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Seasonal movements of migratory and resident female moose (*Alces alces*) in north-central British Columbia, Canada

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Abstract

Ungulate habitat use and movements are highly variable among individuals, populations, and regions. Factors that influence annual and seasonal movements are important to understand for management purposes. Within some populations, moose (*Alces alces*) are known to migrate between seasonal ranges, generally in response to changes in the environment. A total of 45 female moose were fitted with GPS collars between March 1, 2014, and February 28, 2018, in and around the John Prince Research Forest in north-central British Columbia, Canada, to determine the prevalence and timing of migration. Using the model-based net squared displacement approach, we classified 67 (74%) annual trajectories as migratory, of which 43 (48%) were migrant and 24 (27%) were mix-migrant. We classified 22 annual trajectories (24%) as resident and one (1%) as a disperser. Moose with migratory trajectories exhibited a consistent pattern of leaving their winter range (WR) in April and returning from November to February after spending the majority of the year in their non-winter range (NWR). There was a significant negative correlation between mean monthly elevation and mean monthly snow on the ground for migratory moose. The mean distance separating migratory moose WR and NWR ranges (δ) was 32 km (SD = 30 km) but varied greatly from a minimum of 5 km to a maximum of 61 km. We discuss the potential implications of our results on surveys used to estimate moose population abundance and trends. We contend that a better understanding of moose seasonal habitat use patterns would aid moose management, help delineate important seasonal rangelands and migration corridors, inform population survey designs, and expand our understanding of moose populations in general.

Keywords Migration · Net squared displacement · Spatial ecology · Animal movement · Ungulate · Management · Moose

Introduction

Ungulates around the world undertake migrations in response to a variety of exogenous factors (Hebblewhite and Merrill 2009; Singh et al. 2010; Mose et al. 2013; Mysterud 2013; Lendrum et al. 2014; Peters et al. 2019). Some of

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the most well-known examples include the great wildebeest (*Connochaetes taurinus*) migration of the Serengeti (Pennycuick 1975) or the large migrations of caribou (*Rangifer tarandus*) across the Canadian and Alaskan Arctic (Fancy et al. 1989; Nicholson et al. 2016). These events involve the movements of vast numbers of individuals across generally predictable routes and large distances, but they are not the only ungulates on the move. Seasonal migration on a smaller spatial and more individualistic scale occurs in a variety of ungulate species across the world (White et al. 2007; Cagnacci et al. 2011; Gaidet and Lecomte 2013; Sawyer et al. 2016). Dingle and Drake (2007) argued the need to recognize different types and degrees of migration and contended that classic examples of migration may be the most extreme within a range of migration patterns that occur at different spatial and ecological scales.

Movements and habitat use by ungulates are highly variable among individuals, populations, and regions (Cagnacci et al. 2011). Optimal foraging theory predicts that habitat

use and selection are determined by the need for animals to maximize their net energy intake in order to increase fitness (Emlen 1966; MacArthur and Pianka 1966). Predator avoidance theory predicts that the perceived threat or fear of predators causes animals to use habitats that offer greater protection even if that requires reductions in optimal foraging (Brown et al. 1999; Laundré et al. 2001). While optimal foraging, predator avoidance, or a combination of the two and other factors may be the ultimate cause of animal movements, seasonal changes in the environment are often the predominant proximal influence (van Moorter et al. 2016; Rolandsen et al. 2017). For example, in colder climates, snow influences seasonal movements in most animals (Ericsson et al. 1999; Mysterud 2013) because it increases the energetic costs of locomotion (Parker et al. 1984).

Migration in moose (*Alces alces*) has been well documented in some areas and a variety of seasonal movement strategies may exist within a single population (i.e., partial migratory population) (Edwards and Ritcey 1956; Sweanor and Sandegren 1989; Andersen 1991; Ball et al. 2001; Demarchi 2003; Safronov 2009; Bunnefeld et al. 2011; Singh et al. 2012; White et al. 2014). Migration is energetically costly but may confer other benefits which leads to trade-offs between resident and migratory life-history strategies (Hebblewhite and Merrill 2009). For example, calf survival of migratory moose was greater than calf survival of resident moose in Alaska, supporting the predator avoidance hypothesis (White et al. 2014). Rolandsen et al. (2017) found migratory moose grew bigger and produced more twins than residents, suggesting enhanced fitness benefits of migration likely due to better foraging conditions in summer ranges, supporting the optimal foraging theory. The green wave hypothesis (Merkle et al. 2016) and density dependence have also been suggested as potential drivers of moose migration. While the ultimate causes of moose migration are complex and may be spatially and temporally specific, the proximate cause is usually related to seasonal changes (van Moorter et al. 2016; Rolandsen et al. 2017), including snow accumulation (Lundmark and Ball 2008; Poole and Stuart-Smith 2006). Moose may also switch between different life-history strategies annually (e.g., migrant one year, resident the next; Borowik et al. 2020) which could be related to seasonal variation or even individual age (Singh et al. 2012).

Moose in British Columbia (BC), Canada, are hunted by Indigenous peoples for food and social and ceremonial purposes and by licensed hunters for food and recreation (Kuzyk 2016). They also act as an important food source for several large carnivore species; therefore, acting as keystone species in some ecosystems (Gillingham and Parker 2008). The timing, causes, and prevalence of moose migration in BC are not well understood but are known to occur (Hatter 1950). Edwards and Ritcey (1956) described elevation and distance migration in moose living in the Wells Grey area of central BC. Demarchi (2003) described a partial migratory moose population in the Nass Valley in which migratory individuals moved to higher elevation sites prior to calving in the spring and down to lower elevation winter ranges, overlapping with residents, when snow started to accumulate in the fall/early-winter.

It is important to understand different life-history strategies, movements, and habitat use in order to effectively manage a population (Cagnacci et al. 2011). The presence and variable timing of migration between years may influence population estimates and resultant management actions (e.g., setting sustainable harvest levels). Aerial stratified random block (SRB) surveys used by provincial wildlife managers in BC are typically conducted in early-winter when sightability is optimal. These surveys, however, may not represent the density and spatial distribution of moose during the fall hunting season as encounter rates of moose during surveys are dependent on moose movements and survey timing (Singh et al. 2016). Investigating the prevalence, timing, and causes of moose migration in BC can help improve survey design and may contribute towards a better understanding of moose ecology in the region. This can be particularly relevant in areas where recent declines in some populations have been reported (Kuzyk et al. 2018) or in areas where increasing moose densities have become a management focus as a result of apparent competition with endangered woodland caribou (*Rangifer tarandus caribou*; Serrouya et al. 2017).

For this study, we analyzed location data from 45 female moose collared in and around the John Prince Research Forest (JPRF) in north-central BC as part of a larger provincial study investigating factors influencing moose population declines (Kuzyk and Heard 2014). We analyzed these data specifically to assess if, when, and to what extent collared individuals exhibited different seasonal movement strategies and the role of snow accumulation on migration. Our specific hypothesis was that female moose would demonstrate characteristics of a partially migratory population (i.e., some individuals would migrate while others would not). Furthermore, we predicted that migratory moose would move to lower elevations as snow depth increased, which could lead to differences in migration timing between years due to seasonal variation in the timing and amount of snow accumulation. We also predicted that some moose may switch life-history strategies between years (e.g., resident one year, migratory the next).

Materials and methods

Study area and population

The JPRF is located approximately 50 km north of Fort St. James in north-central BC within the territories of the

Tl'azt'en Nation and Nak'azdli Whut'en Nation (Fig. 1). It is one of five study areas of a larger provincial study of female moose, encompassing a total of 6461 km² including the JPRF (165 km²) and surrounding crown and private land (Kuzyk and Heard 2014). This study area is within the Sub-Boreal Spruce biogeoclimatic zone, which is characterized by a continental climate with cool summers and long cold winters (Meidinger and Pojar 1991). Mean daily average temperatures (1981–2010) were 3.5 °C and ranged from a monthly mean daily average of −9.5 °C in January to 15.4 °C in July. Mean annual precipitation was 487.2 mm, with 172.7 cm of it falling as snow (Environment and Climate Change Canada 2018).

A total of 45 female moose were captured using aerial net-gunning or darting and fitted with GPS collars (Vertex Globalstar Survey Collars, Vectronic Aerospace, Berlin, Germany) between December 2013 and January 2017. Collars were either set to record locations once per day ($n = 18$) or twice per day ($n = 27$). All captures were conducted in accordance with the British Columbia Wildlife Act under permit PG13-92390. A detailed description of the study areas and field methods used can be found in Kuzyk et al. (2018).

Data analysis

Bunnefeld et al. (2011) proposed a novel model-based method for classifying and quantifying different types of animal movement behavior. This method models net squared displacement (NSD), the straight-line distance between a starting location and all subsequent locations, over a specified timeframe and compares the fit of the models to five a priori models using Akaike's information criterion (AIC) (see Bunnefeld et al. (2011) and Spitz et al. (2016)). We applied the adapted NSD models of Spitz et al. (2016) to determine whether our moose were migrants, mix-migrants, residents, or dispersers. We excluded the nomad model as nomadism is most likely to occur in unpredictable broad-scale landscapes (Mueller et al. 2011) and is not known to occur in our study population. We also applied the additional constraint that all migratory moose must travel at least 5 km between their seasonal ranges and occupy their second range for at least 90 days. We did this in order to exclude resident moose that were more wide-ranging but do not have distinct seasonal ranges and therefore may be classified as migratory but are a poor fit for migrant or mix-migrant models. We classified trajectories using the model with the lowest AIC score and considered our top model any model in which the second rated model had a ΔAIC of greater than 2 (i.e., non-equivalent model) (Burnham and Anderson 2002) with the exception of migrant and mix-migrant models, which we analyzed together as migratory.

Modelled movement patterns of migrant moose should follow a double sigmoid model where they start in their winter range and remain relatively sedentary (i.e., NSD close to zero) followed by a rapid increase in NSD as they migrate to their non-winter ranges. Once there, NSD plateaus until it decreases rapidly as animals once again return to their

Fig. 1 Location of the John Prince Research Forest (JPRF) and surrounding study area in north-central British Columbia, Canada, with examples of migratory and resident moose collar locations
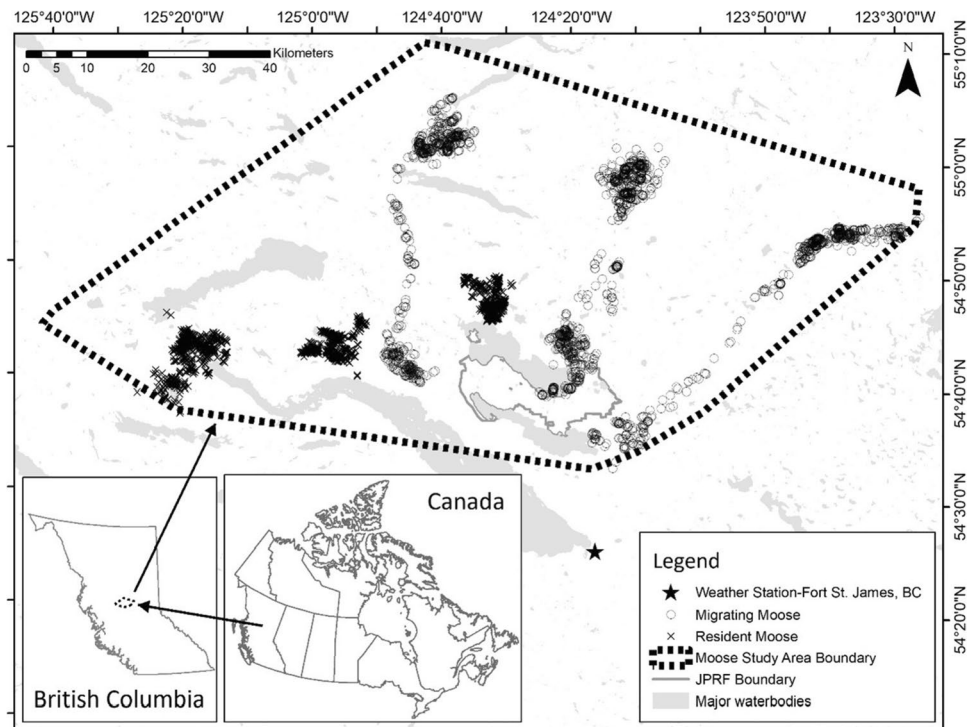
winter ranges. Finally, NSD hits zero when animals have returned to their starting location (Bunnefeld et al. 2011). The mix-migrant model is similar to the migrant model, but the individual does not return to the starting range (Spitz et al. 2016). Patterns of dispersers follow a single sigmoid where NSD increases to a plateau but they do not return to their exact starting range and resident moose have low NSD as they do not move to another range (Bunnefeld et al. 2011).

We used the package "MigrateR" (Spitz et al. 2016) in R version 4.0.3 (R Foundation for Statistical Computing, Vienna, Austria) in order to calculate NSD, compare model fit for each annual trajectory, and calculate model parameters. Spitz et al. (2016) suggest that each trajectory should be less than or equal to a year and include all migratory or other movements (i.e., annual movements begin and end within each annual trajectory). We visually inspected data from our collared moose to see when movements were unlikely to occur and determined that by March of each year most individuals were back in their winter range; we subsequently used March 1–February 28 as our "year." We included all locations from March 1, 2014, to February 28, 2018, in our analysis for a total of four years of study (e.g., March 1, 2014–February 28, 2015 = year 2014). We tested the sensitivity to the starting date by using the "findrlocs" relative net squared displacement (rNSD) tool in MigrateR, which did not lead to a different classification for any trajectories and we therefore used the standard starting date of March 1 for all individuals.

When a collared moose died or a collar failed, it was not included in that years' analysis so those proximal movements would not be included. We defined a collar day as one 24-h period in which a female moose was equipped with a functioning collar. For migratory individuals (migrant and mix-migrant), we defined the starting/first range as the winter range and the second range as the non-winter range. Mix-migrants had a third range, which was the winter range to which they returned at the end of each study year which differed from their starting winter range.

We compared mean monthly elevation of resident and migratory moose for each month by combining elevation data from all years of study and tested for differences using a Wilcoxon rank-sum test (Wilcoxon 1945). To calculate mean monthly snow on the ground for each month of the study, we took the mean of the daily snow on the ground from the federal government weather station in Fort St. James, BC (Environment and Climate Change Canada 2019). We used a linear regression model to assess the relationship between mean monthly snow on the ground and mean monthly elevation for migratory trajectories across all four years of study. We used a one-way analysis of variance (ANOVA; Fisher 1925) to assess whether there were differences in the timing of the start or end date of the spring and winter migration between years.

Results

We received a total of 20,559 locations via satellite from 45 collared female moose over 36,904 collar days during the four years of study resulting in a mean fix-rate of $68\% \pm 0.02\%$ standard error. Using the model-based NSD approach, we classified 67 (74%) annual trajectories as migratory, of which 43 (48%) were migrant and 24 (27%) were mix-migrant (see Fig. 2 for example and Supplementary Information Table 1). We classified 22 annual trajectories (24%) as resident and one (1%) as a disperser. We observed one incident of an individual switching between migrant and resident trajectories between years and one

Fig. 2 Net squared displacement (NSD) models for a migrant GPS-collared cow moose in the John Prince Research Forest, north-central British Columbia, ranked by Δ Akaike information criterion (ΔAIC) and its locations on its winter range (March 1–April 16, 2017) and non-winter range (April 27–November 3, 2017)
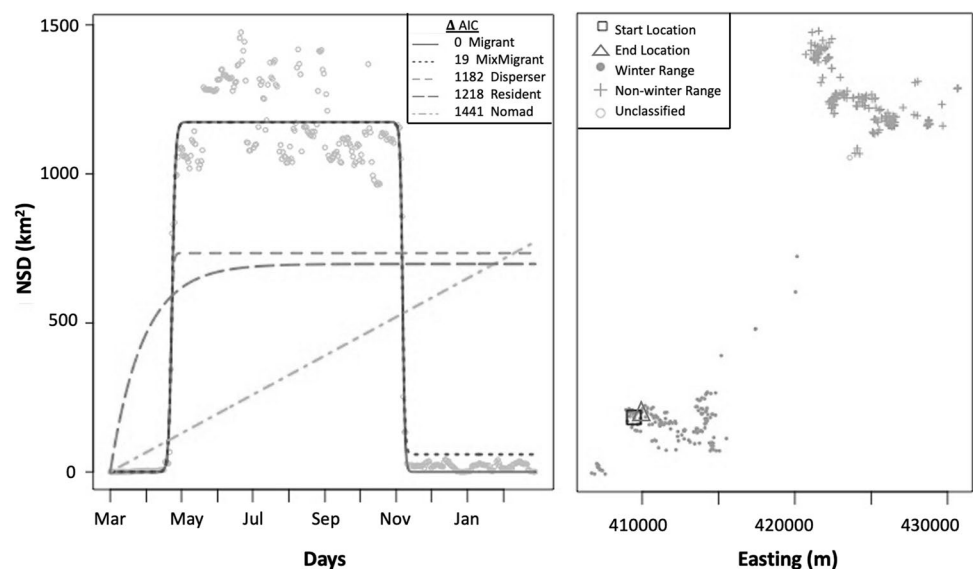
switch between migrant and disperser. The mean distance separating migratory moose WR and NWR ranges (δ) was 32 km (SD = 30 km) but varied greatly from a minimum of 5 km to a maximum of 61 km. The mean NSD of resident moose (γ) was 20.7 km^2.

Elevation and snow accumulation

Migratory moose were at higher monthly median elevations than residents from April to January (Wilcoxon-rank sum: W > 5000, p < 0.01). There was no difference in median monthly elevation for February or March (Wilcoxon-rank sum: W > 5000, p > 0.5). Migratory moose were at their highest mean elevation in August (1021 m) and lowest in February (789 m). The largest drop in mean monthly elevation for migratory trajectories was 88 m and occurred between November and December when they were generally returning to their winter ranges. The greatest gain in mean monthly elevation for migratory moose was 125 m and occurred between April and May when they were leaving their winter ranges.

The annual elevational patterns of moose with migratory trajectories generally corresponded with snow depth (Fig. 3). The mean monthly elevation for migratory moose was negatively correlated with mean monthly snow on the ground ($F_{1,46} = 42.25$, $R^2 = 0.48$, p < 0.001). As snow accumulation increased, migratory moose moved to lower elevations, reaching their lowest mean monthly elevations when snow accumulation was highest and highest mean monthly elevations when there was no snow on the ground.

Migration timing

Moose with migratory trajectories exhibited a consistent pattern of leaving their WR in April and returning from November to February after spending the majority of the year in their NWR (mean ρ = 199 days; Table 1). The minimum number of days a migratory moose spent on its NWR was 100 days. There was no statistically significant difference in the start date ($F_{3,63} = 1.22$, p = 0.311) or end date ($F_{3,63} = 0.86$, p = 0.462) of the spring migration or the start date ($F_{3,63} = 1.31$, p = 0.278) or end date ($F_{3,63} = 1.23$, p = 0.308) of the winter migration between years.

Discussion

The results of our model-based NSD analyses determined that female moose in our study area exhibited four different movement strategies. Female moose exhibited migratory, mixed-migratory, disperser, and resident strategies. The vast majority (98%) of the annual movement trajectories fell into either one of the migratory classes (74%) or were found to be resident (24%). Migratory individuals traveled farther distances and spent most of the year at higher elevations than those classified as resident. In addition, we also observed some switching between movement strategies which demonstrates some level of plasticity. Multiple movement strategies for the same individuals in different years have been seen in other moose populations where physiological and environmental factors may have affected an individual's propensity to migrate (Singh et al. 2012; Rolandsen et al. 2017).

Fig. 3 Mean monthly elevation for GPS-collared female moose with migratory and resident annual trajectories in the John Prince Research Forest, north-central British Columbia, for the 4-year study period (March 1, 2014–February 28, 2018), as well as mean monthly snow on the ground from the Fort St. James weather station (Environment and Climate Change Canada 2019). Error bars for migratory mean monthly elevation represent + 1 standard deviation (SD) and − 1 SD for resident mean resident elevation
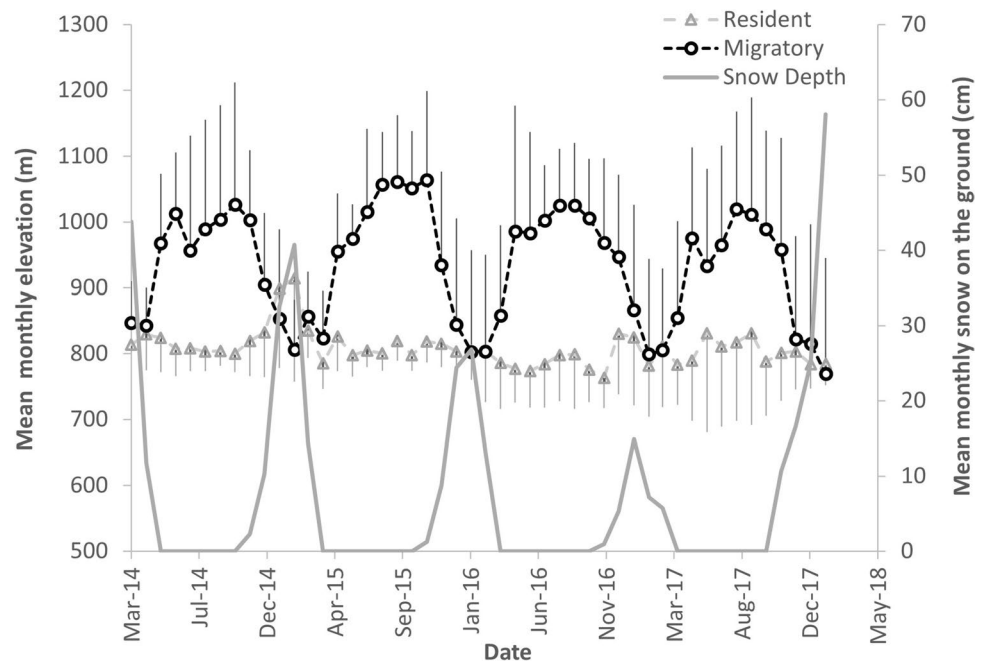
Table 1 Mean migration parameter estimates (with standard deviations (SD) for GPS-collared female moose with migratory trajectories in the John Prince Research Forest, north-central British Columbia, over the 4-year study period (March 1, 2014–February 28, 2018). θ, midpoint of departing movement; $\theta2$, midpoint of returning movement; Φ, time to complete 1/2 to 3/4 of departing movement; $\Phi2$, time to complete 1/2 to 3/4 of returning movement; ρ, duration of occupancy on second (non-winter) range

	2014	SD	2015	SD	2016	SD	2017	SD
Sample size (**n**)	10	-	9	-	25	-	23	-
Spring migration—start	Apr-21	14	Apr-14	20	Apr-08	21	Apr-04	33
Spring migration—end	May-28	38	May-23	29	May-10	24	May-18	41
θ (days)	68	27	64	13	54	16	59	28
$\theta2$ (days)	288	30	295	36	302	41	280	30
Winter migration—start	Nov-11	33	Dec-03	31	Dec-02	43	Nov-17	29
Winter migration—end	Jan-03	19	Jan-07	45	Jan-22	49	Dec-29	47
Φ (days)	6.2	8	6.6	7	5.3	5	6.6	7
$\Phi2$ (days)	7.5	5	5.6	5	6.9	7	5.7	7
ρ (days)	185	43	206	37	213	50	188	54

One trajectory was identified as a disperser but its movements might not have been accurately classified from an ecological perspective. This individual stayed on its NWR until March, much longer than all migratory individuals; it then made a quick long-distance movement away from its WR of the previous year and subsequently died shortly after our timeframe cut-off for that season. A subsequent mortality investigation confirmed that this individual was pursued and killed by predators.

In our study area, migratory distances varied between individuals but moose generally followed the same annual movement patterns with high fidelity to migration corridors between low elevation winter ranges and high elevation summer ranges. In a landscape heavily impacted by industrial forestry, migrators likely encountered movement challenges unknown to resident moose with landscape patchiness and roads affecting the movement choices made by migrating individuals (Borowik et al. 2020). The impacts of industrial forestry activities on moose movements through corridors and seasonal range use in both the short term and long term remain to be studied, but should be addressed soon, especially in the face of recent declines in some populations and with increasing levels of landscape disturbance (Kuzyk et al. 2018).

Moose in many populations have shown seasonal elevation movements (Demarchi 2003; Poole et al. 2007; Lundmark and Ball 2008; Leblond et al. 2010). If snow depth is the proximal driver of migration in this population, climate change may alter seasonal movement patterns by decreasing the time and proportion of precipitation that falls as snow in the interior of BC (Schnorbus et al. 2012; Shrestha et al. 2012). Singh et al. (2012) contended that decreased snow associated with climate change may alter moose migratory behavior. Given this potential climate-associated landscape change, future habitat suitability for some migratory species may expand (Rivrud et al. 2019).

The migratory moose in this study moved to their higher elevation non-winter ranges prior to calving, which is generally recognized as taking place from mid-May to mid-June in this region (Poole et al. 2007; Gillingham and Parker 2008; Kuzyk et al. 2018). Moose calves in our study area are predated by bears and other predators (Rea et al. 2019; Kuzyk et al. 2018), possibly influencing movement by female moose to higher elevations to reduce risk of predation to their calves. Poole et al. (2007) proposed that female moose that do not move to higher elevations for calving may trade off a reduction in predation risk for increased forage quality while selecting habitat features that offer protection at a finer scale. The ultimate causes of migration in this and other populations require more research including investigations into the role of green-up and moose densities.

Migratory ungulates have shown a pattern of highly coordinated spring movements, when accessing vegetation green-up at higher elevation summer ranges (Borowik et al. 2020), and more variable fall/early-winter timing, when returning to lower elevation winter ranges (Mysterud 2013). Moose in our study followed this same pattern with the timing of spring migration more consistent across individuals and years than fall/early-winter. In general, migratory moose returned to their lower elevation winter ranges earlier in years when November and December snow depths were greater, supporting the theory that snow accumulation may be the proximal cause of seasonal movements (Poole and Stuart-Smith 2006; Singh et al. 2012). One limitation of our study was the limited snow data used in our analysis. We obtained snow depths from one station located just outside the study area; although this did not provide fine scale data, we do believe it is reflective of the general trend in snow accumulation that the moose in our study would experience within and between study years.

The prevalence of migration along with annual changes in the timing of migration may affect moose spatial

distributions and influence population assessments that are often conducted during the fall/early-winter migration period. For example, the Fort St. James (FSJ) stratified random block (SRB) survey that includes our study area was last surveyed in 2011 and 2016 (Cadsand et al. 2012; Klaczek et al. 2017). The "2011 FSJ survey" occurred from January 26 to February 3, 2012, and produced a population estimate of 5945 moose (Cadsand et al. 2012). The "2016 FSJ survey" occurred from January 5 to 11, 2017, and estimated 3513 moose, a 40% decline from the 2011 survey (Klaczek et al. 2017). There was a considerable difference between years in total snow accumulation up to the end of January; specifically, 2016 (11 cm) had less snow than 2011 (40 cm). Based on our snow depth findings, we predict earlier migration to winter ranges in 2011 and later in 2016. This is supported by our 2016 collar data where during a winter with low snowpack only 9 of 25 migratory moose had moved into their WR by January 11 (2 days before the end of the aerial survey). The three-week difference between survey dates in 2011 and 2016, snow depth differences between years, and late migration in 2016 may have combined to influence survey results.

Inconsistent survey timing combined with annual variation in migration timing could result in inclusion of migratory moose in population counts in some years and not in others. The implications of this would be hard to estimate but could result in misinterpretation of population trends. These potential misinterpretations could be even more complex when we consider that animal movements could cross multiple management units or administrative jurisdictions (Meisingset et al. 2018). To maintain consistency and accuracy among years, we recommend aerial surveys in our study area be conducted in February, if possible, when the majority of moose have completed their winter migration and are on their WR, or a year-specific correction factor be developed to account for differences in the timing of seasonal movements between years. This issue may not be limited to moose and could be a factor in several other ungulate species in similar systems that exhibit partial migration such as elk (*Cervus canadensis*: Hebblewhite and Merril 2009), white-tailed deer (*Odocoileus virginianus*: Fieberg et al. 2008), and mule deer (*Odocoileus hemionus*: Lendrum et al. 2013).

Although caribou have been mostly extirpated from our study area (Santomauro et al. 2012), moose have become an important management focus where they overlap with populations of at-risk woodland caribou (Serrouya et al. 2017). This is particularly relevant when moose migrate to higher elevation summer caribou habitat (Anderson et al. 2018) and wolves follow them preying on both moose and caribou (Serrouya et al. 2017). Since migration patterns that we detected in our study area are likely to occur in other parts of BC, we recommend further research of moose migratory behaviors in areas where mountain caribou are threatened.

In a recent review of partial migration in ungulates, Berg et al. (2019) asserted the need for more empirical studies to test the mechanisms of this complex phenomenon. Although there appears to be some recognition by biologists, hunters, and First Nations that moose in BC move between seasonal home ranges, there is little understanding of the prevalence, mechanisms, timing, and impacts of these movements on moose population biology. We contend that a better understanding of moose seasonal habitat use patterns may aid moose management and we recommend that future studies seek to elucidate moose migration behaviors by sex, age class, and geographic distribution. Information on seasonal movements of moose can help delineate important seasonal rangelands and migration corridors, help pinpoint range overlaps between species, and help managers interpret population survey data in ways that would not be possible without such information.

Data availability The data associated with this manuscript are part of a larger project in partnership with the Government of British Columbia.

Code availability Not applicable.

Declarations

Ethics approval Research ethics and capture permit were obtained under the British Columbia Wildlife Act (#PG13-92390).

Consent to participate Not applicable.

Consent for publication Not applicable.

Conflicts of interest The authors declare no competing interests.

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