patterns with the NSD technique for any individual moose.

The 2 methods for determining migratory status are highly disparate and caution

is required when comparing results. GPS and VHF locations were also used to determine if individual moose utilized conservation units (GAAR, KNWR), the DHCMA exclusively, or multiple units.

Winter severity was classified from the total number of days with snow and snow depth as recorded in Bettles, Alaska. The categories were mild (<135 days with ≥ 30 cm snow or <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 snow, >100 days with ≥ 60 cm, or >30 days with ≥ 90 cm snow).

Annual and winter home ranges for GPS-collared moose were determined by establishing fixed kernels using the 95% utilization distribution and least square cross validation method for smoothing using ArcGIS (ESRI, Redlands, CA; Worton 1989, Seaman and Powell 1996). There were insufficient data to develop kernels for VHF collars.

RESULTS

Moose Relocation Data

In total we captured 120 adult moose (27 bulls and 93 cows); 58 in March 2008, 10 in October 2008, 15 in November 2009, and 37 in April 2011. One presumed capture myopathy (adult cow in 2008) was censured. There were 52 southern moose and 67 northern moose providing ~265 moose-years of data to analyze allopatric migration and movements among conservation units. Aerial telemetry flights yielded 2119 high-quality relocations (positive visual identification). GPS collars were deployed on 14 northern cow moose in 2008 (25 moose-years of data), 2 in 2009 (2 moose-years), and 2 in 2011 (2 moose-years); 8 GPS collars were deployed on southern cows (8 moose-years of data) and 11 on northern bulls in 2011 (18 moose-years). In total, the 37 GPS units collected 71,675 locations.

Migration

Allopatry of winter and summer ranges and the migratory status of 86 cows and 21 bulls were ascertained through the use of both VHF and GPS data. Of the 10 moose with only a single year of data, 2 displayed non-migratory behavior and 8 displayed mixed-migratory behavior. Using only GPS data for NSD-based models, we determined

the migratory status of 20 cows and 11 bulls; 25 had 2–4 years of data (5 non-migratory, 8 migratory, and 12 mixed) and 6 had only a single year of data (4 non-migratory, 1 migratory, and 1 mixed). Non-migratory, migratory and mixed-migratory strategies were exhibited in varying proportions by sex, location, and methodology (Fig. 2).

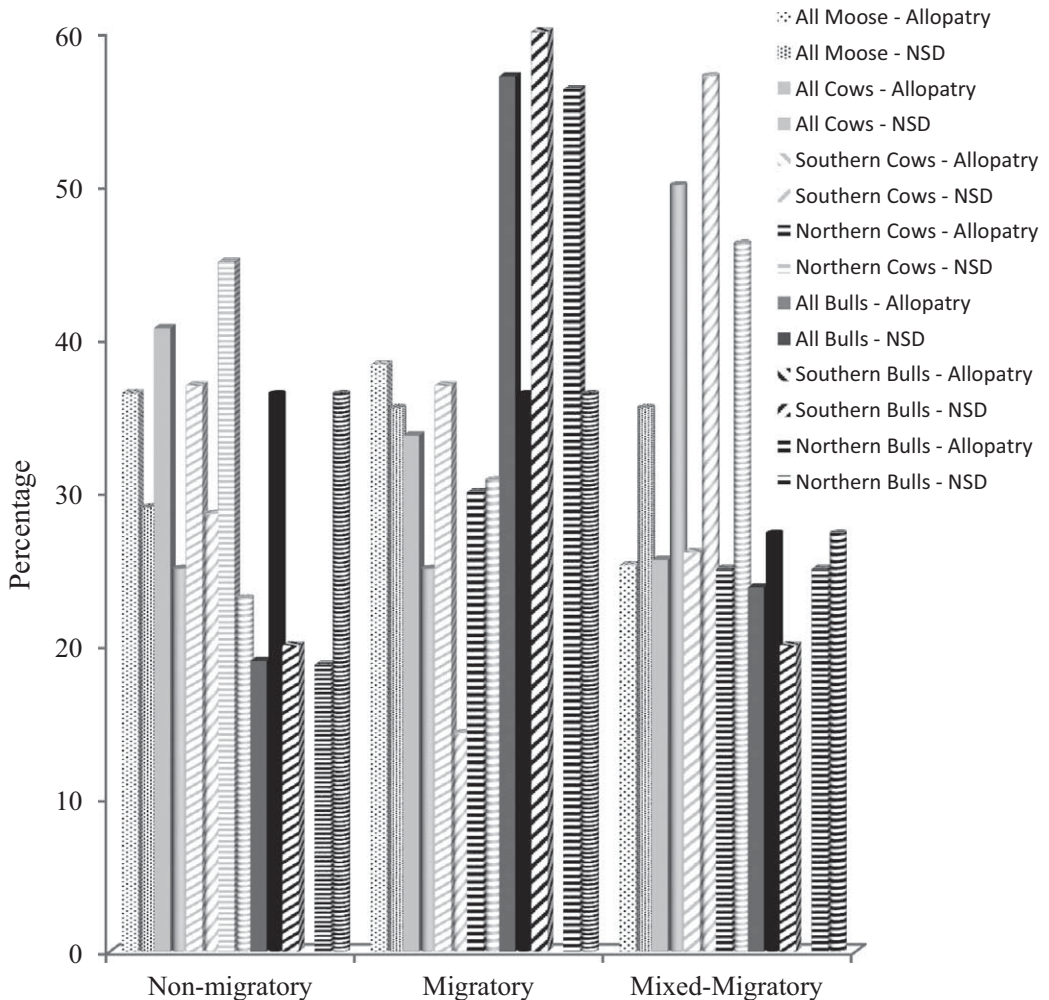


Fig. 2. Percentages of non-migratory, migratory, and mixed-migratory moose in the upper Koyukuk River drainage, northcentral Alaska, 2008–2013. Light bars represent cows and darker bars represent bulls. Rectangular shaped bars represent percentages determined by winter and summer range allopatry, and cylindrical bars represent those calculated by net squared displacement (NSD) methods outlined by Bunnefeld et al. (2011). Percentages associated with southern moose are represented with diagonal striping, and northern moose are represented by horizontal striping; stippled bars represent all moose combined. Note: missing bars occur where n = 0.

Mean distances moved between successive summer and winter locations were 2.5 times greater for migratory cows (n = 86) than non-migrators (Table 1). Migratory southern cows (n = 46) tended to move less between summer and winter locations than migratory northern cows (n = 40; Table 1). Migratory distances (mean per individual) for all cows ranged from 557–88,402 m. Bulls (n = 21) had a similar relative pattern with individual mean distance between summer and winter locations ranging from 2,886–52,624 m (Table 1). Summer ranges of both sexes were located in all cardinal directions relative to winter ranges; however, 59% of winter ranges of migratory moose were located north of summer ranges. Net displacement (ND) of GPS-collared moose (mean per individual) ranged from 10,970–94,972 m for cows and 13,060–52,660 m for bulls (means in Table 1). Only 45% of moose were categorized with the same migratory pattern using the NSD techniques when compared to the winter-summer range allopatry analysis. Although we did not detect any movements that led to dispersal or forays outside the study area, we also

did not collar younger moose that would be more likely to undertake measurable dispersal movements.

Home Range

The mean annual home ranges were 243.5 ± 96.9 km² for GPS-collared cows (n = 21; range = 106.5 – 498.3 km²) and 262.0 ± 67.7 km² for GPS-collared bulls (n = 11; range = 185.7 – 400.9 km²). As expected (July 2005), home ranges of cows (n = 4; 305.0 ± 47.2 km²) calculated from 1 GPS location/day were larger than cows (n = 17; 228.9 ± 22.9 km²) with 3 locations/day. The mean home range size of non-migratory (NSD technique) cows was ~10–15% smaller (n = 5; 228.1 ± 45.2 km²) than that of migratory cows (n = 7; 247.9 ± 38.2 km²) or cows with mixed-migration strategies (n = 8; 261.7 ± 35.7 km²). Non-migratory (n = 4; 260.3 ± 33.4 km²) and migratory (n = 4; 295.9 ± 33.4 km²) bulls conformed to this same pattern; bulls with mixed-migration strategies had home ranges about 25% smaller than other bulls (n = 3; 219.0 ± 38.5 km²). The mean annual home range was smallest for cows found primarily within the KNWR (n = 5; 199.6 ± 63.0 km²),

Table 1. Distance (mean ± SE) between summer and winter locations (allopatry) and net displacement (ND; sensu Bunnefeld et al. 2011) of cow and bull moose for the entire and portions of the upper Koyukuk River drainage study area, northcentral Alaska, 2008–2013.

Methodology	Location/Sex	Non-migratory (m)	Migratory (m)	Mixed Migratory (m)
Allopatry	All Cows	8621 ± 2241	21598 ± 2462	17598 ± 2827
Allopatry	Southern Cows	7697 ± 2233	16128 ± 2233	18619 ± 2658
Allopatry	Northern Cows	9494 ± 3809	29347 ± 4665	16373 ± 5110
Allopatry	All Bulls	5923 ± 5923	15709 ± 3419	18820 ± 5297
Allopatry	Southern Bulls	5015*	906 ± 3261	2886*
Allopatry	Northern Bulls	6226 ± 7176	17644 ± 4143	22804 ± 6215
ND	All Cows	23584 ± 8410	49046 ± 8410	29084 ± 5947
ND	Southern Cows	16526 ± 7663	15604*	40430 ± 5419
ND	Northern Cows	28290 ± 10197	57406 ± 8831	21520 ± 7210
ND	Northern Bulls	22267 ± 6473	37757 ± 6473	22808 ± 7474

*N = 1, no SE reported.

increased in size in the DHCMA ($n = 11$; $227.9 \pm 88.5 \text{ km}^2$), and was largest for cows ($n = 3$; $279.1 \pm 77.4 \text{ km}^2$) in the GAAR. The 2 cows that utilized both KNWR and the DHCMA had the largest annual home ranges ($384.9 \pm 160.0 \text{ km}^2$). All 11 GPS bulls were collared in GAAR and had larger average annual home ranges than cows in GAAR. East of GAAR, home ranges often overlapped the Dalton Highway and Trans-Alaska Pipeline System (TAPS).

For all GPS moose, winter home ranges were slightly larger ($n = 32$; $24.2 \pm 13.0 \text{ km}^2$) in mild winters than moderate ($n = 36$; $20.2 \pm 8.6 \text{ km}^2$) and severe winters ($n = 11$; $21.0 \pm 9.0 \text{ km}^2$). Using only 3 locations/day data, we similarly found larger winter home ranges during mild than moderate winters, and smallest ranges during severe winters ($23.3 \pm 12.5 \text{ km}^2$, $19.4 \pm 7.0 \text{ km}^2$, and $16.4 \pm 8.1 \text{ km}^2$, respectively). Cows appeared to be more sensitive than bulls to severe weather; their winter home ranges were $24.2 \pm 13.7 \text{ km}^2$, $19.0 \pm 7.7 \text{ km}^2$, and $16.4 \pm 8.0 \text{ km}^2$ in mild, moderate and severe winters, respectively. No GPS bulls were collared during a severe winter, but their winter home range sizes were nearly identical in mild and moderate winter ($20.9 \pm 9.3 \text{ km}^2$, $20.2 \pm 8.6 \text{ km}^2$, respectively).

Movement Relative to Conservation Units

VHF and GPS data ($n = 116$ moose) were combined to examine movements in and around GAAR, KNWR, and the DHCMA. Thirty-two moose stayed exclusively within the confines of KNWR, including all 5 bulls originally collared there. An additional 21 used KNWR and areas outside the refuge, and of these, only 1 bull and 2 cows (14.3%) were also found within the DHCMA; 1 cow primarily used the DHCMA (1 location within KNWR) and 1 bull primarily used the GAAR. Two (1 bull and 1 cow) of these 21 moose used

GAAR extensively and did not enter the DHCMA, and the cow consistently migrated from GAAR in the winter to calve within KNWR. The GAAR had 16 moose (10 bulls and 6 cows) that stayed within its borders and 24 that moved in and out of the area; of the 24, 9 bulls and 11 cows (83.3%) moved into the adjacent DHCMA (Fig. 1). Nonetheless, most (~70%) moose using the GAAR and DHCMA resided primarily in one or the other unit, with a single or few relocations falling in the other. Moose located commonly in both units had home ranges with measurable overlap of both. Robust migratory movements between these 2 units were not detected for bulls or cows.

DISCUSSION

Moose in the upper Koyukuk River drainage exhibited partial migration (25–34% of cows and 36–57% of bulls), similar to other areas in Alaska (van Ballenberghe 1977, Osborne and Spindler 1993, Mauer 1998, White et al. 2014). However, the proportion of moose that were migratory in the upper Koyukuk River (35–38%) was less than in the lower drainage (Osborne and Spindler 1993) or the eastern Brooks Range (Mauer 1998). Similarly, the distances traveled from winter to summer range by our migrators (22 km for cows and 16 km for bulls) were less than those measured in adjacent studies (31–123 km; Osborne and Spindler 1993, Mauer 1998) or elsewhere in Alaska (see review in Mauer 1998). Our NSD calculations revealed longer migration distances than obtained by simply comparing mid-summer to mid-winter locations (range allopatry). Although not directly comparable to earlier studies because migration was calculated differently, moose in the upper Koyukuk River drainage exhibited migratory behavior less frequently than moose elsewhere in the region, and migrated shorter distances. This may be due to lower moose density, differences in habitat quality and

distribution, and/or physiographic differences between study areas.

However, moose migration patterns are more complicated than parsing individuals into migratory or non-migratory categories. In addition to partial migration, we documented that a large segment (26–50% of cows and 24–27% of bulls) exhibited a mixed-migration strategy (i.e., migratory behavior only in certain years), and that the annual strategy varied individually. Our estimates are conservative as a portion of our population was classified during a single year only. This phenomenon was documented in southcentral Alaska and believed related to snow depth (van Ballenberghe 1977). Alternatively, adaptive migration may convey fitness benefits especially in highly variable climates (e.g., our study area) and in rapidly changing environments such as the Arctic. However, migration strategy does not appear to be unilaterally linked to environmental conditions because not all our moose, or entire populations in other areas (van Ballenberghe 1977, Ball et al. 2001), respond similarly in a given year. As our analyses reveal and as expected (Singh et al. 2012, Fryxell and Holt 2013), a mix of migratory strategies are displayed by sympatric moose under varied environmental circumstances.

The mixed-migration strategies we detected highlight the importance of long-term studies and procuring an adequate sample size. The migratory characteristics of a study population would probably not be categorized accurately by short duration studies because mixed-migratory behavior could be erroneously categorized as either migratory or non-migratory behavior (Dettki and Ericsson 2008). Long-term, more focused studies are required to determine if migratory strategy is a behavioral trait acquired from maternal experience as documented elsewhere (e.g., Sweanor and Sandegren 1988). If migratory strategy is a

learned behavior, it would explain, in part, why multiple strategies exist.

Our results also reveal that the methodology used to determine migratory status is important because:

“Migratory behavior is persistent and straightened out movement effected by the animal’s own locomotory exertions or by its active embarkation upon a vehicle. It depends on some temporary inhibition of station keeping responses but promotes their eventual disinhibition and recurrence” (Kennedy 1985, Dingle and Drake 2007).

The NSD technique appears to more robustly and objectively parse moose migratory status relative to this definition. However, the NSD requires data beyond identifying if summer and winter locations are allopatric. Because the allopatric technique is simpler, requires less data, and has been used in past studies, we employed it to make more direct comparisons to regional studies. Because both techniques have positive and negative aspects, identifying objectives and definitions are key in determining which is more appropriate for a specific study.

We found home ranges to be larger in the northern part of our study, which was consistent with past studies (see review by Hundertmark 1997). Highly variable seasonality and climatic conditions in the north where forage productivity is lower, and habitat is patchier due to more rugged and higher terrain, may foster migratory behavior and larger home ranges (Ballard et al. 1991, Hundertmark 1997). The size of home ranges appeared to be influenced by winter severity as smaller home ranges occurred in harsher winters.

Our study was promoted by public concern about moose moving between conservation units (GAAR and KNWR) and areas with different hunting regulations and accessibility, such as the DHCMA. Peak movement rates of bulls occurred from mid-September through early October (Joly et al.

2015) coinciding with much of the hunting season; presumably this timing of bull movement stimulated public concern. Exposure of KNWR moose to the DHCMA was negligible, likely a result of the separation (>10 km apart) of the units in most areas and smaller home ranges of moose in that area. In contrast, GAAR and the DHCMA shared a common boundary and a large proportion (50%) of the moose collared in GAAR used both units. Nonetheless, a preponderance of these moose resided primarily in either unit, with a single or a few relocations at the edge of the adjacent unit. Moose that spent large portions of time in both units had home ranges that measurably overlapped both units. With a single exception, we did not detect regular or substantial migratory movements between the DHCMA and GAAR or the more distant KNWR.

This study was the first of its kind in this region of Alaska and these data provide a basis for evaluating moose movements relative to harvest concerns and distribution of the moose resource, specifically in our study area. Understanding the spatial ecology of moose improves the understanding of moose ecology, behavior, and demographic and genetic processes. It is also critical to developing a comprehensive management program (Hundertmark 1997), especially where harvest allocation, resource damage, and local management issues are influenced by seasonal migration and distribution of moose.

ACKNOWLEDGEMENTS

This project was promoted by public subsistence and wildlife advisory groups. Funding was provided by the National Park Service, US Fish and Wildlife Service, Alaska Department of Fish and Game, and the Bureau of Land Management. We thank pilots T. Cambier, M. Spindler, M. Webb, P. Zaczkowski, C. Cebulski, L. Dillard, P. Christian, A. Greenblatt, H. Bartlett,

N. Guldager, D. Sowards, and S. Hamilton for making this project possible and safe. S. Backensto, J. Burch, J. Caikoski, K. DeGroot, J. Dillard, M. Flamme, A. Morris, C. Harwood, T. Hollis, E. Julianus, H. Kristenson, J. Lawler, N. Pamperin, T. Paragi, K. Rattenbury, C. Roberts, L. Saperstein, G. Stout, and many others provided critical assistance with project implementation. We thank G. Stout for his contributions to project management and insights into the ecology of moose within the region. N. Bywater, C. Harwood, S. Miller, R. Sarwas, and A. Quist provided database and GIS expertise. We appreciate the constructive reviews by E. Addison, R. Churchwell, and anonymous reviewers. All moose captures adhered to State of Alaska Animal Care and Use Committee (ACUC) guidelines (#07–11).

LITERATURE CITED

- AVGAR, T., G. STREET, and J. M. FRYXELL. 2013. On the adaptive benefits of mammal migration. *Canadian Journal of Zoology* 91: 481–490.
- BALL, J. P., C. NORDENGREN, and K. WALLIN. 2001. Partial migration by large ungulates: characteristics of seasonal moose Alces alces ranges in northern Sweden. *Wildlife Biology* 7: 39–47.
- BALLARD, W. B., J. S. WHITMAN, and D. J. REED. 1991. Population dynamics of moose in south-central Alaska. *Wildlife Monographs* 114: 1–49.
- BUNNEFELD, N., L. BORGER, B. VAN MOORTER, C. M. ROLANDSEN, H. DETTKI, E. J. SOLBERG, and G. ERICSSON. 2011. A model-driven approach to quantify migration patterns: individual, regional and yearly differences. *Journal of Animal Ecology* 80: 466–476.
- CAIKOSKI, J. 2010. Units 25A, 25B, and 25D moose. Pages 611–642 in P. Harper, editor. Moose Management Report of Survey and Inventory Activities 1 July 2007 – 30 June 2009. Alaska Department

- of Fish and Game. Project 1.0 Juneau, Alaska, USA.
- DETTKI, H., and G. ERICSSON. 2008. Screening radiolocation datasets for movement strategies with time series segmentation. *Journal of Wildlife Management* 72: 535–542.
- DINGLE, H., and V. A. DRAKE. 2007. What is migration? *Bioscience* 57: 113–121.
- FRYXELL, J. M., and R. D. HOLT. 2013. Environmental change and the evolution of migration. *Ecology* 94: 1274–1279.
- HUNDERTMARK, K. J. 1997. Home range, dispersal and migration. Pages 303–335 in A. W. Franzmann and C. C. Schwartz, editors. *Ecology and Management of the North American Moose*, Wildlife Management Institute, Washington, DC, USA.
- JOLY, K. 2005. The effects of sampling regime on the analysis of movements of overwintering female caribou in east-central Alaska. *Rangifer* 25: 67–74.
- , T. CRAIG, M. S. SORUM, J. S. McMillan, and M. A. SPINDLER. 2015. Variation in fine-scale movements of moose in the upper Koyukuk River drainage, Northcentral Alaska. *Alces* 51: 97–105.
- KENNEDY, J. S. 1985. Migration: behavioral and ecological. Pages 5–26 in M. A. Rankin, editor. *Migration: Mechanisms and Adaptive Significance*. *Contributions in Marine Science* 27 (suppl.). University of Texas, Austin, Texas, USA.
- LAWLER, J. P., L. SAPERSTEIN, T. CRAIG, AND G. STOUT. 2006. Aerial moose survey in upper Game Management Unit 24, Alaska, fall 2004, including state land, and lands administered by the Bureau of Land Management, Gates of the Arctic National Park and Preserve, and Kanuti National Wildlife Refuge. National Park Service Technical Report NPS/AR/NR/TR-2006-55, Fairbanks, Alaska. 30 pp.
- MAUER, F. J. 1998. Moose migration: north-eastern Alaska to northwestern Yukon territory, Canada. *Alces* 34: 75–81.
- MUELLER, T., K. A. OLSON, G. DRESSLER, P. LEIMGRUBER, T. K. FULLER, C. NICOLSON, A. J. NOVARO, M. J. BOLGERI, D. WATTLES, S. DEStEFANO, J. M. CALABRESE, and W. F. FAGAN. 2011. How landscape dynamics link individual- to population-level movement patterns: a multispecies comparison of ungulate relocation data. *Global Ecology and Biogeography* 20: 683–694.
- OSBORNE, T. O., AND M. A. SPINDLER. 1993. Moose population identification study. Three Day Slough, Koyukuk National Wildlife Refuge, Alaska, Game Management Unit 21D. Progress Report 93-3. US Fish and Wildlife Service, Fairbanks, Alaska, USA.
- SEAMAN, D. E., and R. A. POWELL. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* 77: 2075–2085.
- SINGH, N. J., L. BORGER, H. DETTKI, N. BUNNEFELD, and G. ERICSSON. 2012. From migration to nomadism: movement variability in a northern ungulate across its latitudinal range. *Ecological Applications* 22: 2007–2020.
- SWEANOR, P. Y., and F. SANDEGREN. 1988. Migratory behavior of related moose. *Holarctic Ecology* 11: 190–193.
- VAN BALLEMBERGHE, V. 1977. Migratory behavior of moose in southcentral Alaska. *Transactions of the 13th International Congress of Game Biologists* 13: 103–109.
- WHITE, K. S., N. L. BARTEN, S. CROUSE, and J. CROUSE. 2014. Benefits of migration in relation to nutritional condition and predation risk in a partially migratory moose population. *Ecology* 95: 225–237.
- WORTON, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70: 164–168.