Seasonal habitat use, habitat selection, and migratory behaviours of Stone’s sheep (*Ovis dalli stonei*) in northern British Columbia, Canada

by

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Abstract

Habitats and migration corridors used by wildlife have become increasingly modified by anthropogenic disturbances, and in many cases have resulted in population declines and local extirpations. To conserve ungulate populations, management strategies often focus on identifying and mitigating disturbances in critical habitats and seasonal ranges. The Cassiar Mountains of northern British Columbia, Canada are home to a spatially structured population of Stone's sheep (*Ovis dalli stonei*) composed of small bands (groups) of sheep dispersed throughout the region. The Cassiar Mountains are largely unaltered by human land-use and disturbance, however, more recent increases in recreation and potential resource development expansions might threaten critical habitats and alter seasonal movements of the Cassiar population. My objectives in this study were to identify lambing events, estimate habitat selection during critical lambing and nursery periods, and examine the seasonal space-use and migratory patterns of 18 collared female Stone's sheep to identify areas of high conservation priority. I assessed individual movement patterns and used vaginal implant transmitters to identify lambing events from 2018 to 2020. Females gave birth from May 3rd to June 14th, which was within the expected lambing season of northern mountain sheep. I estimated habitat selection during each female's lambing and nursery periods at two spatial scales; first, at the home range scale, by fitting resource selection functions, and second, at a finer scale constrained by individual movement by modelling integrated step selection functions. I found habitat selection was consistent across scales. During lambing and nursery periods, females selected southwest slopes in rugged, steep terrain at mid elevations, demonstrating selection for landscape features that facilitate predator avoidance. Further, during the nursery period, females exhibited selection for intermediate greenness, and unexpectedly, for habitats near roads, likely due to nursing females accessing nutritionally important mineral licks adjacent to roads in the area. To evaluate the seasonal space-use and migration behaviours of Stone’s sheep, I estimated Brownian bridge movement models to delineate winter and summer ranges, migration corridors, and stopover sites. Next, I classified individual migration strategies based on seasonal geographic and altitudinal movements between summer and winter ranges. Variation in migration strategies did not occur across individuals, but rather across bands, suggesting migratory diversity in the Cassiar population is driven by the distribution of resources and topography within the local landscapes of different bands. Due to two bands crossing a major highway during spring and fall migrations, I recommend installing road signage and speed reductions near these areas to reduce road-strike mortality risk and potential impacts to connectivity. Further, I recommend mitigating disturbances in delineated migration corridors, seasonal ranges, and suitable lambing and nursery habitats to better conserve Stone’s sheep in the Cassiar Mountains.

Preface

This thesis is original work by Grace Enns. Field and wildlife handling was conducted in accordance with the Canadian Council on Animal Care (CCAC) guidelines and approved by the University of Alberta Animal Care and Use Committee (AUP00002992).

To date, no manuscripts have been submitted for publication. A version of Chapter 2 will be submitted for publication in the *Journal of Wildlife Management* and includes B. Jex and M. Boyce as co-authors. For this manuscript, B. Jex organized field work, collected data, and provided input on writing. G. Enns conducted fieldwork, collected data, conducted analyses, and wrote the manuscript. M. Boyce supervised the research, and provided feedback on analyses and writing.

A version of Chapter 3 will be submitted for publication in *Global Ecology and Conservation* with B. Jex and M. Boyce as co-authors. For this manuscript, B. Jex organized field work, and collected data. G. Enns conducted fieldwork, collected data, conducted analyses, and wrote the manuscript. M. Boyce supervised the research, provided feedback on analyses and writing.

Dedication

I dedicate this thesis in memory of my grandma, Gladys Enns. Although she couldn’t be here in person to see me complete this master’s degree, I know she has been with me every step of the way.

I would also like to dedicate this thesis to my mom and my greatest cheerleader, Sue Enns. Without your constant support, love, and encouragement this journey would not have been possible.

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This thesis would not have been possible without the generosity, support, and encouragement from many people. First, I would like to thank the Dease River, Kaska & Tahltan First Nations and Good Hope community for welcoming our team into their traditional territories, and helping make this project a success. This project would not have been possible without the generous funding and in-kind support from many partners, including the Wild Sheep Foundation & Affiliates, Habitat Conservation Trust Foundation, Wild Sheep Society of British Columbia & Affiliates, Safari Club International - Northern Alberta Chapter, the Abbotsford Fish & Game Club, Northwest Guide Outfitter Association, Tahltan Guide Outfitters Association, Natural Sciences and Engineering Research Council, and British Columbia Ministry of Forest, Lands, Natural Resource Operations and Rural Development.

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Chapter 1 - Introduction

Thinhorn sheep (*Ovis dalli*) are found in mountainous landscapes throughout northwestern Canada and Alaska, and are generally associated with open, high-elevation, rugged terrain (Geist 1971, Bunnell 2005, Jex et al. 2016). Stone's sheep (*O. d. stonei*) is a subspecies of thinhorn sheep found almost entirely within northern British Columbia (BC) (Sim et al. 2016). Populations of Stone's sheep often occur in inaccessible and remote mountain ranges with limited human interactions and disturbances. While considerable research has been conducted on bighorn sheep (*O. canadensis*), only a few studies have focused on the ecology of Stone's sheep (Geist 1971, Luckhurst 1973, Seip 1983, Dale R. Seip and Bunnell 1985, Walker et al. 2006, 2007, Hengeveld and Cubberley 2012, Thacker 2020). Despite this limited research, these studies provide a baseline description of habitats, seasonal movements, social behaviours, and health status of Stone's sheep.

One of the first and highly influential studies on Stone's sheep in British Columbia was conducted by Geist (1971) and provided a thorough description on the social behaviours and general habitat use of Stone's sheep, Dall's sheep (*O. d. dalli*), and Rocky Mountain bighorn sheep (*O. c. canadensis*). Following this, Seip (1983) and Seip and Bunnell (1985) provided important insights on Stone's sheep foraging behaviours, diet, and seasonal altitudinal movements in response to plant phenology. Information on the use of mineral licks by Stone's sheep and other ungulates, including elk (*Cervus elaphus*), moose (*Alces alces*), and mountain goats (*Oreamnos americanus*), was addressed in Ayotte (2004) and Ayotte *et al.* (2006, 2008). These studies highlighted the strong influence mineral licks have on the spatial distributions and movement behaviours of mountain ungulates. Walker et al. (2007) provided the first seasonal habitat selection study on Stone's sheep located in the Beta-Prophet watersheds in the Muskwa–Kechika Management Area (MKMA) of northern BC. This study found Stone's sheep exhibited similar habitat selection to other northern mountain sheep populations, and showed strong fidelity to their different seasonal ranges (Walker et al. 2007). And most recently, Thacker (2020) investigated the health of thinhorn sheep throughout western Canada and Alaska, including 3 populations of Stone's sheep in northern British Columbia. Thacker (2020) emphasized the naivety of thinhorn sheep to diseases carried by domestic ruminants (e.g., *Mycoplasma ovipneumoniae*), and provides a baseline for future health monitoring of thinhorn herds.

Although these studies cover a variety of information on Stone's sheep ecology, I identified two knowledge gaps in Stone's sheep research, which are the main focuses of this thesis. First, little is known about the habitat selection of female Stone's sheep during critical life stages, like lambing and nursing periods. And secondly, there is much to learn about the seasonal movement patterns of Stone's sheep, and the locations and characteristics of their seasonal ranges and migration routes.

Our study takes place in the Cassiar Mountains, located in northern interior BC in the traditional territories of the of the Dease River and Kaska First Nations. Good Hope Lake, Cassiar, and Jade City townsites are located within the study area and are located along Highway 37, which is the only highway passing through the Cassiar Mountains, facilitating travel between southern BC and the Yukon. A native Stone's sheep population of approximately 175 sheep resides within the Cassiar Mountains (*B. Jex; pers. comm.*). This population is spatially structured with small bands of Stone's sheep dispersed throughout the mountain ranges. The Cassiar population is suspected to be in decline (*B. Jex; pers. comm.*), but little scientific research has been conducted on the population, and so, this decline has not been confirmed and no cause has been identified.

The Cassiar Mountains experience varying levels of human disturbance, such as highway traffic on Highway 37, localized gold placer-mining, a small-scale jade mine operating on the footprint of the Cassiar Asbestos Mine, an unreclaimed open-pit asbestos mine that closed in 1992, recreational motorized vehicle use (e.g., snowmobile, quad), hiking, camping, and hunter harvest. Despite these disturbances, most of the Cassiar Mountains remains largely intact and unaltered from human land-use and disturbance. Recent increases in recreational activities (e.g., motorized vehicle use and tourism) and potential interest in future resource extraction, might threaten habitats and health of the Cassiar population (Jex et al. 2016).

The Cassiar Stone's Sheep Project was established in 2017, and was a collaborative effort with the Province of British Columbia, Forest, Lands, Natural Resource Operations and Rural Development (FLRORD) wildlife biologists, provincial veterinarians, the Tahltan Guide Outfitters Association, local community and First Nations, the University of Alberta, and

University of Calgary. This project had two overall objectives; to develop baseline data on the health, and seasonal habitat use of the Cassiar Stone's sheep population. In 2020, the health assessment for the Cassiar population was completed by Dr. Caeley Thacker under the supervision of Dr. Doug Whiteside, Dr. Kathreen Ruckstuhl, and Dr. Helen Schwantje (see Thacker 2020 for more information).

The second component of the Cassiar Stone's Sheep Project, and my work in this thesis, is focused on investigating the spatial habit use, habitat selection and movement behaviours of adult female Stone's sheep in the Cassiar Mountains. In Chapter 2, I identified the timing and locations of lambing events of collared female Stone's sheep, and evaluated the habitat selection of critical lambing and nursery habitats. I estimated habitat selection across two spatial scales; broadly, across individual home ranges using resource selection functions (RSF; Manly et al. 2002), and at a finer spatial scale, constrained by individual movements using integrated step selection analyses (iSSA; Avgar et al. 2016). Lastly, I developed predictive maps of relative habitat suitability for lambing and nursery habitats within the Cassiar Mountains.

In Chapter 3, I examined the various geographic and altitudinal migration tactics used by Stone's sheep in the Cassiar Mountains. I also delineated the locations and temporal use of winter and summer ranges, migration corridors, and stopover sites along the migration route. Recent evidence suggests native migration routes and migratory populations are declining and disappearing worldwide, and is most often attributed to anthropogenic influences (Berger 2004, Bolger et al. 2008, Harris et al. 2009). Our study provided a unique opportunity to evaluate migratory behaviours and seasonal habitat use of native mountain ungulates in an environment with limited exposure to disturbance.

The findings from this thesis can assist The Province of British Columbia (BC), local First Nations Governments and regional wildlife biologists in mitigating overlap of human disturbance in areas of high conservation priority. In 2004, the Province of BC and local First Nations Governments developed the Dease-Liard Sustainable Resource Management Plan (SRMP) to sustainably manage the Dease and Liard River watersheds, including the Cassiar Mountains (Govt of British Columbia Ministry of Sustainable Resource Management 2004). Results from this thesis might be important contributions to future iterations of the Dease-Liard SRMP, and other land-planning initiatives in the Cassiar Mountains.

Chapter 2 - Stone's sheep (*Ovis dalli stonei*) lambing and nursery habitat selection

INTRODUCTION

Identifying and protecting habitats used by wildlife during critical life stages is important to the management and conservation of populations. In particular, the habitats used by maternal females during parturition and while rearing young can influence the survival of juvenile ungulates (Moorter et al. 2009, Wiedmann and Bleich 2014, Fryxell et al. 2020). Recruitment of juvenile ungulates is a main driver of ungulate population growth and demographics (Gaillard et al. 2000, Raithel et al. 2007, DeCesare et al. 2012, Gilbert et al. 2020). Predation is the primary cause of juvenile ungulate mortality (Ballard et al. 1981, Linnell et al. 1995) with newborns typically facing the greatest risks of predation during their first few weeks after birth (Gaillard et al. 2000, Raithel et al. 2007, Grovenburg et al. 2011). Hypothermia is another prominent cause of neonate mortality in northern/temperate environments from exposure to harsh environmental conditions like snowfall, rain, wind, and cold temperatures (Wehausen et al. 1987, Linnell et al. 1995, Smith et al. 2014). Because of this, mothers generally select birthing and rearing sites that facilitate predator avoidance and provide suitable microclimates for their newborn (Festa-Bianchet 1988*a*, Bowyer et al. 1998, Van Moorter et al. 2009). Female ungulates often return to these suitable natal ranges in following years (Geist 1971, Etchberger and Krausman 1999, Whiting et al. 2012). In addition, anthropogenic disturbance has been found to influence female habitat selection during parturition and rearing periods (Singh et al. 2010, Dzialak et al. 2011, Kaze et al. 2016), and also can cause declines in newborn survival (Phillips and Alldredge 2000, Wiedmann and Bleich 2014). Delineating the timing and habitat use of parturient females during critical reproductive stages can help wildlife managers and land-use planners prevent temporal and geographic overlap of anthropogenic disturbances in suitable reproductive habitats and known natal areas, and inform future management and conservation strategies (Smith et al. 2015, Severud et al. 2019, Robinson et al. 2020).

During critical lambing and nursery periods, female mountain sheep (*Ovis canadensis* and *O. dalli*) generally select habitats and exhibit behaviours that may help avoid predators to improve their newborn's survival, as well as their own fitness (Bunnell 1982, Festa-Bianchet 1988*a*, Rachlow and Bowyer 1998). Mountain sheep give birth and isolate with their newborn lamb in rugged, steep terrain at high elevations where predation risk to their neonate is lower

(Geist 1971, Bunnell 1982, Festa-Bianchet 1988*a*). At northern latitudes, ungulates typically give birth within constrained periods in the spring coinciding with the onset of the growing season, and that generally avoids harsh climatic conditions (Berger 1979, Bunnell 1980, Thompson and Turner 1982, Festa-Bianchet 1988*b*). During the nursery period, immediately following the lambing period, mothers and young leave lambing habitats and join other females and young in nursery groups (Geist 1971, Karsch et al. 2016). Nursing mothers face high energetic demands in the first months of lactation (Millar 1977). As a result, mothers have been found to favour areas with quality forage and access to mineral licks (Ayotte et al. 2008), while also selecting habitats that provide adequate escape terrain (steep, rugged terrain) to facilitate predator evasion (Rachlow and Bowyer 1994, Bleich et al. 1997, Hamel and Côté 2007).

Understanding the habitat selection behaviours of female ungulates is a key component of identifying critical reproductive habitats. Resource selection functions (RSFs) and step selection analyses (SSA) are powerful tools to evaluate the habitat selection of animals. RSFs have been used by researchers to examine mountain sheep habitat selection (DeCesare and Pletscher 2006, Walker et al. 2007, Bleich et al. 2009), and to predict the suitability of habitats across regions of interest to identify high conservation priority areas (Smith et al. 2015, Poole et al. 2016, Robinson et al. 2020). Generally, RSFs quantify habitat selection by comparing habitat features at locations an animal has visited ('used locations') with habitat features at random locations assumed to be available to an animal ('available locations') (Manly et al. 2002). RSFs can be estimated at many scales, with a common approach following a 3rd-order selection approach (Johnson 1980), where an animal's home range is assumed to be the domain of availability, and available locations are randomly sampled within that domain (Manly et al. 2002). RSFs are an important tool for managing wildlife as they can be used to predict habitat suitability across large spatial extents; however, RSFs are often limited in their ability to evaluate habitat selection at fine scales. Step selection analyses (SSAs) are another type of resource selection analyses that constrain the domain of availability based on an animal's movements (Fortin et al. 2005). In an SSA, an animal's path of movement is split into discrete steps, where a 'used step' is the linear connection between subsequent GPS locations collected at fixed time intervals (Fortin et al. 2005, Thurfjell et al. 2014). SSAs compare habitat variables at used steps with variables at random steps using conditional logistic regression. Random steps begin at the start of each used step and are generated from empirical distributions of an animal's movement parameters: step lengths (the euclidean distance of a step), and turning angles (the angular deviation of successive steps). The domain of availability in a SSA is constrained around an animal's current location at a specific point in time based on the animal's movement patterns. For this reason, SSAs provide an opportunity for investigators to assess the habitat selection of animals within constrained, localized scales that are more realistically available to them (Fortin et al. 2005). Integrated step selection analyses (iSSA) incorporate movement parameters into a SSA to estimate movement in the model in addition to habitat selection (Avgar et al. 2016). Ecological functions carried out by animals often take place over differing temporal and spatial scales (e.g., foraging vs. long-distance migration), thus the resources that influence an animal's habitat selection patterns may vary across spatial extents (Boyce et al. 2006). Estimating habitat selection of animals using both RSFs and iSSAs allows researchers to investigate the mechanisms influencing habitat selection across large and fine scales, respectively.

Stone's sheep (*Ovis dalli stonei*) are one of two subspecies of thinhorn sheep (*O. dalli*) and are found predominantly in northern British Columbia, Canada (Demarchi and Hartwig 2004, Sim et al. 2016, 2019). While there is considerable information on lambing and nursery behaviour and habitat use by bighorn sheep (*O. canadensis;* Geist 1971, Festa-Bianchet 1988*a*, Bangs et al. 2005*a*, Whiting et al. 2012, Smith et al. 2015*a*, Karsch et al. 2016, Robinson et al. 2020) and Dall's sheep (*O.d. dalli*; Rachlow and Bowyer 1991, 1994, Rachlow and Bowyer 1998*b*), less is known about Stone's sheep habitat selection during reproductive periods. Most Stone's sheep populations are found in remote areas with sparse human populations and are exposed to little anthropogenic disturbance relative to many populations of bighorn sheep (Geist 1971, Bunnell 2005, Walker et al. 2006, Jex et al. 2016). However, expanding interests in resource development (e.g., mineral extraction, oil and gas development), recreational activities (e.g., motorized vehicle use and tourism), and potential increases in highway traffic in northern British Columbia, may impact the suitability of reproductive habitats for Stone's sheep, creating a need to identify the locations of suitable lambing and nursery habitats and areas of traditional use (Jex et al. 2016). Identifying potential suitable habitat, and mitigating the effects of anthropogenic disturbances in Stone's sheep habitats used to give birth and rear young, would help ensure these critical habitats remain intact for future generations.

Our first objective was to understand habitat selection during the lambing and nursery periods of female Stone's sheep in the Cassiar Mountains of northern British Columbia using

RSFs and iSSAs. To fulfill this objective, we used GPS relocated data to evaluate the movement behaviours of female Stone's sheep to identify the timing and locations used during lambing and nursery periods. We then estimated habitat selection during lambing and nursery periods at the home range scale using 3rd-order RSFs, and at a finer scale constrained by individual movements using iSSAs. We predicted parturient female Stone's sheep would select lambing habitats in escape terrain at high elevations to minimize predation risk, on warmer, southwest-facing slopes to access areas free from snow, and at far distances from roads to minimize exposure to anthropogenic disturbances. Next, we predicted mothers would select nursery habitats near escape terrain to reduce predation risk, and far from roads to avoid disturbance. We also predicted they would select habitats with high-quality foraging opportunities to meet the high energetic demands of lactation.

Our second objective was to develop predictive maps of suitable lambing and nursery habitats for Stone's sheep in the Cassiar Mountains using our top performing RSFs for lambing and nursery periods, to identify areas of high conservation priority. Predicting the locations of lambing and nursery habitats could provide regional wildlife managers and land-use planners with valuable insight into critical Stone's sheep range, and may be an important contribution to the Dease-Liard Sustainable Resource Management Plan established in 2004 by local First Nations Governments and the Province of British Columbia to sustainably manage resources and the land occurring in the Dease and Liard River watersheds (Govt of British Columbia Ministry of Sustainable Resource Management 2004), which includes the Cassiar Mountains.

Our last objective was to identify consistencies or differences in habitat selection patterns exhibited by maternal Stone's sheep across large and fine scales based on the estimates of our top performing RSFs and iSSAs. If females exhibit consistent patterns of habitat selection across all scales, our predictive maps will delineate habitats that are likely suitable for females at both home range and fine scales. In contrast, if females exhibit habitat selection patterns that differ greatly across scales, this may suggest that habitats suitable for females identified at the home range scale may differ from suitable habitats at fine scales, during lambing and nursery periods.

METHODS

Study area

Characterized by wide valleys and high mountain peaks, the Cassiar Mountains encompass approximately 4301 km^2 of interior northwestern British Columbia (Pojar & McKinnon 2013). The Cassiar Mountains are located within the territories of the Dease River, Kaska and Tahltan First Nations; and in the vicinity of Cassiar, Jade City, and Good Hope Lake town sites. Our study was concentrated in the north-central portion of the Cassiar Mountains across an area of 2090 km^2 within the Dease River First Nation Territory (Figure 2.1) managed as Crown land under the Dease-Liard Sustainable Resource Management Plan that was established in 2004 by local First Nations Governments and The Province of British Columbia (Govt of British Columbia Ministry of Sustainable Resource Management 2004).

The Cassiar Mountains support a diverse and intact predator-prey system, including ungulate populations of Stone's sheep, mountain goats (*Oreamnos americanus*), moose (*Alces alces*), caribou (*Rangifer tarandus*), and occasionally mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*). Predators to these ungulate populations include grizzly bears (*Ursus arctos*), black bears (*U. americanus*), wolves (*Canis lupus*), coyotes (*C. latrans*), golden eagles (*Aquila chrysaetos*), Canada lynx (*Lynx canadensis*) and wolverines (*Gulo gulo*).

Despite human impacts, the Cassiar Mountains have remained largely unmodified due to the region's limited access and small resident populations, but interest in recreation and resource development in the area is rising. Current human impacts in the Cassiar Mountains includes small-scale jade mining operations in the Troutline Creek valley and portions of the previous Cassiar Asbestos Mine footprint; widespread mineral exploration and active gold placer-mining sites; vehicle traffic along Highway 37 (paved highway facilitating travel between British Columbia and the Yukon Territory); motorized vehicle use (e.g., snowmobile, all-terrain vehicle); hiking; front-country and backcountry camping; helicopter activity; and resident and non-resident hunter harvest of Stone's sheep (Jex et al. 2016).

The inter-montane climate of the Cassiar Mountains is harsh with long, cold winters and short, cool summers. The mean annual temperature in the subalpine zone ranges between -0.7 to -0.3°C, with only one month of the year reaching mean temperatures above 10°C. Mean annual precipitation ranged between 460-700mm with snowfall accounting for 35-60% of precipitation (Geist 1971, Meidinger and Pojar 1991).

The Cassiar Mountains occur in the Boreal Cordillera ecozone with three distinct ecosystems, and elevations ranging from 650 to 2280m above sea level. The montane ecosystem occurs at the lowest elevations (650-900m), containing a mixture of white spruce (*Picea mariana),* black spruce (*P. glauca*), Engelmann spruce (*P. englemannii*), lodgepole pine (*Pinus contorta*), willow (*Salix* spp.), dwarf birch (*Betula glandulosa)*, and trembling aspen (*Populus tremuloides*). The subalpine ecosystem occurs above the montane ecosystem (900-1500m), dominated by white spruce, willow, stunted dwarf birch, and subalpine fir (*Abies lasiocarpa*). Lastly, the alpine ecosystem occurs above treeline (>1500m) characterized by rocky terrain and sparse vegetation consisting of grasses, sedges, alpine-flowering plants, herbs, bryophytes, lichens, and few subalpine fir in stunted form (Meidinger and Pojar 1991).

Data collection

In the winters of 2018 and 2019, we captured 19 female Stone's sheep by helicopter net gun and fitted them with Iridium GPS collars (model G2110E2, Advanced Telemetry Systems (ATS), Isanti, MN, USA). We programmed the collars to collect individual locations at 2h (2018) or 1h (2019) intervals over a span of 30 months or until an individual died. We estimated the age of captured individuals based on their horn annuli. Next, we assessed for pregnancy using a portable ultrasound (model Ibex Pro, E.I. Medical Imaging, Loveland, Colorado, USA), and pregnant females (*n* =17) were fitted with a vaginal implant transmitter (VIT) (*Neolink*, ATS). Capture and animal handling procedures were in accordance with BC Ministry of Forests, Lands, and Natural Resource Operations protocols, and approved by the Animal Care and Use Committee at the University of Alberta (no. AUP00002992). To ensure we did not include 'capture effects' and erroneous GPS locations, we removed GPS locations collected 0-96 hours after captures, and collected with ≤ 2 satellites (251 locations) (D'Eon and Delparte 2005, Lewis et al. 2007, Frair et al. 2010).

Estimating the lambing and nursery periods

To estimate the lambing and nursery periods we first estimated parturition dates, and then assessed the consistency of our estimates with corresponding VIT expulsions and photos captured by trail cameras. We used parturition dates to define lambing and nursery periods of individual female-years to be incorporated into our habitat selection analyses (RSFs and iSSAs).

GPS relocation data used to estimate lambing and nursery periods were collected from 36 female-years during the spring and summers of 2018 – 2020.

Estimating parturition dates. – During parturition, female ungulates generally exhibit an abrupt and sustained decline in movement rates while giving birth, nursing, and isolating at their parturition site (Long et al. 2009, Brook 2010). This common movement pattern exhibited by parturient females can be used to identify probable parturition events in ungulates. Thinhorn sheep generally give birth between early-May to late-June (Bunnell 1982, Thompson and Turner 1982, Rachlow and Bowyer 1991). Parturient females travel away from the herd to a lambing site before giving birth, and then remain at or near the lambing site for days to weeks after parturition (Geist 1971, Rubin et al. 2020). While parturient mountain sheep give birth and isolate at their lambing site, their movement rates decline abruptly over a sustained period of days, estimated between 1 - 7 days in length (Geist 1971, Shackleton and Haywood 1985). Abrupt and sustained declines in movement rates also are indicative of parturition events in other ungulates and have been used by researchers to identify parturition (Ferguson and Elkie 2004, Long et al. 2009, Peterson et al. 2018). Based on this, we identified potential lambing events for each female-year by identifying abrupt and sustained changes in individual movement rates during the lambing season.

We identified a lambing event had occurred if a female's movement rate abruptly declined and remained <50% of her mean movement rate during the lambing season (May 1 – June 30) for ≥36 hours. Female-years that did not exhibit a decline in movement rates <50% of their lambing season movement rate for ≥36 hours were identified as barren that year. In the few situations where a female-year exhibited two probable lambing events, we identified the period with the lowest median movement rate as the lambing event. If the median movement rates of both probable lambing events differed by 10m/hr or less, we chose the period with the greatest number of days with movement rates <50% of the mean lambing season movement rate. After we identified lambing events, we used the time stamp from the first rounded hour of the lambing event to identify the parturition date. Some collared females had parturition dates within multiple study years, and we treated these females during each year as independent female-years.

Defining lambing and nursery periods. – We defined the lambing period as the time a female occupies lambing habitat. The lambing period began on a female's estimated parturition date and ended when she exhibited an abrupt movement away from the lambing habitat that was >500m and did not return. To estimate the lambing period, we first calculated net displacement (m) from the estimated birth site for each female-year (Figure 2.2). The birth site was determined from the location used during a female-year's estimated lambing date. Next, we fit a piece-wise linear regression to each female-years' net displacement (Walker et al. 2020) to identify when a female exhibited an abrupt increase in distance travelled away from the lambing site without returning (Figure 2.3). We fit a piecewise regression to the net displacement of each female-year beginning from the estimated time of birth until 24 hours after the female reached a net displacement of 1000m. This allowed us to identify lambing periods with various durations (e.g., 2-day vs. 11-day lambing period).

We validated lambing period estimates using known VIT expulsion dates and photos from trail cameras placed on high traffic sheep trails when available for a female-year. We considered that parturition dates and lambing periods were validated if a VIT expulsion occurred within the duration of a female-year's estimated lambing period. We were unable to validate lambing periods during non-capture years because we did not re-capture collared females in subsequent years to equip them with an additional VIT. In addition to using VITs to validate our lambing period estimates, we used trail cameras to visually confirm the presence of lambs-at-heel with collared females. We deployed 10 trail cameras on sheep trails in the subalpine and alpine from late June 2019 to July 2020 to capture photos of collared females and young. We identified collared females captured on trail camera photos based on ear tags and individual markings, and then documented the presence or absence of a lamb-at-heel with each collared female to provide further support for our estimates of parturition dates and lambing periods (Figure 2.4).

Next, we defined the nursery period as the 30-day duration immediately following the lambing period. We chose a 30-day duration following the lambing period to represent the nursery period, because it encompasses the early and middle phases of lactation, when nursing females experience the highest energetic demands from lactation (Berger 1979, Bunnell 1982, Festa-Bianchet 1988*b*), that is likely to influence their habitat selection during this time. We were unable to confirm the survival of young throughout the lambing and nursery periods, and as a result, we assumed all female-years with an estimated birthdate had a newborn lamb-at-heel throughout the entire lambing and nursery periods with subsequent validation from trail camera photos.

Landscape variables

We assembled a suite of landscape variables that we expected to influence Stone's sheep habitat selection, particularly during the lambing and nursery periods. Topographic variables were calculated from the Canadian Digital Elevation Model (CDEM) with 20m spatial resolution from Natural Resources Canada, and included elevation (m), slope (°), northness and eastness, and terrain ruggedness. We calculated northness and eastness as the cosine and sine of aspect in radians, respectively, which represent aspect on a continuous scale from -1 to 1 with values closer to 1 representing more northern or eastern aspects (Roberts 1986, Domaç and Süzen 2006). We calculated vector ruggedness measures (VRM; Sappington et al. 2007) from the CDEM to represent terrain ruggedness.

We included an exponential decay function of distance to roads as a predictor covariate in our habitat selection analyses to account for highway and road disturbance throughout the study area. We acquired a Digital Road Atlas from the British Columbia Ministry of Forests, Lands, Natural Resource Operations and Rural Development and combined the 8 classes of roads depicted in the study site, which included resource, highway, recreation, service, restricted, arterial, local and trail roads. We calculated the Euclidean distance from roads (m) from each 20m pixel, and then, following Nielsen et al. (2009), transformed distance to roads (*d*) into exponential decays in the form of e^{-ad} where α was set to 0.002, and took the inverse of these values. We used the inverse of a decay function of Euclidean distance to roads rather than the Euclidean distance to roads to ensure the effect of roads would be represented in habitats near roads, and road effects would decline precipitously at farther distances from roads (>600m from roads = minimal road effects). All topographic and road layers were created using the 'SpatialEco' and 'raster' packages in R v. 4.0.3 (Evans 2019, Robert J. Hijmans 2019, R Core Team 2020) and the Euclidean distance toolset in ArcGIS 10.7 (ESRI 2019).

We used normalized difference vegetation index (NDVI) as a predictor covariate to represent vegetative greenness. NDVI is a standardized measure of vegetative greenness, calculated from the near-infrared and visible wavelengths reflected by vegetation (Tucker and Sellers 1986, Pettorelli et al. 2005). NDVI values were formatted on a 0 to 1 scale, and in our study low values (<0.3) generally indicating barren areas with sparse vegetation, and rocky terrain; moderate values (0.3-0.6) corresponding with grass and shrublands; and high values (>0.7) representing areas with high greenness, such as dense shrub cover and forest cover. We used NDVI in two ways in our home range and fine-scale habitat selection analyses. First, we developed annual maximum NDVI layers ($NDVI_{max}$) for each study year (2018-2020) from Moderate Resolution Imaging Spectroradiometer (MODIS) satellite imagery (MOD10A1) collected in 16-day increments at from April to September (months when minimum snow fraction is reduced) at 250m spatial resolution. We used $NDVI_{max}$ as a predictor covariate in our iSSAs. Next, we calculated a maximum NDVI layer for the entire study period ($NDVI_{total\_max}$) by calculating the mean NDVI value at each pixel from the 2018-2020 $NDVI_{max}$ layers. We used this $NDVI_{total\_max}$ layer as a covariate in our home range RSFs, rather than the $NDVI_{max}$ layers from each year, so we could develop a predictive map of suitable habitats over the entire study period, rather than annually, to be more applicable for management and planning.

Habitat-selection analyses

We evaluated habitat selection during the lambing and nursery periods at the home range scale using 3rd-order RSFs (Johnson 1980), and at a finer scale using iSSAs (Avgar et al. 2016), respectively.

Home range habitat modelling. – We estimated habitat selection at the home-range scale based on a use/available design using mixed-effect RSFs fitted with logistic regression:

$$w(\mathbf{x}) = \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots.. + \beta_n x_n)$$

where w is the relative probability of selection and β_i are the selection coefficients for a vector, $\mathbf{x}$, of predictor covariates x_i (Manly et al. 2002, Johnson et al. 2006). We used female-year as a random effect in all candidate models to address individual-based differences in selection that could not be identified otherwise (Gillies et al. 2006).

We estimated population-level RSFs across all study periods, by comparing habitat variables of used and available resource units (spatial pixels) within the home range of each female-year. We identified ‘used’ resource units as the GPS locations collected from female-years. We defined the domain of availability (home range) as the area within a 95% kernel density estimate (KDE) calculated from each female-year’s GPS locations during the spring and summer seasons combined (May 1 – Aug 31). We randomly selected 10 'available' locations within an individual's domain of availability for every used location. Next, we extracted all habitat variables at used and available locations, and then centered and standardized each variable. We screened predictor covariates for collinearity using a Pearson correlation test. There were no strong correlations between variables ($| r | > 0.7$), thus, all variables were included in model selection. We developed 17 candidate models, which incorporated variables that we had hypothesized are biologically relevant and influential to habitat selection by maternal females during these reproductive periods (Appendix 2.1). Before modelling the RSFs, we determined whether habitat selection was best estimated using elevation, slope, and $\mathrm{NDVI}_{\mathrm{max\_total}}$ as linear or squared terms to account for the selection of intermediate variables. We determined habitat selection at the home range scale was best explained using a linear term of $\mathrm{NDVI}_{\mathrm{max\_total}}$, and squared terms of elevation and slope. Because elevation and slope influence female mountain sheep habitat selection during lambing and nursery periods (Bangs et al. 2005*a*, Smith et al. 2015, Karsch et al. 2016, Robinson et al. 2020), we designed a base model that included elevation and slope to be included as covariates in the other candidate models. Next, we designed 15 candidate models from the base model, including a global model, that incorporated additional covariates we hypothesized would influence maternal habitat selection including ruggedness, northness, eastness, NDVI, and an exponential decay function of Euclidean distance to roads (Appendix 2.1).

We estimated the candidate model set using logistic regression in the lme4 package (Bates D, Mächler M, Bolker B 2015) in R v. 4.0.3 (R Core Team 2020). We conducted model selection with Akaike's Information Criterion corrected for small sample size (AICc), calculated AICc scores and Akaike weights (Akaike 1974) for each candidate model, and the best predictive models were identified with the lowest AICc scores and highest Akaike weights. We considered top models to be competitive if their AICc scores differed by less than two ($\Delta\mathrm{AICc} < 2.0$) (Burnham and Anderson 2002), and we identified the top model as the competing model with greatest parsimony. We validated the top lambing and nursery models using five-fold cross validation and Spearman's rank correlation ($\bar{r}_s$) to assess each model's predictive ability (Boyce et al. 2002).

From the top lambing and nursery models, we identified relative selection or avoidance of landscape variables based on the sign (+/-) of the parameter estimates (β_i), and significant selection or avoidance was identified when the 95% confidence intervals of a parameter estimate did not overlap zero. Lastly, we evaluated the habitat selection exhibited by individual female-years in the top lambing and nursery models in Appendix 2.6, but do not present the findings here as most female-years exhibited consistent patterns to the top population-level models.

Fine-scale habitat modelling. – We evaluated fine-scale habitat selection during lambing and nursery periods by estimating population-level iSSAs from used steps and random steps for each female-year. We identified 'used' steps from the observed GPS locations collected from each female-year during the lambing and nursery periods separately. We removed used steps from the analysis if they lacked a preceding step. Next, we generated 10 random steps for every used step originating at the same start point of each used step. Random steps were generated by randomly sampling from a gamma distribution of an individual's observed step lengths, and a Von Mises distribution of observed turning angles (Fortin et al. 2005, Avgar et al. 2016). Step lengths are the Euclidean distance of a step, and turning angles are the difference in headings of successive steps. The domain of availability in an iSSA, the spatial domain where random steps are generated, is constrained based on individual's movement parameters and changes with each used step that an animal takes.

We extracted covariates from the endpoints of all used and random steps to estimate the habitat selection of female Stone's sheep, rather than estimating their movement. We used the 'amt' package (Signer et al. 2019) in R v. 4.0.3 (R Core Team 2020) to extract covariates to the used and random steps, which included elevation, slope, ruggedness, northness, eastness, and an exponential decay function of distance to roads. We also extracted the annual maximum NDVI ($NDVI_{max}$) from 2018, 2019, or 2020 that corresponded with the timestamp of each step. We centered and standardized all covariates, so the mean was set to 0 and the standard deviation to 1. We assessed covariates for collinearity using a Pearson correlation test, and because there were no significant correlations between covariates ($| r | > 0.7$), we included all covariates into the models.

Next, we developed a global iSSA model that was fit to the population using conditional logistic regression. We developed one global model, rather than developing candidate model sets, because a global model allowed us to identify patterns of selection exhibited by females in response to each covariate, which we then could contrast with the habitat selection patterns exhibited by females in the home range scale RSFs. We included all predictor covariates into the global iSSA that we hypothesized were influential and biologically relevant to females during these periods. Unlike the RSFs estimated for the lambing period, we did not include the exponential decay function of distance to roads into the lambing iSSA, because no females had roads near their used or random steps during this time. Before modelling, we investigated using elevation, slope, and $NDVI_{max}$ as linear or squared terms, to allow for the selection or avoidance of intermediate values. We determined iSSA was best estimated with slope as a linear term, and squared terms for elevation and $NDVI_{max}$. For iSSA we included step length as the movement covariate included into the global models.

Each global model used female-years as a random effect to address individual variation in habitat selection, like in our home range habitat selection models (Gillies et al. 2006). We used conditional logistic regression to estimate the global models using the 'lme4' package (Bates D, Mächler M, Bolker B 2015) in R v. 4.0.3 (R Core Team 2020). We identified population-level selection of each covariate based on the sign (+/-) of the parameter estimates (β_i) from the lambing and nursery period global models, and defined significant selection or avoidance if the 95% confidence intervals of a parameter estimate did not overlap zero.

RESULTS

Data collection

We collared 18 adult female Stone's sheep in the winters of 2018 and 2019. Collared females were monitored over a mean of 260 days (range: 30, 880) at 1h (2019) or 2h (2018) fixes, resulting in 169,591 locations. Locations collected over the three-year study covered 2090 km^2. The mean age of collared females was 5.4 years (range: 4 - 8 years) at time of capture (Appendix 2.4). We determined 17 captured females were pregnant (94%) during captures, and equipped them with a VIT. We could not incorporate the expulsion data from 5 VITs because the female had died before giving birth ($n = 2$) or the VIT was prematurely expelled before April 15th of the capture year ($n = 3$).

We retrieved 1,665 GPS relocations from 23 female-year lambing period. The mean number of GPS relocations per female-year during the lambing and nursery period was 60 (range: 12-130) and 656 (range: 335-712), respectively. These GPS relocations were incorporated into our habitat selection analyses.

Estimating the lambing and nursery periods

We identified 23 parturition events out of a possible 32 during the lambing seasons of 2018 (*n* = 4), 2019 (*n* = 13), and 2020 (*n* = 6) based on female movement, resulting in a mean parturition rate of 0.72 across years (Table 2.1). The mean and median parturition date pooled across years was May 22nd and May 14th, respectively (range: May 3 – June 14; Table 2.1). All parturition dates occurred within the expected lambing season of thinhorn sheep (May 1 – June 15th), however parturition dates were more synchronous in 2019 (see Appendix 2.2 for more information on timing and synchronicity of parturition dates across study years).

Females remained in lambing habitat for a mean of 5.2 days, ranging from 1.5 to 11.3 days (Table 2.1). During the lambing period, females exhibited low movement rates with a mean movement rate of 38 m/hr (range: 0-1607.7m/hr). The mean movement rate during the nursery period was 176 m/hr (range: 0-2934 m/hr), which was substantially larger than lambing period movement rates.

Our parturition date estimates were consistent with VIT expulsion dates and trail camera photos. We found 13/23 estimated female-years estimated to have given birth had a corresponding VIT expulsion (Appendix 2.4), and all VIT expulsion dates occurred within the estimated lambing events. Most female-years expelled VITs within 24h of the first hour timestamp of their lambing period (*n* = 10; 76.9%), however some female-years (*n* = 3; 21%) arrived at their lambing site earlier and expelled their VIT after 24h of the first timestamp of their lambing period ranging from 29h to 96h after. Although these three parturition date estimates exceed the 24h threshold we set for validation, we believe our estimations of the lambing period are an accurate representation of the duration females use lambing habitat, whether prior, during, or after a birth has occurred. Because all VIT expulsions occurred within our estimated lambing periods, we concluded that this approach was successful at estimating lambing periods based on evaluating changes in female Stone's sheep movement patterns. We were unable to assess the consistency of VIT expulsion dates for the remaining 11/23 female-years that lacked corresponding VIT expulsion data.

Trail camera photos of collared females on sheep trails in 2019 and 2020 captured ≥1 photo of 12 collared female-years estimated to have given birth that year. From these photos, we confirmed the presence of a lamb-at-heel with all 12 collared females, thus providing evidence that 12/23 females had given birth as predicted, and their lambs had survived until the date the photo was taken. Figure 2.4 provides an example of trail camera photos that confirm the presence of a lamb-at-heel with a collared female.

Habitat-selection analyses

Home range habitat modelling. – Habitat selection by female Stone's sheep was influenced by elevation, slope, NDVI, northness, eastness, ruggedness, and exponential decay function of distance to roads. The top competing model during the lambing period was Model 3 (Model 3, Table 2.3), which outcompeted the next-ranked model (Global, Table 2.3) as the most parsimonious model albeit lacking the NDVI term. The top model estimating habitat selection during the nursery period was the Global model (Global, Table 2.3) with a difference in AICc > 821 indicating it was the most competitive model out of the candidate model sets. Model results for all 17 candidate resource selection models and null models for lambing and nursery periods can be found in Appendix 2.3. Top models for the lambing and nursery periods had excellent predictability with $\bar{r}_s = 0.967$ ($n = 5$, $P < 0.0001$) and $\bar{r}_s = 0.857$ ($n = 5$, $P < 0.01$), respectively (Appendix 2.5).

As we predicted during the lambing period, Stone's sheep females strongly selected intermediate (mid) elevations relative to available elevations indicated with a positive elevation term, and negative squared elevation term that did not overlap zero (Table 2.4). The mean elevation selected was 1635m located in the alpine. We also found females significantly selected habitats with steep slopes and rugged terrain on southwest aspects, and exhibited strong avoidance of habitats near roads (Table 2.4 and Figure 2.5).

During the nursery period, females exhibited similar habitat selection patterns with strong selection for intermediate elevations, steep slopes, rugged terrain, and southwest aspects (Table 2.4 and Figure 2.6). We found an elevation of 1674m to be the most strongly selected elevation by nursing mothers based on our estimate of relative selection strength, which is almost equal to the optimal elevation selected by females during the lambing period. Unexpectedly, we found that females with roads located close to their available locations (< 200m; $n = 11$), exhibited significant selection for habitats near roads during the nursery period, unlike the avoidance of roads exhibited during the lambing period. We also found nursing females selected for habitats with low NDVI values relative to available areas (Table 2.4 and Figure 2.6). Lastly, we used the top models from the lambing and nursery periods to develop predicted relative habitat suitability maps for parturient Stone's sheep in the Cassiar Mountains during the lambing and nursery periods as demonstrated in Figures 2.7 and 2.8.

During most female-years, ewes exhibited the same habitat selection patterns as the population-level models during the lambing and nursery periods. Because there was little variation in habitat selection among female-years, we only present the population-level models for each reproductive period. Additional information on habitat selection at the home range scale by female-year is provided in Appendix 2.6.

Fine-scale habitat modelling. – As we expected, shorter step lengths over 2h fix rates were moved during the lambing period, with the mean step length of 78m (range: 0 – 3211m). The mean step length during the nursery period was 351m (range: 0 - 5869m).

During the lambing period, the iSSA habitat selection was significantly influenced by slope, ruggedness, and aspect (Table 2.5 and Figure 2.6). Like the 3rd-order RSF, females did not significantly select or avoid NDVI during the lambing period. Unlike the 3rd-order RSFs, we did not observe a significant selection or avoidance of elevation by females in the iSSA.

During the nursery period, all covariates incorporated into our global step selection model significantly influenced female habitat selection (Table 2.5 and Figure 2.6). Like the 3rd-order RSF, nursing mothers significantly selected for intermediate elevations, steep slopes, rugged terrain, and southwest-facing aspects. Nursing mothers also exhibited significant selection for intermediate NDVI, unlike the home range RSF that identified females selected low NDVI. Surprisingly, nursing mothers that had used and available steps located near a road (< 200m; *n* = 11), exhibited significant selection for habitats near roads, as also demonstrated in the 3rd-order RSF estimates.

Individual females generally exhibited similar fine-scale habitat selection patterns to the population level habitat selection patterns during the lambing and nursery periods. Because the population-level step selection models represent the overall trends in habitat selection by most female years, we only presented the top population-level step selection models for each reproductive period.

DISCUSSION

With this study, we provide the first evaluation of resource selection by maternal Stone's sheep during critical lambing and nursery life stages within individual home ranges, and at a finer scale constrained by individual movement. We identified the characteristics of suitable habitats used by female Stone's sheep when giving birth and rearing young in the Cassiar Mountains, to identify areas with high conservation priority. Maternal sheep were influenced by topography, vegetative productivity, and distance to roads during these critical reproductive life stages. Our study also offers new insight into habitat selection patterns across home range and at fine spatial scales. Female Stone's sheep exhibited similar habitat selection across spatial scales, providing support for the use of 3rd-order RSFs to estimate habitat selection and to identify the characteristics and locations of suitable habitats for important lambing and nursery stages.

Timing of lambing events

We identified the parturition dates of Stone's sheep based on abrupt and sustained declines in individual movement rates during the lambing season. Assuming annual reproduction, we identified 23 lambing events out of a possible 32 during the 2018-2020 lambing seasons. The median parturition date was May 14th, and ranged from May 4th to June 14th. These parturition dates are similar to parturition documented for other thinhorn and bighorn populations at northern latitudes, which typically occur between May 1 to June 15th (Bunnell 1980, Thompson and Turner 1982, Festa-Bianchet 1988*c*, Rachlow and Bowyer 1991, Grigg et al. 2017). As we expected, all females exhibited lower movement rates and remained in close spatial clusters during the lambing period, likely to recover physiologically, nurse and bond with their newborn lamb, and likely to reduce predator detection of neonates (Geist 1971, Shackleton and Haywood 1985, Bleich et al. 1997). We found females varied from 1.5 to 11.3 days spent in lambing habitats after giving birth, which differs from other studies that identify females remaining with their newborn in lambing habitat for only 1-2 days (Shackleton and Haywood 1985) or 5-7 days after birth (Geist 1971). Factors that influence the length of the lambing period among individuals are unknown, but it seems logical that this would be linked to a combination of predator avoidance, female and lamb body conditions, and forage availability. We provide additional information on the timing, synchronicity, and duration of lambing events exhibited by females across study years in Appendix 2.2.

Lambing period

As expected, females selected habitats with steep slopes and rugged terrain to give birth and isolate with their young during the lambing period, at both the home range and fine scales. Our results suggest maternal females in the Cassiar Mountains select habitat and terrain features that offer better protection from predation for themselves and their young. These findings corroborate studies that identified slope and ruggedness as essential features of escape terrain used by mountain sheep to evade predators (Geist 1971, Bleich et al. 1997), especially in the first days postpartum when lambs are less mobile and most vulnerable to predation (Krausman and Leopold 1986, Hass 1989, Berger 1991). Previous work on lamb mortality by Berger (1991) documented predation on bighorn lambs occurred more frequently in open or flat terrain (71%), rather than in rugged or steep terrain (22%), suggesting females that give birth and isolate with their young in rugged, steep habitats may improve their newborn's survival. In addition to providing escape routes for females and young, escape terrain may also provide additional concealment cover used as hiding cover for newborns to further reduce predator detection (Bangs et al. 2005*b*, Karsch et al. 2016). The main predators of thinhorn sheep young are golden eagles, wolves, grizzly bears, black bears, wolverine, Canadian lynx and cougars (*Puma concolor*) (Geist 1971, Nette et al. 1984, Bunnell 2005, Koizumi and Derocher 2019). Grizzly bears and wolves are less agile in precipitous, rugged terrain compared to mountain sheep. Because of this, female Stone's sheep favour rugged, steep terrain possibly to reduce detections by grizzly bears and wolves, and to be able to escape if they approach. We did not have the data to incorporate predator densities and predation risk from the study site into our habitat selection analyses. However, Walker et al. (2007) found grizzly bear and wolf predation risk influenced habitat selection by female Stone's sheep in the Muskwa–Kechika Management Area (MKMA) in northern British Columbia during the lambing season (May 15 - June 14). The Cassiar and MKMA are in close geographic proximity and occur across similar latitudes, and because maternal Stone's sheep in the Cassiar Mountains show strong selection for giving birth and isolating with their young in precipitous terrain, we suspect parturient Stone's sheep in the Cassiar Mountains are also influenced by predation risk that includes grizzly bears and wolves. Future evaluations of grizzly and black bear, wolf, golden eagle, and wolverine predation on newborn lambs in the Cassiar Mountains might improve our understanding of lambing habitat selection, and Stone's sheep lamb recruitment.

At the home range scale, we found maternal Stone's sheep selected lambing habitats at intermediate elevations, with the average elevation used during lambing events was 1635 m. Similar to our findings, maternal desert bighorns in the Peloncillo Mountains in New Mexico (Karsch et al. 2016), and female Stone's sheep in the MKMA (Walker et al. 2007), selected lambing habitats at intermediate elevations within their home range. We suggest females in the Cassiar Mountains might select lambing sites at intermediate elevations to reduce the risk of being detected by a predator. Golden eagles have been observed to predate on thinhorn neonates (Nette et al. 1984). The habitats in rugged, steep terrain at intermediate elevations in the Cassiar Mountains likely provide greater concealment cover (e.g., overhang and cave-like features) than ridgelines and mountain peaks, so females may avoid high elevations to reduce detections by golden eagles. Females selecting for mid elevations is consistent with predator avoidance as grizzly bears and wolves generally use habitats in lower elevations during the spring.

While at the fine scale females likewise selected intermediate elevations, this was not statistically significant (the confidence intervals overlapped zero), unlike our RSF estimates at the home range scale. This could lead one to believe elevation is not an important variable in lambing habitat, contrary to our findings at the home-range scale. Instead, we offer an alternative explanation: because the spatial extent of available habitats in the iSSA is constrained based on distributions of step lengths and turning angles during low-movement phases, results can show non-significant selection or avoidance of variables – despite their true importance. Scale is important when investigating habitat selection of wildlife, because habitat selection often varies across different scales as landscape features provide different functions at different scales (Boyce 2006). The used steps for the lambing period iSSA were tightly clustered because this is a period of low movement. Low movement during lambing periods was consistent with the expected movement patterns of females during parturition because females remain isolated in lambing habitats following giving birth and nursing their young for multiple days (Geist 1971, Shackleton and Haywood 1985). As a result, lower movement rates were observed during the lambing period with the median movement rate for all female-years of 20.3m/hr, resulting in short step lengths. The 'available steps' were located near used steps because they were generated based on the distribution of these short step lengths. As a result, the endpoints of used and available steps had the same or similar elevations, and lacked the heterogeneity necessary to reveal selection or avoidance of various elevations. Generally, topographic variables tend to be selected across large spatial scales (Boyce 2006).

Mountain sheep are habitat specialists distributed across mountainous and rugged landscapes that are highly influenced by the topography of an area. As a result, fine-scale resource selection analyses might not be able to account for the selection of landscape features by mountain sheep that are more variable at larger scales like elevation (Boyce et al. 2003). iSSAs are a powerful tool to assess habitat selection and movement behaviours at finer scales that are more representative of the habitats available to an individual at specific points in time (Avgar et al. 2016). However, our results suggest it is important to assess habitat selection during low-movement lambing periods at broader spatial scales, like the home range scale, in addition to using iSSAs, because iSSAs are less suited to evaluate the influence of covariates that are homogenous at fine spatial scales (e.g., elevation).

Throughout the lambing period, females consistently selected southwest aspects at home range and fine scales. Generally, southwest aspects receive the greatest amount of solar radiation, and as a result provide microclimates that are warmer, drier, and free of snow cover earlier in the spring (Albon and Langvatn 1992*a*). Hypothermia is a known cause of mortality in neonatal lambs (Wehausen et al. 1987, Smith et al. 2014). A newborn's ability to thermoregulate can be hindered by cold temperatures, snowfall, and rain (Giest 1971, Wehausen et al. 1987), which frequent the Cassiar Mountains during the lambing season. Smith et al. (2015) documented bighorn sheep in Black Hills, South Dakota selected birthing sites on southern aspects that may have provided microclimates that were warmer with less snow cover to reduce the risk of hypothermia. The similar selection for southwest-facing lambing sites exhibited by the Cassiar Stone's sheep, may have also occurred to reduce the risks of hypothermia in neonates.

An alternative explanation for the selection of southwest aspects may be that maternal females select these habitats to access better foraging opportunities, since new vegetation growth generally emerges earlier on southern slopes (Albon and Langvatn 1992*a*). We incorporated metrics of NDVI as a covariate in our analyses to investigate the influence of vegetative productivity on female habitat selection during the lambing period. Our results suggest females are not heavily influenced by forage quality during lambing periods, as females showed no significant selection for NDVI at the home range or fine scale. These findings corroborate studies that suggested maternal females select habitat features during lambing that improve newborn survival by minimizing predation risk and protection from weather elements, and trade-off access to quality forage (Geist 1971, Bunnell 1980, Festa-Bianchet 1988*c*). Recognizing that the use of NDVI to assess forage quality has limitations, we could not draw strong conclusions about the strength of vegetation on lambing habitat selection. The NDVI layers incorporated into this study had coarse resolutions (250m x 250m) compared to our topographic variables, which limited our ability to assess the availability and quantity of preferred forage types at local scales; the level where sheep selection of foraging areas generally takes place (Boyce 2006). In addition, we included maximum NDVI layers from each year and over the entire study period into our home range and fine scale models, rather than including the 16-day NDVI values collected during lambing periods. We did this to avoid using NDVI values that were contaminated from snow-cover, since some of the 16-day NDVI layers derived in May and June had high levels of snow-cover present. Because of this, the maximum NDVI values at most used and available points included in the RSF and iSSA were derived from summer months (July and August), and likely do not represent the true greenness in May and June when lambing periods took place, potentially explaining the insignificant selection of any NDVI value. Future research should investigate site-specific vegetation quality at local used and available lambing habitats to better understand the influence of vegetation on lambing habitat selection by parturient Stone's sheep.

We predicted females would avoid habitats with roads during lambing periods to avoid vehicle and human disturbance. As we expected, all females with roads in their home ranges (n =11) significantly avoided habitats near roads during the lambing period at the home range scale. The used and generated steps for all females included in the fine-scale analyses (iSSA) were located over 600m from roads (exponential decay of distance to road > 0.95), and because females exhibited avoidance of roads during this period, we did not include an exponential decay function of distance to roads in the fine scale analyses (iSSA). Our results corroborate Smith et al. (2015) that documented female bighorn sheep in South Dakota selected parturition sites located far from roads and residential areas. Maternal sheep can be negatively impacted by anthropogenic disturbances, and have been documented to alter activity patterns (Campbell and Remington 1980, Leslie and Douglas 1980, Papouchis et al. 2001, Sproat et al. 2020), become temporarily displaced (Lowrey and Longshore 2017), and even abandon suitable lambing habitats in response to human activity near lambing ranges (Etchberger et al. 1989, Wiedmann and Bleich 2014). The avoidance of roads at large and fine scales demonstrated by parturient females in our study suggest parturient Stone’s sheep have low tolerance for disturbance during lambing, but it could also be that females avoided roads because roads in the study area were commonly situated in valley bottoms, where predation risks are expected to be greatest. Mountain sheep developing a high level of tolerance to vehicle traffic on roads, likely motivated by a need to access specific benefits (e.g., roadside salt residue), because road traffic occurs in predictable locations, has consistent behaviours, and is not life-threatening (MacArthur et al. 1979, Papouchis et al. 2001). While we cannot conclude whether parturient sheep avoided roads to minimize exposure to road disturbance or to avoid unsuitable lambing habitats located in low elevations, some work undertaken in the Dease Lake, BC area has noted avoidance of areas near industrial roads by ewes with lambs during seasonal movements made during nursery periods (ERM 2018). The Cassiar Mountains currently experiences low levels of anthropogenic disturbance, particularly when compared to the active mining that occurred during the 1960-70s, however there is concern that increased use of off-highway vehicles (OHV) (e.g., snowmobiling, snow-cycling, all-terrain vehicle) could disturb critical ranges for thinhorn populations (Jex et al. 2016). Recreational OHV users are more likely to use areas near lambing habitats that are inaccessible to highway vehicle traffic, which could disturb or displace mothers and newborns during critical lambing and nursery periods. We were unable to quantify spatial and temporal use of OHVs in the Cassiar Mountains to identify the degree to which OHV use occurs near suitable lambing habitats, but use of areas by OHVs has been noted (*pers. comm.*; B. Jex).

Nursery period

Like the lambing period, the nursery period is a critical life stage for ungulates that can influence the fitness and survival of mothers and their young. During the nursery period, mothers face trade-offs between minimizing predation risks on their young and improving their own fitness and nutrition (Festa-Bianchet 1988*a*, Berger 1991, Rachlow and Bowyer 1998) to support the high energetic demands of lactation (Millar 1977, Berger 1979, Bunnell 1982). As we expected, nursing females in our study continued to select nursery habitats in steep, rugged terrain at intermediate elevations, at both home range and fine scales likely to improve their own and their lamb’s collective ability to escape predators. Although lambs develop rapidly and become agile in escape terrain just days after birth (Geist 1971), our results demonstrate that mothers continued to select areas that reduced predation risk during the first month postpartum.

Smith et al. (2014) documented predation on bighorn lambs occurred most frequently 2-3 weeks after birth. Interestingly, Corti and Shackleton (2002) found nursing mothers with young used habitats closer to escape terrain with worse foraging opportunities compared to barren females, suggesting mothers selected for habitats to reduce the risk of predation on their young in preference over habitats that could best support their own nutritional needs. We did not compare habitat selection behaviours from female Stone's sheep with and without young as conducted by Corti and Shackleton (2002), however, our study confirms that Stone's sheep mothers demonstrated significant selection for nursery habitats in and adjacent to escape terrain.

Lactating mothers experience high energetic demands during their first month after giving birth (Millar 1977, Berger 1979, Festa-Bianchet 1988*b*). To produce enough quality milk for their young, nursing Stone's sheep should favour areas with abundant and nutritious foraging opportunities, while also balancing other needs such as predator avoidance (Festa-Bianchet 1988*a*, Berger 1991, Rachlow and Bowyer 1998). As a result, vegetation undoubtedly influences habitat selection by nursing mothers. We found females significantly selected southwest aspects at intermediate elevations in subalpine and alpine zones, at both home range and fine scales, likely to access new forage growth while maintaining proximity to escape terrain. In northern mountain environments southwest aspects receive the greatest amount of solar radiation and typically host warmer and drier microclimates (Albon and Langvatn 1992*a*). Southwest aspects in alpine and subalpine ranges often support the earliest growth of graminoids and forbs (Albon and Langvatn 1992*a*), which are main components of Stone's sheep diet during late spring (D. R. Seip and Bunnell 1985). Throughout the growing season, mountain ungulates migrate altitudinally following the 'green-up' to exploit newly emerging, nutritious vegetation growth that is easier to digest and contains higher crude protein than winter forage (Hebert 1973, Albon and Langvatn 1992*a*, Hebblewhite et al. 2008). High alpine habitats might not provide mothers with as nutritious and abundant foraging opportunities during nursery periods in late spring compared to habitats at mid elevations, which may explain the significant selection for intermediate elevations during nursery periods in our study (from mid-May to late June). Similarly, Seip and Bunnell (1985) found Stone's sheep near Toad River, British Columbia used habitats at intermediate elevations in the subalpine from May to mid-June to access newly emerging, nutritious forage, and then gradually reached higher alpine elevations in late June, July, and August. Although we did not evaluate habitat selection during late summer, we predict

Stone's sheep would continue to migrate altitudinally while following the 'green-up', and thus would select habitats at higher elevations in July and August as observed in other populations of mountain sheep (D. R. Seip and Bunnell 1985, Walker et al. 2007, Merkle et al. 2016, Courtemanch et al. 2017).

Our best predictive models at the home range and fine scales revealed that nursing females selected habitats with low and intermediate NDVI values, respectively. NDVI values varied broadly across available habitats in individual home ranges (range: 0.156-0.8785), and within our study, high NDVI values generally coincided with areas dominated with dense cover of shrubs (e.g., willow) and deciduous and coniferous trees (e.g. spruce, aspen), and lower NDVI values in areas with high rock content, sparse vegetation, and open areas with graminoids and forb species. We expected nursing females would select low to intermediate NDVI to access open habitats dominated by new growth of graminoids and forbs to meet the high energetic demands of lactation and be able to produce sufficient milk for their young. At the home range and fine scales, females consistently avoided areas of high NDVI, which generally coincided with dense woody shrub and tree cover. This corroborates Risenhoover and Bailey (1985) that recorded bighorn sheep in Waterton Canyon, Colorado, avoided tall, dense vegetation cover, and favoured open areas with high visibility, likely to improve their detection of predators. Our home range RSFs identified females selected low NDVI, initially suggesting that nursing females select habitats with little to no primary productivity relative to NDVI in available habitats. However, when we constrained a female's domain of availability in the iSSA, we found females selected habitats with intermediate NDVI, rather than low NDVI. The selection for intermediate NDVI at fine scales reveals that nursing females are influenced by the productivity of available habitats, and do not select areas with low productivity (e.g., barren, rocky areas that provide little to no forage). Resource selection by ungulates in regard to foraging typically occurs at fine spatial scales (Boyce 2006). Assessing resource selection at fine scales with iSSAs provides an opportunity for investigators to better assess the influence of vegetation productivity on habitat selection, which is often challenging to evaluate across large spatial scales often used in second or third order RSFs. Seip (1983) documented Stone's sheep near Toad River, BC foraged predominantly on grasses, sedges, forbs, and some willow in subalpine and alpine ranges in May and June. Similarly, Walker et al. (2006) reported Stone's sheep in the MKMA used herbaceous habitat where they foraged mostly on graminoids and alpine forbs. Our iSSA results support Seip

(1983) and Walker et al. (2006), as maternal females in the Cassiar Mountains selected intermediate NDVI values that most likely correspond with open areas with similar available forage. NDVI can be informative to better understand productivity across landscapes, however it is a limited tool for delineating the specific types or quality of vegetation in local areas. Incorporating site-specific data on vegetation type and quality into our habitat selection analyses may provide better insight on the influence of vegetation on nursing Stone's sheep habitat selection. For this study, NDVI was an appropriate variable to use to investigate the influence of primary productivity on the habitat selection of mothers during the nursery period.

We predicted nursing Stone's sheep with young would avoid habitats near roads during the nursery period to avoid disturbance from highway traffic, however our data suggested nursing females strongly selected areas near roads at both the home range and fine scale; we found 9 collared females-years (6 individuals) used habitats near or along Highway 37 (<50m from road edge) to access natural mineral licks or to cross Highway 37 to access summer ranges. Mountain ungulates are attracted to mineral licks to acquire sodium and other trace elements to counteract mineral deficiencies that occur at the beginning of the growing season when transitioning from their lower-quality winter diets to new, high-quality vegetation (Hebert and Cowan 1971, Jones and Hanson 1985, Parker and Ayotte 2004, Ayotte et al. 2006). In addition, nursing ungulates face high nutritional demands with lactating females estimated to need approximately 40% more sodium than generally required (Staaland et al. 1980). As a result, mineral licks are likely important for the physiology of nursing females and their young. We observed collared nursing females travel from alpine and subalpine ranges to mineral lick sites often in low elevations near valley bottoms as early as May 11th. Based on female movements, we identified a cluster of three main mineral licks located near Highway 37; located within a 500m radius. The first site was the Mud Lake mineral lick, located approximately 1875m from Highway 37, which is a natural lick with multiple areas to obtain mineral soils (Appendix 2.7). The second mineral lick site is also a natural formation located about 25m from Highway 37, and the third is a roadside mineral lick located approximately 5m from the highway edge (Appendix 2.7). The attraction of females to mineral licks near Highway 37 during the nursery period may be of concern, because these sites are likely to expose nursing females and their young to the greatest levels of vehicle traffic within their home ranges. Additionally, Stone's sheep that access natural minerals near Highway 37 may also be attracted to lick remnant salts from the highway that were added in the winter, as demonstrated in Appendix 2.7. Considering wild sheep learn the locations of mineral licks from older sheep (Geist 1971, Festa-Bianchet 1986) we expect these three mineral lick sites near Highway 37 will continue to be important for future generations of Stone's sheep in the Cassiar Mountains.

In addition to the use of road-side mineral licks, we observed 2 nursing females from separate bands travel across Highway 37 at different crossing locations during the nursery period to access summer ranges, suggesting Highway 37 intersects an important movement corridor for some bands of Stone's sheep (Chapter 3). In addition to the inherent mortality risk resulting from vehicle-sheep collisions, disturbances on roads can negatively affect mountain sheep by accelerating energy depletion, impeding movements to resources and seasonal ranges (Papouchis et al. 2001, Keller and Bender 2007), and hindering genetic transfer between populations (Epps et al. 2005). In contrast, multiple studies have demonstrated mountain sheep can adapt and become tolerant of disturbances like highway traffic if the disturbance is predictable, consistent in behaviour, and is not life-threatening (MacCullum and Geist 1992, Papouchis et al. 2001, Jansen et al. 2006, 2009, Bleich et al. 2009). Regardless, the risk of being struck by a vehicle remains, and during the duration of our fieldwork, a non-study female was hit and killed by a vehicle using Highway 37 (*pers. comm.;* B. Jex). Females in this study are not known to experience negative effects from vehicle traffic on Highway 37, but our results suggest nursing females that accessed mineral lick sites near Highway 37 must be relatively experienced at navigating highway traffic at slower speeds and be somewhat tolerant of vehicle traffic, especially when accessing the roadside mineral lick located less than 10m from the highway edge. Although the Province of British Columbia's Wildlife Accident Reporting System (Sielecki 2010) list any records of road-caused mortalities of Stone's sheep, anecdotal observations from local community members and wildlife biologists reveal Stone's sheep have been killed on Highway 37 from vehicle collisions. Additionally, the Sulphur 8/Mile Stone's Sheep Project in the MKMA of northern British Columbia reported vehicle collisions on the Alaska Highway were the cause of 3/37 mortalities of collared female Stone's sheep in their study from 2005 to 2010 (Hengeveld and Cubberley 2012). These known Stone's sheep mortalities from road collisions suggests the Province of British Columbia's wildlife collision records of Stone's sheep are incomplete (Bunnell 2005). The number of Stone's sheep mortalities from road collisions are expected to be low in the Cassiar Mountains due to the current alignment of the highway with several tight corners requiring vehicles to slow down, and as such are likely not a persistent threat to Stone's sheep populations in general. The Cassiar Stone's sheep herd however is a relatively small population estimated at approximately 175 sheep (*pers. comm.*; B. Jex), and vehicle traffic may be on the rise as more people access winter and summer recreational opportunities in the Cassiar Mountains (e.g., snowmobiling, quadding). Implementing preventative actions may be helpful to minimize potential negative interactions between Stone's sheep and vehicle traffic.

Besides roads, we were unable to evaluate anthropogenic disturbances from other sources in the Cassiar Mountains and their possible effect on female habitat selection during lambing and nursery periods. Other anthropogenic disturbances of concern include OHV use (e.g., snowmobiling, quadding, dirt biking, etc.) and industrial development (e.g., mining, oil & gas) (Jex et al. 2016). OHV use can have negative effects on mountain sheep (Jex et al. 2016), and we suspect if female Stone's sheep are increasingly exposed to OHV use in the Cassiar Mountains, on undesignated trails during critical reproductive periods, this could affect the habitat selection of females with lambs. Additionally, mineral exploration has doubled in British Columbia since 2016 with 50% of all exploration occurring in northwestern British Columbia (British Columbia Mineral and Coal Exploration Survey 2018). Mountain sheep can be negatively affected by mining operations in response to blasting, high vehicle traffic, use of heavy machinery, and increased human presence (Oehler et al. 2005, Bleich et al. 2009, Poole et al. 2016). If anthropogenic disturbances continue to increase in the Cassiar Mountains, this study will provide insight for land-use planners and wildlife managers to identify suitable locations for resource development, like mining, that might reduce much of the negative impacts to critical habitats used by the Cassiar Stone's sheep herd.

MANAGEMENT IMPLICATIONS

Identifying suitable habitats for parturition and nursery periods is important to effectively manage ungulate populations (Dzialak et al. 2011, Smith et al. 2015, Kaze et al. 2016). Biologist and land-planners can minimize the overlap of human disturbances in critical lambing and nursery habitats by implementing mitigation strategies such as vehicle/OHV access restrictions, implementing industrial activity/disturbance windows, and by improving community awareness. We developed predictive maps of suitable lambing and nursery habitats with the top performing

RSFs to identify areas of high conservation priority within the Cassiar Mountains (Figure 2.7 and 2.8). This information can help inform future land and management decisions made by the Province of BC in collaboration with local Dease River, Kaska and Tahltan First Nation Governments, and provincial wildlife biologists. We suggest implementing spatial and temporal closures around suitable lambing and nursery ranges, and incorporating these critical ranges into subsequent iterations of the Dease-Liard Sustainable Resource Management Plan (SRMP) or other land management planning initiatives.

In our study, maternal Stone's sheep generally exhibited consistent patterns of resource selection across scales, suggesting the predictive maps developed from the top performing RSFs identified habitats can be considered suitable for females at both the home range and fine scales. Some inconsistencies in selection patterns were observed at the home range and fine scales, likely resulting from the heterogeneity of specific landscape features (e.g., elevation, NDVI) within the available domains of the RSF and iSSA. Our study highlights the importance of analyzing habitat selection at various scales to better understand the mechanisms driving habitat selection during critical life stages.

Females appeared to avoid areas with roads during lambing, and thus were not exposed to road disturbances during this time. In contrast, many nursing females selected for habitats near roads as that was necessary to facilitate access to mineral lick sites and for travel between seasonal ranges bisected by Highway 37, indicating a level of tolerance for navigating the current levels of road traffic along Highway 37, during the nursery period. However, it is unknown if vehicle traffic on Highway 37 has negative physiological or stress related impacts on nursing females in the Cassiar Mountains. We recommend land-planners, wildlife biologists, and local Indigenous Governments consider implementing traffic directives near areas where mineral lick sites in the Cassiar Mountains exist to prevent disturbance and mortality risks from increasing vehicle traffic, recreation, and industry. Specifically, we recommend managers consider installing road signage and speed reductions on short segments of Highway 37 near the mineral lick sites and at known road crossings, to improve public safety, reduce the risk of nursing Stone's sheep and lambs being killed from vehicle collisions, and ensure migratory corridors connecting seasonal ranges are not further impacted by highway traffic in the future.

TABLES

Table 2.1. Parturition rate (*n* = female-years), mean ($\bar{x}$) and range of parturition dates, and the mean ($\bar{x}$) and range of lambing period durations in days of collared Stone's sheep per study year in the Cassiar Mountains, British Columbia, Canada, 2018-2020.

	Parturition		**Parturition dates**		**Lambing period duration (days)**	
Study year	**Rate**	***n***	$\bar{x}$	**Range**	$\bar{x}$	**Range**
2018	0.67	4	30 May	4 May – 14 June	6.6	5.6 – 9.7
2019	0.93	13	14 May	3 May – 2 June	4.9	1.7 – 8.6
2020	0.43	6	31 May	13 May – 14 June	6.5	1.5 – 11.3
Total years	0.68	23	22 May	3 May – 14 June	5.6	1.5 – 11.3

Table 2.2. Top 5 ranked resource selection models and null models for the lambing and nursery periods estimated from Stone's sheep female-years (*n* =23) in the Cassiar Mountains, British Columbia, Canada from 2018-2020. Variables included in each model are displayed along with number of covariates (K), Akaike's Information Criterion corrected for small sample size (AICc) scores, and difference in AICc scores (Δ AICc) between consecutive models. All ranked models for the lambing and nursery periods are displayed in Appendix 2.3.

Period	**Rank**	**Model**	**Variables** [a]	***K***	**AICc**	**Δ AICc**
Lambing	1	Model3	EL + EL^2 + S + N + E + R + RDS	7	7713.39	0.00
	2	Global	EL + EL^2 + S + NDVI + N + E + R + RDS	8	7715.11	1.71
	3	Model1	EL + EL^2 + S + NDVI + N + E + R	7	7911.55	198.16
	4	Model5	EL + EL^2 + S + N + E + R	6	7912.89	199.50
	5	Model6	EL + EL^2 + S + N + E + R + RDS	7	8124.98	411.59
	17	Null	Null	0	10888.04	3174.65
Nursery	1	Global	EL + EL^2 + S + S^2 + NDVI + N + E + R + RDS	9	135408.71	0.00
	2	Model1	EL + EL^2 + S + NDVI + N + E + R	7	136230.32	821.61
	3	Model7	EL + EL^2 + S + NDVI + R + RDS	6	136399.36	990.58
	4	Model3	EL + EL^2 + S + N + E + R + RDS	7	136409.64	1000.85
	5	Model10	EL + EL^2 + S + R + RDS	4	137253.52	1844.80
	17	Null	Null	0	163367.23	27958.43

[a] EL = elevation, S = slope, N = northness, E = eastness, R= vector ruggedness measure, RDS = exponential decay function of Euclidean distance to roads, NDVI = total averaged maximum normalized vegetation index ($NDVI_{total\_max}$) across 2018-2020.

Table 2.3. Population-level variable estimates (β_i) and 95% confidence intervals (CI) from the top-ranked resource selection functions for female Stone's sheep (*n* =23) during the lambing and nursery periods in the Cassiar Mountains, British Columbia, Canada, 2018-2020.

	Lambing period			**Nursery period**		
Variables[a]	***β***	**Lower (95% CI)**	**Upper (95% CI)**	***β***	**Lower (95% CI)**	**Upper (95% CI)**
Elevation	3.05*	2.11	3.99	4.01*	3.78	4.23
Elevation^2	-2.45*	-3.29	-1.61	-2.96*	-3.16	-2.76
Slope	1.39*	1.30	1.48	0.41*	0.39	0.42
$\text{NDVI}_{\text{max\_total}}$				-0.31*	-0.32	-0.27
Northness	-0.57*	-0.64	-0.51	-0.16*	-0.17	-0.14
Eastness	-0.36*	-0.42	-0.29	-0.17*	-0.18	-0.15
Vector ruggedness measure	0.46*	0.42	0.51	0.29*	0.28	0.30
Exponential decay function of distance to roads	3.94*	3.20	4.68	-0.49*	-0.52	-0.46

[a] $\text{NDVI}_{\text{max\_total}}$ = total averaged maximum normalized difference vegetation index across entire study period (2018-2020).

* 95% CI did not overlap 0.

Table 2.4. Population-level variable estimates (*β_i*) and 95% confidence intervals (CI) from the global integrated step selection analyses for female Stone's sheep (*n* =23) during the lambing and nursery periods estimated with integrated step selection analyses in the Cassiar Mountains, British Columbia, Canada, 2018-2020.

	Lambing period			**Nursery period**		
Variables[a]	***β***	**Lower (95% CI)**	**Upper (95% CI)**	***β***	**Lower (95% CI)**	**Upper (95% CI)**
Elevation	0.71	-1.59	3.01	0.99*	0.69	1.31
Elevation^2	-0.40	-2.74	1.95	-0.85*	-1.15	-0.60
Slope	0.26*	0.18	0.35	0.12*	0.10	0.15
NDVI_{max}	-0.41	-1.04	0.23	0.14*	0.01	0.27
NDVI_{max}^2	0.29	-0.35	0.93	-0.18*	-0.31	-0.05
Vector ruggedness measure	13.07*	7.60	18.54	18.77*	17.08	20.46
Northness	-0.45*	-0.56	-0.33	-0.14*	-0.16	-0.11
Eastness	-0.21*	-0.35	-0.08	-0.06*	-0.08	-0.03
Exponential decay function of distance to roads				-0.10*	-0.14	-0.07
Step length	0.08*	0.02	0.14	0.09*	0.07	0.12

[a] NDVI_{max} = annual maximum normalized difference vegetation index (NDVI) for 2018-2020.

*95% CI did not overlap 0.

FIGURES

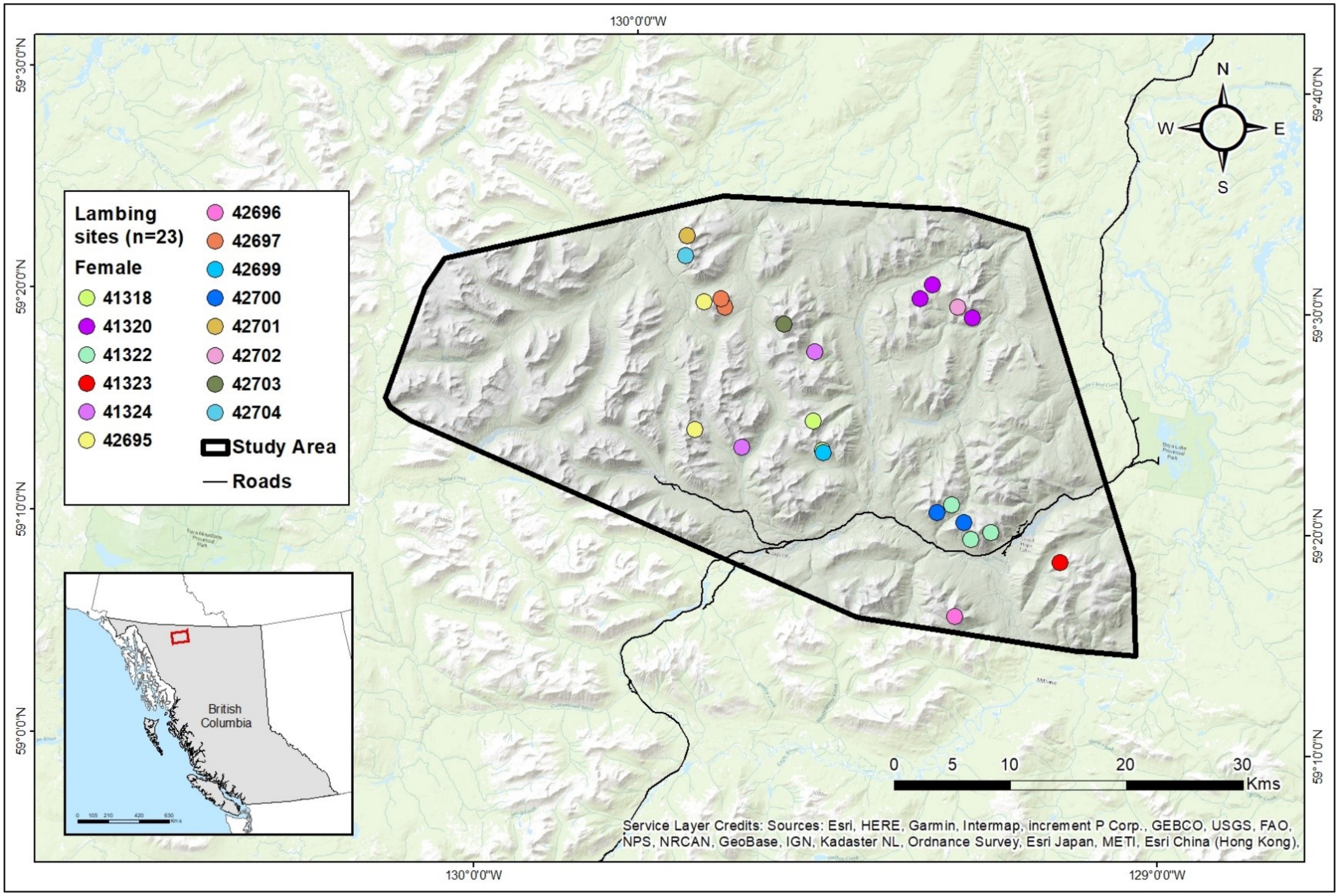

Figure 2.1. Study area and lambing sites (*n*=23 female-years) used by 14 collared female Stone's sheep in the Cassiar Mountains of northern British Columbia, Canada, 2018-2020.

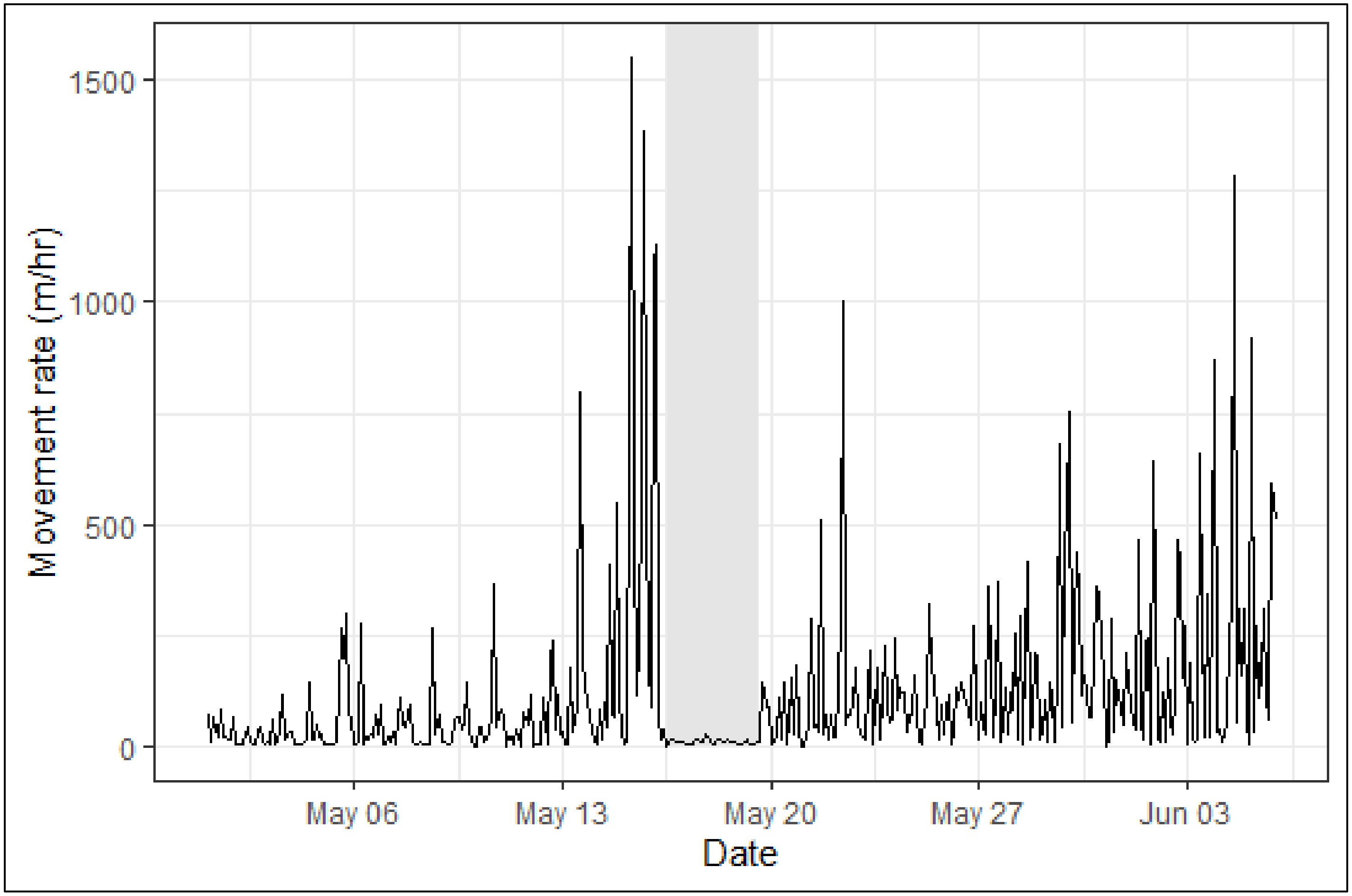

Figure 2.2. Movement rates (m/h) of collared female 42697 from May 1 – June 5, 2019. Parturition date was estimated on May 16, 2019, and the lambing period indicated in grey shading was estimated from May 16 – 19, 2019 based on net displacement from the lambing site.

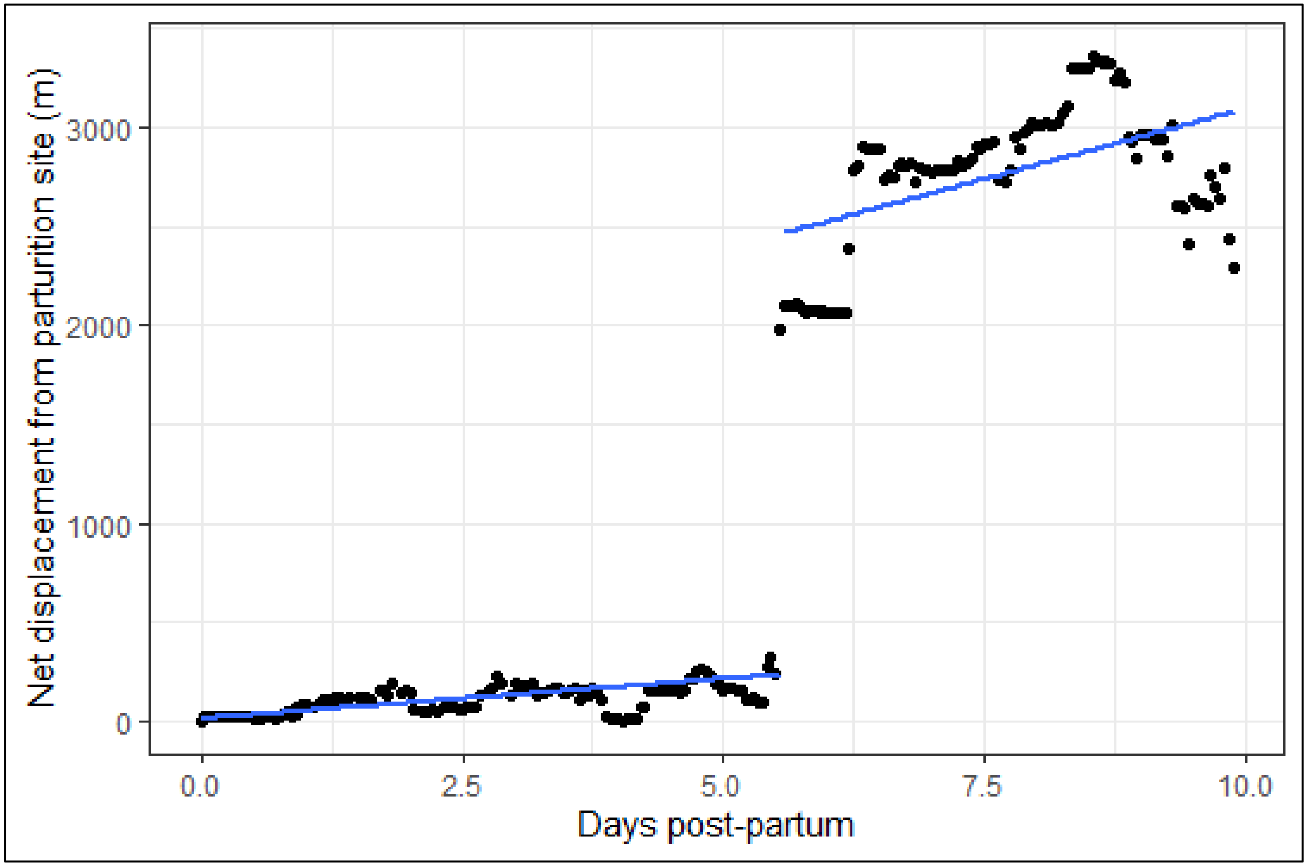

Figure 2.3. Net displacement (m) from the estimated parturition site from collared female 42699 over 10 days postpartum. Piecewise regression was used to identify the days postpartum for which a significant break in net displacement occurred, indicated by a blue line.

Figure 2.4. Captured trail photos of collared female 42700 followed by a lamb-at-heel on June 28, 2019, at 7:50pm on a sheep trail used to access a mineral lick site near valley bottom in the Cassiar Mountains, British Columbia, Canada.

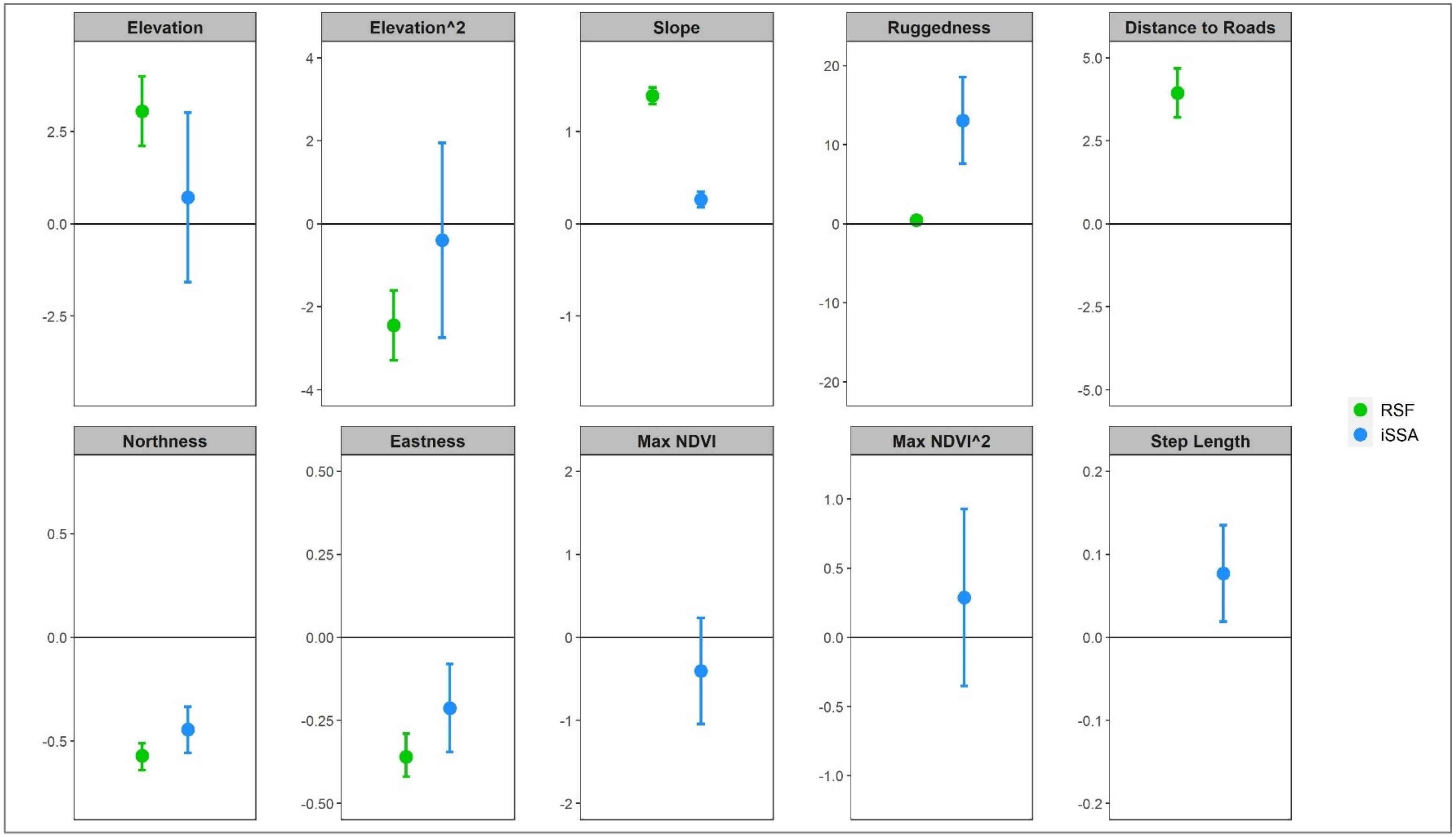

Figure 2.5. Scaled parameter estimates from the top-ranked resource selection functions (RSF) shown in green and integrated step selection analyses (iSSA) shown in blue for lambing periods of female Stone's sheep (*n*=23 female-years) in the Cassiar Mountains, British Columbia, Canada, 2018-2020. Error bars indicate 95% confidence intervals for scaled parameter estimates and significant covariates are indicated with error bars that do not overlap zero. Parameters include elevation (m), elevation^2, slope (°), average maximum NDVI values ($NDVI_{max}$) calculated from 2018-2020 maximum NDVI, ruggedness calculated as vector ruggedness measures, northness, eastness, and the inverse of an exponential decay function of distance to roads.

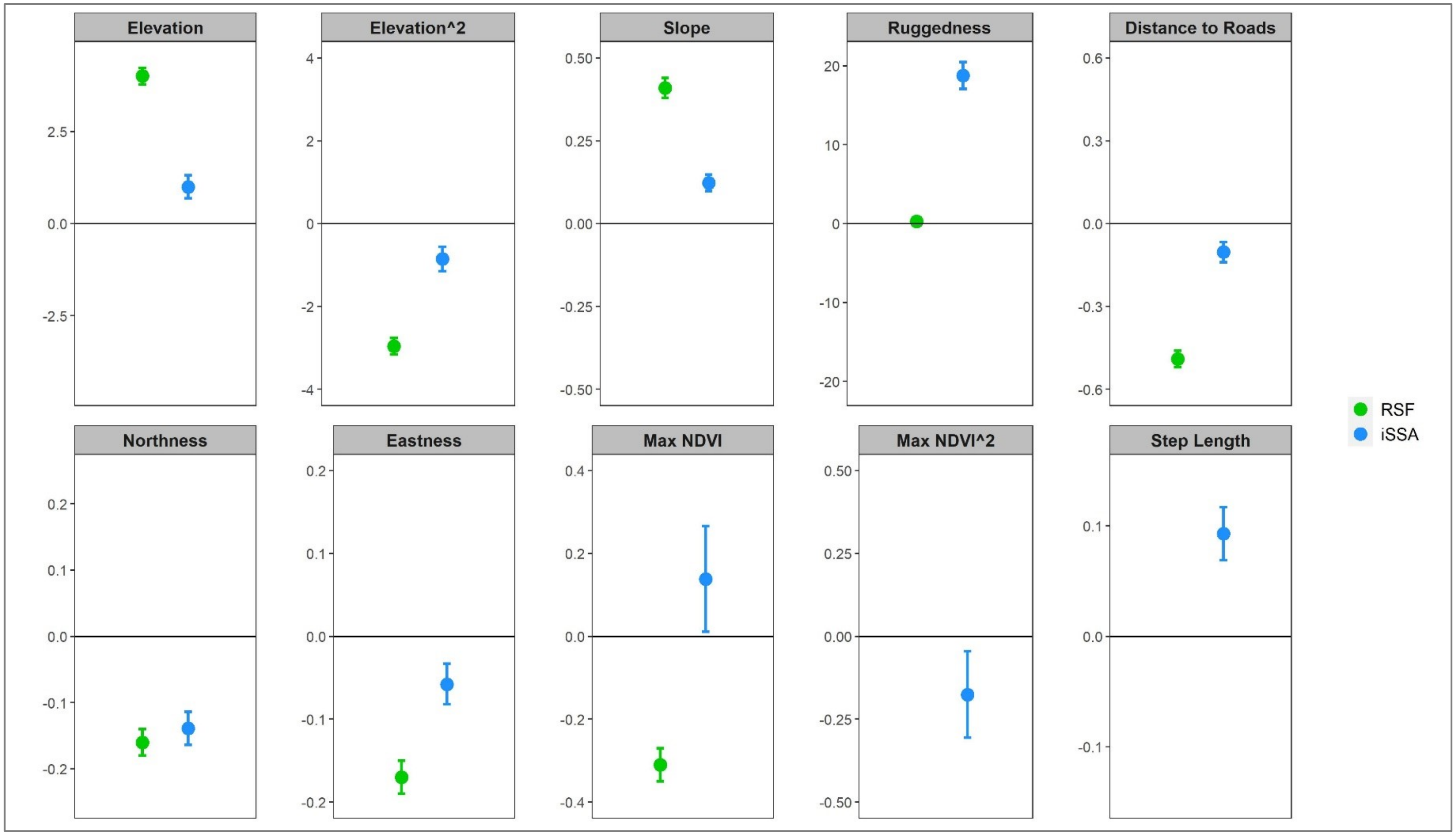

Figure 2.6. Scaled parameter estimates from the top-ranked resource selection functions (RSF) shown in green and integrated step selection analyses (iSSA) shown in blue for nursery periods of female Stone's sheep (*n*=23 female-years) in the Cassiar Mountains, British Columbia, Canada, 2018-2020. Error bars indicate 95% confidence intervals for scaled parameter estimates and significant covariates are indicated with error bars that do not overlap zero. Parameters include elevation (m), elevation^2, slope (°), average maximum NDVI values (NDVI$_{max}$) calculated from 2018-2020 maximum NDVI, ruggedness calculated as vector ruggedness measures, northness, eastness, and the inverse of an exponential decay function of distance to roads.

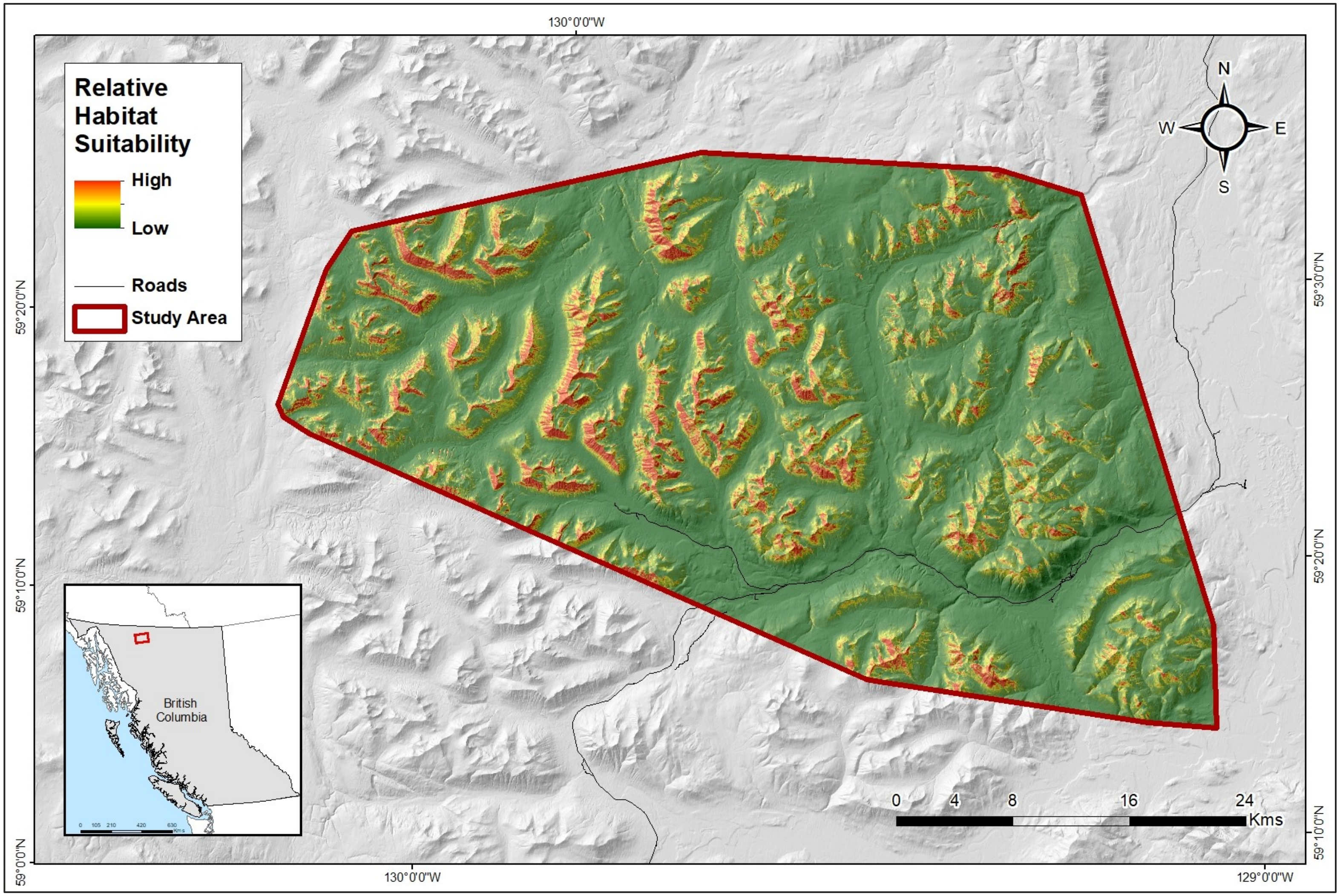

Figure 2.7. Relative lambing habitat suitability calculated from the top-performing resource selection function estimated from collared parturient Stone's sheep (*n*=23 female-years) during the lambing period in the Cassiar Mountains in northern British Columbia, Canada, 2018-2020.

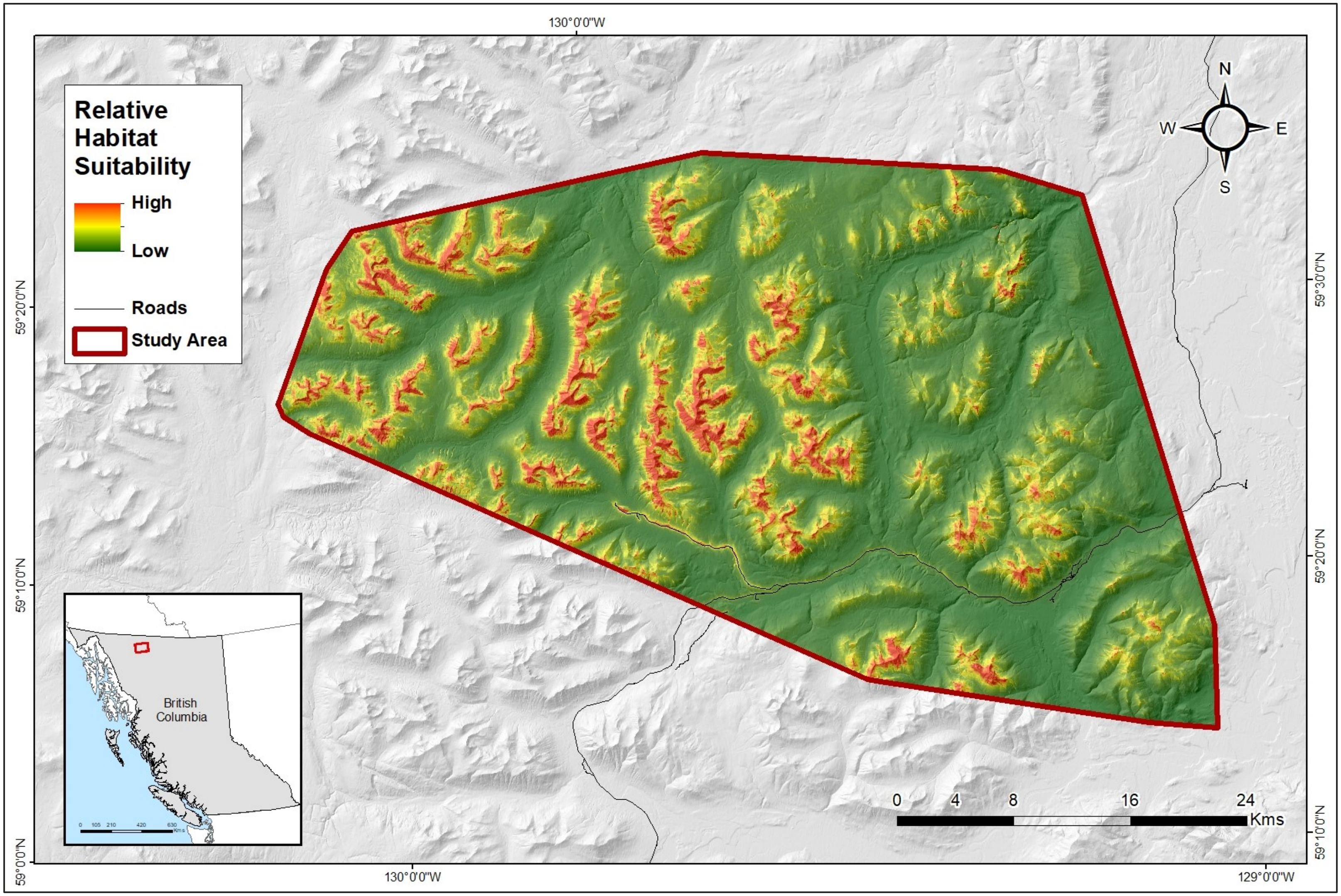

Figure 2.8. Relative nursery habitat suitability calculated from the top-performing resource selection function estimated from collared Stone's sheep (*n*=23 female-years) during the nursery period in the Cassiar Mountains in northern British Columbia, Canada, 2018-2020.

Chapter 3 - Diverse migration strategies and seasonal habitat use of Stone's sheep

INTRODUCTION

Migration is common across taxa and has evolved in response to spatial and temporal variation of resources (Fryxell and Sinclair 1988, Berger 2004). During the growing season, mountain ungulates often migrate to different ranges and across elevations in synchrony with plant phenology to maximize their intake of new, high-quality forage growth (Fryxell and Sinclair 1988, Fryxell 1991, Hebblewhite et al. 2008). Migration also can be an adaptation to reduce predation risk (Fryxell and Sinclair 1988, Hebblewhite and Merrill 2011), or to access critical resources distributed in specific locations across a landscape (e.g., mineral licks; Heimer 1973, Ayotte et al. 2008). Migration is not only fundamental to the fitness and demographics of migratory ungulate populations (Fryxell and Sinclair 1988, Berger 2004), but also to ecosystem processes and nutrient dynamics (Helfield and Naiman 2001, Holdo et al. 2007). However, ungulate migrations are declining and disappearing worldwide (Berger 2004, Bolger et al. 2008, Harris et al. 2009). This loss of migratory behavior is often attributed to disturbances such as, overhunting (Milner-Gulland et al. 2001), habitat loss on seasonal ranges (Harris et al. 2009), barriers that impede movement along migratory routes (e.g., highways, fences; Sawyer et al. 2013, Seidler et al. 2015), and climate change (Middleton et al. 2013, Aikens et al. 2020). In North America, migratory ungulates continue to experience unprecedented levels of human disturbance, creating a need for identifying and conserving migration routes and seasonal ranges used by ungulate populations (Berger 2004, Thirgood et al. 2004, Harris et al. 2009).

Migrations by North American ungulates can vary from short to extensive geographical distances to reach distinct seasonal ranges (Berger 2004). Some ungulates, such as mule deer (*Odocoileus hemionus*), will gradually migrate to summer ranges while remaining at stopover sites along the migration route for multiple weeks to forage on newly emerging, nutritious plant growth ('surfing the green wave') (Sawyer et al. 2009*b*, 2011, Merkle et al. 2016). In comparison, some ungulates tend not to use stopover sites altogether, or only for short durations to restore depleted energy stores, rest, and reduce predation risk before continuing on with their migrations (Bischof et al. 2012), similar to stopover use by avian migrants (Kuenzi et al. 1991, Bauer et al. 2008). In addition to migrating to distinct ranges across geographic distances, mountain ungulates often exhibit traditional altitudinal migration (Hebert 1973, Albon and

Langvatn 1992*a*). In the summer, mountain ungulates migrate to high elevation ranges to exploit emerging, highly nutritious forage (Seip 1983, Albon and Langvatn 1992*b*). In the winter, many ungulates then descend to low elevations to avoid deep snow, reduced mobility, and colder temperatures often associated with high elevations in winter (Tilton and Willard 1982, Festa-Bianchet 1988*a*). In contrast, some populations of mountain ungulates do not winter at low elevation, but instead migrate to high elevation ranges, where they winter on windswept grasslands and ridgelines that provide access to forage, improved locomotion and reduced predation risk (Poole et al. 2016, Courtemanch et al. 2017). Courtemanch et al. (2017) defined this less-common pattern of altitudinal migration as "abbreviated altitudinal migration".

Many ungulates learn migrations and seasonal movement patterns from older generations and culturally transmit 'landscape knowledge' on the distribution of resources within their range (Jesmer et al. 2018). Thus, native populations of migratory ungulates often exhibit strong fidelity to historical ranges and migration routes, as demonstrated by many North American ungulates, such as elk (*Cervus elaphus*; Hebblewhite and Merrill 2007, Cole et al. 2015), pronghorn (*Antilocapra americana*; Rudd et al. 1983, Sawyer et al. 2002), mule deer (Sawyer et al. 2009*b*, 2011), and bighorn and thinhorn sheep (*Ovis canadensis, O. dalli;* (Geist 1971, Festa-Bianchet 1986, Sawyer et al. 2009*b*). Populations of native ungulates often display the greatest migratory diversity across individuals, in contrast to newly introduced (e.g., translocated) or augmented populations (Lowrey et al. 2019). This occurs because native populations have longer durations of time to gain landscape knowledge and to continue to adapt diverse migration strategies that bolster individual fitness (Lowrey et al. 2019). Partial migration in ungulate populations often involves individuals sharing a winter range, but then in spring, a portion of the population migrates to allopatric summer ranges while the remaining population remains on the sympatric winter range (Fryxell and Sinclair 1988). Recent findings on individual diversity in the life-histories of anadromous fish and avian migrants revealed that migratory diversity is advantageous for the long-term sustainability of populations (Webster et al. 2002, Schindler et al. 2015). Individual diversity improves population and ecosystem stability (Schindler et al. 2010, Griffiths et al. 2014), reduces risk and improves resilience in the wake of stochastic and unpredictable conditions (e.g., drought, human-caused habitat loss) (Gilroy et al. 2016, Morrison et al. 2016), and can reduce density dependent competition and predation risk (Leech et al. 2017, Lowrey 2018). Migratory diversity in ungulates may include individual variation in the timing of migrations, geographic routes and distance travelled during migrations, seasonal ranges, use of stopover sites, and the frequency of visits between seasonal ranges (e.g., vacillating migration; Denryter et al. 2021). Despite the importance of migratory diversity, little research has examined the diversity among individual migration strategies in ungulate populations (Lowrey et al. 2019). Losing migratory diversity in native ungulate populations could result in severe consequences to long-term population sustainability and ecosystem stability (Webster et al. 2002, Schindler et al. 2010, 2015), would likely eradicate long-evolved migration strategies that may never be restored (Jesmer et al. 2018), and could result in formerly occupied habitats becoming alienated and lost to herd memory through localized extirpations. Identifying and conserving migratory diversity within native ungulate populations may be essential for effective management and maintaining the resilience of migratory ungulate populations.

A native population of Stone's sheep (*O. d. dalli*) resides in the Cassiar Mountains of northern interior British Columbia, Canada. The Cassiar population is spatially structured; composed of small bands of Stone's sheep that occupy distinct winter ranges and only overlap with other bands in spring and summer months and sometimes during the rut. The Cassiar Mountains are relatively remote with little anthropogenic disturbance, and consequently, most of the Cassiar population is expected to use long-evolved, native migration patterns that have not been significantly altered by human influences. Little information is known about the migrations and seasonal movement patterns of the Cassiar population, and Stone's sheep populations in general. Because of this, documenting a baseline for Stone's sheep migrations and seasonal movement patterns is necessary for informing Stone's sheep management and land-planning decisions in northern British Columbia. In addition, evaluating migration across individuals in the Cassiar population provides a unique opportunity to examine natural migration strategies evolved by native ungulates in an environment with little, widespread human disturbance. In this study, we identified migration routes and seasonal ranges used by the Cassiar population, and classified females by their geographic and altitudinal migration strategies.

Migratory diversity among individuals can benefit individual fitness by reducing density-dependant competition and predation (Leech et al. 2017; Lowrey et al., 2018; Singer et al., 2000), and improve population resilience and sustainability (Griffiths et al., 2014; Schindler et al., 2010). Because of these benefits associated with individual migratory diversity, and since partial migration is often exhibited in native ungulate populations (Lowrey et al. 2019), we predicted individuals in the Cassiar population would exhibit diverse migratory strategies and seasonal movements across bands.

Greater trophic diversity occurred in threespine stickleback (*Gasterosteus aculeatus*) when the availability and diversity of resources (prey) within lakes was highest, demonstrating how distribution and diversity in resources can drive the adaptation of diverse behaviours (Bolnick and Ballare 2020). Like threespine stickleback exposed to varying resources within different lakes, sheep bands in the Cassiar Mountains are structurally distributed across the Cassiar Mountains, and thus, are exposed to varying distributions of resources (e.g., quality forage, mineral licks), topography, and predation pressure. Because of this, we also predicted bands would vary in migratory behaviours and seasonal movements in response to their diverse local landscapes. If diversity in migration behaviours occurred among bands, it would suggest resource distribution and landscape topography drives diversity in migration and seasonal movements.

METHODS

Study area

The Cassiar Mountains span approximately 4301km^2 of interior northwestern British Columbia, Canada (Pojar and MacKinnon 2013), and are located near the townsites of Cassiar, Jade City, and Good Hope Lake, within the Dease River, Kaska and Tahltan First Nations territories. Our study area spanned 2090 km^2 in the north-central ranges of the Cassiar Mountains. Most of the land in the Cassiar Mountains is managed as Crown land and is managed through the Dease-Liard Sustainable Resource Management Plan (Govt of British Columbia Ministry of Sustainable Resource Management 2004) developed by the Province of British Columbia and local First Nations Governments.

The Cassiar Mountains are found within the Boreal Cordillera ecozone, and are comprised of three ecosystems occurring across different elevations (Meidinger and Pojar 1991). At the lowest elevations (650-900m) is the montane ecosystem, which consists of black spruce (*P. glauca*), white spruce (*Picea mariana),* Engelmann spruce (*P. englemannii*), lodgepole pine (*Pinus contorta*), trembling aspen (*Populus tremuloides*), dwarf birch (*Betula glandulosa*), and willow (*Salix* spp.). The subalpine ecosystem ranges from 900-1500m and contains white spruce, willow, dwarf birch in krummholz form, and subalpine fir (*Abies lasiocarpa*). Above treeline (>1500m) is the alpine ecosystem consisting of rocky, rugged terrain and plant communities comprised of few subalpine fir in krummholz form, grasses, sedges, alpine-flowering plants, lichens, and bryophytes (Meidinger and Pojar 1991). The Cassiar Mountain climate is cool and short summers and cold, lengthy winters. Average subalpine temperatures rang form -0.7 to -0.3°C throughout the year, and typically only 1 month experiences temperatures about 10°C. Average annual precipitation ranged from 460-700mm and snowfall accounted for 35-60% of it (Geist 1971, Meidinger and Pojar 1991).

The Cassiar Mountains host a diverse array of large predators and ungulates. Predators of Stone's sheep found in the Cassiar Mountains include golden eagles (*Aquila chrysaetos*), grizzly bears (*Ursus arctos*), black bears (*U. americanus*), wolves (*Canis lupus*), coyotes (*C. latrans*), wolverines (*Gulo gulo*) and lynx (*Lynx canadensis*). Species of ungulates include Stone's sheep, moose (*Alces alces*), mountain goats (*Oreamnos americanus*), caribou (*Rangifer tarandus*), and sometimes elk (Ce*rvus elaphus*) and mule deer *(Odocoileus hemionus*).

Most of the Cassiar Mountains have remained relatively unaltered from anthropogenic disturbance because of low human densities present and the limited access to much of the area. The limited anthropogenic land-use in the Cassiar Mountains includes traffic on Highway 37, a small-scale jade mine operating in Troutline Creek valley and areas on the abandoned Cassiar Asbestos Mine, active gold placer-mining, Indigenous/resident/non-resident hunter harvest, and various recreation, such as recreational motorized vehicle use (e.g., by snowmobile, all-terrain vehicle), hiking, and camping (Jex et al. 2016). Although the Cassiar Mountains exhibited relatively low human disturbance, there is increasing interest in recreation, especially motorized vehicle use and tourism, and potential for increased mineral extraction.

Captures and GPS relocation data

We captured adult female Stone's sheep by helicopter net-gun in February 2018 and February to April in 2019. All individuals were collared with Iridium GPS collars (model G2110E2, Advanced Telemetry Systems (ATS), Isanti, MN, USA) that collected relocations at 1h (2019) and 2h (2018) fixes. Capture and animal handling procedures were in accordance with BC Ministry of Forests, Lands, and Natural Resource Operations protocols, and approved by the Animal Care and Use Committee at the University of Alberta (no. AUP00002992). GPS collars collected relocation data from the time of captures until September 2020, unless an individual died before the end of the study or if their collar malfunctioned or the batteries died. We removed erroneous GPS relocations and relocations that could have been influenced by capture effects by removing relocations collected in the first week after captures, locations collected with ≤ 2 satellites (251 relocations), and locations with movement rates >20km/h (2 relocations) (D'Eon and Delparte 2005, Lewis et al. 2007, Frair et al. 2010).

Timing of spring and fall migrations

To determine the timing of spring and fall migrations we visually identified abrupt changes in net squared displacement (NSD) and GPS relocations from the winter range (Cole et al. 2015). To calculate NSD, we determined a start date and location from which Euclidean distances were calculated from for the subsequent GPS relocations. We used March 15 as the start date because we assumed Stone's sheep would be residing on their winter range at that time. However, for individuals collared in early April 2019, we defined their NSD start date as one week after the April capture efforts, and we assumed these individuals would still be occupying their winter ranges at this time.

We determined the start and end dates of spring migrations for each female-year by visually identifying abrupt movements away from winter range indicated by substantial increases in NSD (Poole and Lamb 2020), and then we visually confirmed that the female moved away from the winter range to a spatially distinct (non-overlapping) range for at least 30 days (Eggeman et al. 2016, Poole and Lamb 2020). We identified the start and end dates of fall migrations when female's NSD sharply declined near zero, and visually confirmed the female had returned to the winter range for at least 30 days (Eggeman et al. 2016). We defined the winter season for migrants as the period between the end date of fall migration and the start date of spring migration, and similarly, we defined summer as the period between the end of spring migration and start of fall migration. We could not distinguish a winter and summer season for residents because they do not exhibit obvious migrations to seasonal ranges, so we defined resident summer and winter seasons based on the timing of the spring and fall migrations of standard migrants. The resident summer season was defined as the time between the 66th and 33rd percentiles of spring migration end dates and fall migrations start dates of standard migrants, respectively (Poole and Lamb 2020). Similarly, the winter season for residents was defined as the time between the 66th and 33rd percentiles of fall migration end dates and spring migration start dates of standard migrants, respectively (Poole and Lamb 2020).

Summer and winter ranges

We developed summer and winter 95% utilization distributions (UDs) by calculating Brownian bridge movement models (BBMM; Horne et al. 2007) at 100x100m resolution using the GPS locations from each female-year during the summer and winter seasons. To do this, we used the kernel Brownian bridge home range estimation function (Calenge 2015) in R v. 4.0.3 (R Core Team 2020). We defined the first smoothing parameter, $\sigma 1$, using the R function *liker* (Horne et al. 2007), and the second, $\sigma 2$, as 30m (Frair et al. 2010, Kittle et al. 2015).

We used the winter 95% UDs to determine which females were in the same bands. We determined that females were in the same band if their winter ranges overlapped >70% and visually confirmed that they frequently moved together and occupied the same ranges.

Fidelity to winter ranges

We assessed whether females exhibited fidelity to their winter range in subsequent years. To do this, we compared each female's winter range in 2019 with the winter range used in their collar year. If a female's winter ranges had ≥ 50% overlap, we determined she expressed fidelity to her winter range. We also assessed the fidelity exhibited by females with multiple years of collar data (n = 4) to gain more insight on fidelity to winter ranges over time.

Stopover sites and movement corridors

We identified migration corridors and stopover sites used by migrating Stone's sheep during spring and fall migrations by estimating BBMMs (Horne et al. 2007). Similar to the summer and winter UDs, we delineated migration corridors 95% UDs at 100x100m resolution for all spring and fall migrations by estimating BBMM (Horne et al. 2007) using female relocations during spring and fall migrations. In the models, we also included the relocations collected 24h before and after the start and end dates of our defined migrations as suggested by Sawyer et al. (2009*b*). As defined in the summer and winter BBMMs, we defined $\sigma 1$ using the *liker* function (Horne et al. 2007), and $\sigma 2$ as 30m (Frair et al. 2010, Kittle et al. 2015).

Next, we delineated stopover sites from the migration corridors for each female-year. We defined stopover sites as habitat patches located along the migration route that are spatially distinct (non-overlapping) from summer and winter ranges. Stopover sites are identifiable as a spatial cluster of GPS relocations located on the migration route, collected over multiple hours to weeks. We identified stopover sites as the top 12% percentile of each migration UD (Monteith et al. 2018). In the results, we describe different use of migration routes and stopover sites exhibited by the collared individuals in this study.

Evaluating migration strategies

To evaluate migration strategies, we calculated parameters using each female's summer and winter UDs. First, we calculated percent overlap and area of overlap (km^2) between the winter and summer range for each female (Fieberg and Kochanny 2005, Poole and Lamb 2020). Next, we calculated the Euclidean distance between the centroid of each female's summer and winter UDs (Cagnacci et al. 2015, Poole and Lamb 2020). Lastly, we calculated the mean elevations used by each female during the summer and winter, and then calculated the difference in mean elevations between seasons.

To better define migration strategies used by the Cassiar Stone's sheep population, we classified individuals into broad classes of migration strategies. Because mountain ungulates often migrate over geographic distances and elevations (altitudinal migration), we classified females into geographic migration classes (4 classes; long-distance migrants, short-distance migrants, vacillating migrants, or resident), and then into altitudinal migration classes (3 classes; traditional migrants, abbreviated migrants, or residents). We discuss these geographic and altitudinal migration strategies in more detail below. Consequently, each females received 2 migration strategy classifications.

Geographic migration

To first account for geographic migration, we classified individuals as residents or geographic migrants based on different seasonal range parameters (see below). Females were classified as geographic migrants (long-distance, short-distance, or vacillating) if they occupied non-overlapping summer and winter ranges for at least 30 days (Ball et al. 2001, Eggeman et al. 2016), and had <20% overlap between summer and winter ranges. We further classified geographic migrants as either long-distance migrants or short-distance migrants depending on whether their Euclidean distance between range centroids was >10km, or ≤10km, respectively

(Mysterud 1999, Berger 2004). Figure 3.1 provides an example of the NSD of a long-distance migrant and resident.

Vacillating migration was described by Denryter et al. (2021) as occupying a spatially distinct range for most of the summer, but returning (‘vacillating’) to the winter range ≥ 2 times. Because of this, we classified vacillating migrants by visually inspecting the NSD and relocation data from the geographic migrants and residents, to see if the individual predominantly used a distinct summer range, but ‘vacillated’ between seasonal ranges at least twice. We looked for this pattern in geographic migrants *and* residents, because it is possible vacillating migrants would be improperly classified as residents, because their vacillations may result in high overlap between ranges, despite occupying separate summer ranges during most of summer. Figure 3.1 provides an example of the NSD of a vacillating migrant.

As a result, we classified females into 4 different classes of geographic migration strategies, including: long-distance migration, short-distance migration and vacillating migration, and residency.

Altitudinal migration

Our second classification of migration strategies accounted for altitudinal migration. To do this, we classified individuals as traditional altitudinal migrants, abbreviated altitudinal migrants, or residents. Females were classified as a traditional altitudinal migrant if they exhibited a change in mean elevation > 250m between the summer and winer seasons (Poole and Lamb 2020). Abbreviated altitudinal migration consists of a spring altitudinal migration from low-elevation spring ranges to high-elevation summer ranges, then individuals descend to low-elevations in the fall, and then migrate again from low-elevation fall ranges to high-elevation winter ranges (Courtemanch et al. 2017). We identified abbreviated altitudinal migrants as individuals that exhibited a spring and fall altitudinal migration from low-elevations to high-elevations in summer and winter. To do this, we evaluated each female’s seasonal patterns of elevation use throughout the year, by visually examining each female’s mean daily elevations calculated over a 14-day moving window (e.g., Figure 3.2). Lastly, we classified individuals as resident if they did not exhibit clear seasonal changes in elevation, or if they did not use elevations that ranged over 150m throughout the year.

As a result, we classified females into 3 different classes of altitudinal migration strategies, including: traditional altitudinal migrants, abbreviated migrants, and residents. Therefore, all females were given two classifications to characterize their geographic and altitudinal migration strategies.

RESULTS

Capture and GPS data

We captured and radio collared 18 female Stone's sheep in 2018 and 2019. We collected a total of 169,591 GPS relocations from February 2018 – September 2020. Because we were evaluating migrations and seasonal range use, we removed females that did not have a full year of data. If a female did not have relocations collected for at least 30 days during the winter season, because of mortality, the collar malfunctioned or the battery died, we removed the female from the analyses. As a result, we included 16 females in the analyses, and 2 females were removed. For individuals monitored over 2+ migration seasons (n = 4), we present the findings from their second migration season in 2019 so we can compare with the other females collared in 2019.

We determined these 16 collared females were spatially distributed across 9 bands (Appendix 3.1). Most bands consisted of 2 collared females, however there were 2 bands with only 1 individual, and 1 band with 3 individuals.

Timing of spring and fall migrations

The median start and end dates of spring migration for standard migrants was 12-June and 19-June respectively, and during the fall migration they were 20-September and 07-October respectively (Table 1). The summer season for residents was defined as June 26 – August 26th, and the winter season as October 11th – June 6th (Table 1). The length of time it took females to migrate varied between individuals and bands (see below). Generally, females from the same band migrated together or within a few days of one another. More information on the dates of spring and fall migrations for each female can be found in Appendix 3.2.

Summer and Winter Ranges

The mean area of the summer range across individuals (n = 16) was 4909m^2 and ranged from 2027m^2 to 9887m^2. Similarly, the winter range had a mean area of 4401m^2 and ranged from

$1878m^2$ to $9120m^2$. Migrants had the largest home ranges, while residents generally had the smallest. All summer and winter ranges are depicted in Figure 3.3.

Almost all females within the same band (15 females; 8 bands) used the same winter and summer ranges. However, one band with 3 collared females exhibited partial migration; where one female exhibited a long migration to a distinct summer range, while the other 2 females were classified as residents.

Fidelity to winter ranges

All 16 females across 9 bands returned to the same winter range where they were collared in the previous year, resulting in a 100% fidelity rate to their winter range. Additionally, all females with multiple years of collar data (n = 4), returned to the same winter range each year, further supporting this 100% fidelity rate.

Additional seasonal ranges

Four females from two bands used a spatially distinct spring or fall range in addition to their summer and winter ranges. One of the bands with two females travelled to a spatially distinct range that was not en route to their summer range. These females left their winter range on June 6th, but rather than using a stopover site en route to their summer range to the west, both females migrated to a spring range that was southeast of their winter range (Figure 3.4). This spring range was an additional 16km from the summer range compared to their winter range. This spring range was located close to Highway 37 and has a known mineral lick nearby. Both females remained at their spring range for about 14 days before travelling to the summer range on June 26. Interestingly, both females gave birth in 2019 on May 11th and 22nd (Chapter 2); thus, this spring stopover site was not used as a lambing/natal range. During the fall migration, both females travelled directly to their winter range and did not return to this spring range.

The second band had two collared females that used an additional range during the spring, fall and rut (‘spring/rut range’) (Figure 3.5). These females migrated from their winter range located south of Highway 37 to this spring/rut range in mid-June after giving birth, and remained for multiple weeks before migrating to their summer range. In early October, they migrated back to the spring/fall range where they remained for two months before returning to winter range. The dates they occupied this separate range coincide with expected peak rutting dates (November 16-19) in the Cassiar population based on backdating the population's peak lambing date of May 14 (Chapter 2) by 173-176 days as advised in Krausman and Bowyer 2003. This was the only band in this study to use rutting grounds that were spatially distinct from their winter range.

Migration routes and stopover sites

We mapped 8 migration corridors used by 12 geographic migrants from 8 different bands (Figure 3.6). The mean duration of spring migration was 8.5 days ranging from 1 to 26 days. Fall migrations were longer with a mean duration of 14.9 days and varied more across females than spring migrations from 2 to 59 days in length. We observed that 8 of 12 migrants from 4 bands used spring stopover sites while migrating to their summer range (Figure 3.6), and 11 of 12 migrants from all 9 bands used fall stopover sites. Females from the same band generally used the same stopover sites and over similar lengths of time. In contrast, bands varied in the length of time they used stopover sites. Some bands tended to use stopovers for short durations (<48 hours) and then continued their migrations, while other bands remained for multiple weeks before completing their migration. Interestingly, 4 of the 8 bands that used stopover sites during the spring did not return to the same stopover sites during their fall migrations, but instead travelled directly to their winter range or used different stopover sites.

Migration strategies

Geographic migrants

We first classified 12 females from 8 bands as geographic migrants, and 4 females from 2 bands as residents (Table 3.2). Geographic migrants exhibited little overlap between ranges with a mean of 2.9% (SE=1.3), while residents exhibited great amounts of overlap between seasonal ranges with a mean of 48.6% (SE=10.5) ranging from 25.6 to 74.8% (Table 3.2).

Geographic migrants varied substantially in the distances travelled between summer and winter ranges with a mean distance of 17.5km (SE=3.4) during spring and fall migrations, ranging from 6.2km to 45.9km (Table 3.2). In contrast, the mean Euclidian distances between seasonal ranges for residents was 2.1km (SE=0.3; Table 3.2). Most females travelled similar distances during spring and fall migrations as others in their band (Appendix 3.1). Of the 12 geographic migrants, we further classified 8 females as long-distance migrants, and 2 females as short-distance migrants, and 2 as vacillating migrants.

Altitudinal migration

The mean elevation used by females during this study was 1643m ± (SE=7.8). We found the collared females varied substantially in the elevations used throughout the year, which ranged from 772m to 2264m (Appendix 3.3). We found little variation in the elevations used between the summer and winter ranges with a population-level mean Δ elevation of 94m (SE = 15.5; range: 4-282m) (Table 3.2; Appendix 3.3). Most Stone's sheep did not occupy low elevation winter ranges that differed notably from summer range elevations, except for one female that was the only individual classified as a traditional altitudinal migrant (Appendix 3.3.3).

To assess for abbreviated altitudinal migration, we visually inspected each female's elevation use and GPS relocations. We found almost all females exhibited abbreviated altitudinal migration. As we expected, almost all females (n = 15) descended to lower elevations in mid-April to mid-May relative to their elevation-use during the whole year, likely following the spring green-up, and then gradually moved upwards over multiple weeks until arriving at high-elevation summer ranges in mid-July or August. All 15 females exhibited an increase in elevation of at least 100m from spring to summer months (Appendix 3.3.2.- example of a female's large altitudinal migration during the spring). Next, we found many females (n = 14) occupied intermediate to high elevations in winter months, typically from February 1 to April 15, relative to their elevation use throughout the rest of the year (Figure 3.2). Generally, these 14 females descended from high summer ranges to lower elevations during the fall and rut (September 15 - December 15), and then migrated > 100m back up to high winter ranges (Figure 3.2). Consequently, we defined 14 of 16 females as abbreviated altitudinal migrants. One female was classified as a traditional altitudinal migrant, and another female was defined as a resident because she remained within 150m of elevation throughout the entire year and did not exhibit clear seasonal changes in elevation use (Appendix 3.3.3).

DISCUSSION

Maintaining individual variation in migratory behaviours can be important for long-term population sustainability, and resilience to stochastic and unpredictable conditions (Webster et al. 2002, Schindler et al. 2010, Lowrey et al. 2019). Individual variation can develop as an adaptation to spatial variation in resources (Bolnick et al. 2020), yet we found no diversity in migration strategies across individuals, but rather across bands. Yet, similar to the Bolnick et al.

(2020) observation, spatial variation in resources and topography create opportunity for sheep among bands to have variable migrations and movement patterns.

Some ungulate populations show partial migration, with diverse migratory behaviours among individuals within a herd unit (Berg et al. 2019). However, we found almost all individuals within a band exhibited similar migratory movements, and thus, a partial migration pattern was not generally supported. The lack of individual diversity within bands suggests female individuals in the same band tend to adopt the same seasonal movements, possibly because these movements are best adapted to the distribution of resources and topography within their local landscapes, or because moving together as a gregarious unit helps reduce predation risk (Berger 1978, Festa-Bianchet 1986).

Among bands, we observed varying geographic migration strategies, including long-distance migration, short-distance migration, vacillating migration, and resident behaviour. Within these classes, we continued to observe variation among bands. For example, the 8 long-distance migratory bands varied in the distances travelled from 10.5km up to 46km, with some bands occupying multiple stopover sites for long durations and others bypassing stopovers altogether. These diverse movement patterns exhibited by different bands in the Cassiar population reflects the ability of ungulates to adopt movement patterns, likely over many generations (Jesmer et al. 2018), in response to the spatiotemporal heterogeneity of their local landscapes.

Ungulates adapt migration strategies that improve their fitness by accessing separate seasonal ranges that provide quality forage, critical resources (e.g., minerals or water), or to lower predation risks (Fryxell and Sinclair 1988, Ayotte et al. 2008, Hebblewhite et al. 2008, Mysterud et al. 2011). Although we cannot identify the mechanisms driving the migration strategies used by the Cassiar population in this study, we hypothesize these migration strategies have evolved to maximize fitness or to navigate pathways across linear features (e.g., lakes and rivers) or around established anthropogenically disturbed sites (e.g., Highway 37, Cassiar town site), and differ between bands in response to the availability and distribution of quality forage, mineral licks, lambing sites, variable predation pressures, landscape characteristics, and environmental conditions (e.g., deep snow accumulation) within each band's range. The forage maturation hypothesis (FMH) predicts that herbivores exhibit migrations during the growing season to maximize intake of new, high-protein forage by moving in concert with plant phenology (Albon and Langvatn 1992*b*, Hebblewhite et al. 2008). The spring migrations of the Cassiar populations may align with the FMH, because all spring migrations occurred during peak growing season (early May to late June), indicating females may have migrated to access better foraging opportunities on their summer range, compared to the available forage on winter range. In contrast, we suspect the 4 females from 2 bands that were residents had sufficient forage available on their winter range, and thus, did not adapt migration to a separate summer range. Regardless of geographic migrations, almost all females (15 of 16) exhibited spring altitudinal migrations. Generally, females descended to lower, subalpine elevations in early spring (Figure 3.2), coinciding with the onset of plant growth in subalpine habitats (D. R. Seip and Bunnell 1985), and then gradually migrated upwards, reaching peak elevations in July and August when peak productivity is expected at high alpine elevations (Seip 1983, Albon and Langvatn 1992*b*). The spring altitudinal migration exhibited by the Cassiar population corroborates many studies that have documented mountain ungulates 'surf the green-wave' during the growing season to maximize energy intake by accessing new forage growth at increasing elevations (Albon and Langvatn 1992*b*, Merkle et al. 2016). Our findings suggest the Cassiar population has likely evolved geographic and altitudinal migrations during the growing season to improve intake of nutritious, high-quality forage growth during the growing season.

We found the Cassiar population rarely exhibited the altitudinal migrations (high-elevation summer range to low-elevation winter range) commonly documented in bighorn populations (Spitz et al. 2017), but instead exhibited abbreviated altitudinal migration. Collared females typically descended from high-elevation summer ranges to lower elevations during the fall, and remained there for multiple months. In January and February, females made a second altitudinal migration to high-elevation winter ranges, where they remained for the winter (Figure 3.2). Similar migrations to high elevation winter ranges have been documented for some sheep populations, including the Elk Valley bighorn population in southern British Columbia (Poole et al. 2016), and the Teton bighorn population in Wyoming, USA (Courtemanch et al. 2017). Both studies found bighorn sheep selected high-elevation winter ranges on south-facing, windswept grasslands and ridgelines near escape terrain. Mountain sheep are strongly affected by winter severity and snow depth during the winter (Richardson et al. 2014), and previous work has linked harsh winters with above-average snowfall to loss in body fat, reduced juvenile survival, and population declines (Stelfox 1975, Burles and Hoefs 1984, White et al. 2008). Poole et al. (2016) suggested the Elk Valley bighorns wintered on high-elevation, south-facing, windswept ranges to avoid deep snow that accumulates at lower elevations in tree cover in this region, that may impact the population's ability to acquire forage, to move, and evade predators (Parker et al. 1984, Dailey and Hobbs 1989). The Cassiar population may also have used high elevations in winter to avoid deep snow at low elevations, and used open, windswept grasslands with greater sun exposure to access better foraging and improved mobility. The use of open, high-elevation winter ranges also might be advantageous in reducing predation risk, because these open areas provide better visibility to detect predators (Poole et al. 2016). Future research could evaluate winter habitat selection to better understand the landscape characteristics that make high-elevations suitable for Stone's sheep in the Cassiar Mountains, and elsewhere, during the winter.

Predation risk is another factor that can influence ungulate migrations (Bergerud et al. 1984, Fryxell and Sinclair 1988, Nicholson et al. 1997). We did not have data available on predator densities or predation risk across the Cassiar Mountains, and consequently, we could not identify if bands migrated to a separate summer range to reduce predation risk. However, we suspect that migratory bands experience high predation risks while migrating (Bolger et al. 2008), considering their migration routes are largely composed of 'risky' habitats located in wide valley bottoms, with little visibility and escape terrain, which is essential for predator evasion by mountain sheep (Geist 1971, Festa-Bianchet 1988*a*, Bleich et al. 1997). Additionally, Stone's sheep are more likely to encounter predators while on their migration route, because these low-elevation routes are expected to overlap with home ranges of wolves, grizzly bears, and black bears. Higher predation risks and elevated deaths from grizzly bears and wolves during migrating was observed during migrations of elk from a partially migratory population in southwestern Alberta, Canada (Hebblewhite et al. 2006, Hebblewhite and Merrill 2007). Long-distance migrants likely expose themselves to substantially higher predation risks during migrations, in comparison to short-distance migrants or residents that rarely travel through 'risky' habitats on valley bottoms. Many migratory females gave birth only 2-8 weeks before migrating to their summer ranges (Chapter 2), meaning these females and their young lambs likely experienced heightened predation risks during the spring migration. Despite the increased predation risks while migrating to a distant summer range and with a vulnerable lamb-at-heel, more females exhibited geographic migration (75%) than resident behaviour. This indicates that many bands have adapted migrations likely because the benefits of migrating to a distinct summer range exceed the potential costs of increased predation risk during migration (Bolger et al. 2008).

Studies have discovered stopover sites can play an important role in the migrations of temperate ungulates (Sawyer et al. 2009*a*, 2011, Blum et al. 2015, Paton et al. 2017, Monteith et al. 2018). Despite this, little is known about the use of stopover sites in bighorn and thinhorn sheep migrations. To our knowledge, our study is the first to demonstrate stopover site use in a Stone's sheep population. We found most migratory bands used stopover sites along their migration route, especially during fall migrations, and while at stopover sites, females remained mostly in subalpine and alpine habitats. Bands varied in the durations spent migrating and using stopover sites during spring and fall migrations (1-59 days). The differing use of stopover sites by bands in the Cassiar population may occur in response to the distribution and availability of forage growth along the migration route and on the summer range. We suggest bands that used stopover sites for multiple weeks during spring migrations may have been timing their migrations and stopover use with the leading edge of spring vegetation growth ('surfing the green-wave') to exploit new, protein-rich forage (Albon and Langvatn 1992*b*, Merkle et al. 2016), as has been demonstrated in mule deer migrations (Monteith et al. 2011, Sawyer et al. 2011, Aikens et al. 2017). In contrast, bands that used stopover sites for only a few days may use stopovers to quickly refuel, rest, and find refuge from predators before continuing their migrations, as commonly documented in the migrations of avian migrants (Klaassen and Lindstrom 1996, Åkesson and Hedenström 2007, Hedenström 2008). In response to linear corridors (e.g., Highway 37) and anthropogenic disturbances, the use of stop-over sites may also allow individuals to time their movements across a disturbance zone in a way that reduces mortality risk and avoids peak disturbance or human activity times (Figures 3.5 & 3.6). It could also be beneficial for Stone's sheep to minimize the time spent migrating, so they can arrive onto their summer range faster, and thus, gain quicker access to the resources provided on the summer range. Although we could not determine the factors that caused bands to adapt different patterns of stopover site use, the existence and use of stopover sites is likely an important component of mountain sheep migrations.

Most migratory bands used only a winter and summer range during the year. However, we observed four females from two bands that occupied separate seasonal ranges in the spring and fall. First, we observed two females from the same band travel and stay on a separate spring range for 3 weeks that was located outside of the migration route to the summer range (Figure 3.4). We suspect this band used their spring range to access minerals from a road-side mineral lick located within the spring range, despite the additional 16km they would have to travel to access their summer range. Mineral licks are an essential resource for mountain ungulates because they provide ingestible sodium and other elements to counter mineral deficiencies that occur when ungulates change from their winter diets to feeding on young, high-protein plant growth in the spring and summer (Jones and Hanson 1985, Ayotte et al. 2006). We did not observe other bands using distinct spring ranges associated with mineral licks, but some females visited known mineral licks during their spring migration and while on their summer ranges (see Figure 3.3 and 3.6). Our findings support studies that suggested the availability and distribution of mineral licks can influence the seasonal movements of mountain ungulates (Hebert and Cowan 1971, Jones and Hanson 1985), especially during the spring and summer when the need for minerals is highest (Heimer 1973, Ayotte et al. 2008). Another band with two females used an additional range in the spring and fall/rut (Figure 3.5). This was the only band that we found used a separate range from the winter range during the rut, and as a result, this range may have important consequences to the band’s reproduction and recruitment.

The Cassiar Mountains have low levels of anthropogenic disturbance, and because of this, we suspect most migration routes used by the Cassiar population have not been drastically altered or lost in response to anthropogenic impacts. However, we observed some females migrate through or occupy ranges on areas that have been modified by human land-use, and could have impacted their space-use patterns. We identified 3 females from 2 bands whose migration routes intersected Highway 37 (Figure 3.6). Consequently, these bands may be exposed to negative effects associated with road disturbance, such as increased mortality risk from road strikes, and other effects associated with highway disturbance like increased energy depletion and stress response, impeded movements to seasonal resources, and reduced genetic transfer (Papouchis et al. 2001, Frid and Dill 2002, Epps et al. 2005, Keller and Bender 2007). We do not know if these bands altered their traditional migration routes when Highway 37 was originally constructed or when it was subsequently paved and upgraded around 2012, or if their current migration routes are the same traditional routes used by past generations. Regardless, both bands are exposed to greater road disturbance during migrations than any other band in the Cassiar Mountains. These bands are currently able to navigate across Highway 37, but we do not know the level to which these bands may be negatively impacted by vehicle traffic on Highway 37. We recommend implementing speed reductions and road signage at the common crossing locations (Figure 3.6) to alert drivers to potential safety risk and reduce the potential for road collisions and other negative effects to result, and ultimately, to help ensure these important migration corridors remain intact (Chapter 2). We found an additional 6 females from 4 bands that occupied summer ranges overlapping with the abandoned open-pit Cassiar Asbestos Mine. This supports the assumption that Stone's sheep can adapt to using areas previously altered by open-pit mining during the summer when other aspects of human activity and disturbance are removed, but we do not know if there are consequences associated with using these abandoned mine sites. Besides these two examples, most Stone's sheep used habitats that were exposed to low levels of human disturbances; however, this may change with increasing recreational activities (e.g., motorized vehicle use, tourism) and potential expansions to resource development.

Ungulate migrations are being affected by anthropogenic influences and disturbances worldwide, resulting in migration loss and declines of migratory populations (Berger 2004, Bolger et al. 2008, Harris et al. 2009). Losing native ungulate migrations because of habitat loss or anthropogenic barriers (e.g., highways, fencing) can diminish population stability and persistence (Whyte and Joubert 1988, Ben-Shahar 1993, Harris et al. 2009); and, if long-evolved ungulate migration strategies are lost, they are likely to be lost indefinitely (Jesmer et al. 2018, Lowrey et al. 2019). In this study, we delineated 8 migration corridors used by migratory bands within the Cassiar Mountains (Figure 3.6). We provide a baseline description of Stone's sheep space-use in the Cassiar Mountains, by classifying geographic and altitudinal migration strategies, and delineating seasonal ranges, stopover sites, and migration corridors. We believe that having these patterns documented should allow managers to mitigate overlap of human disturbance and space-use patterns to help conserve the diverse migration strategies of the Cassiar Stone's sheep population.

TABLES

Table 3.1. Summaries of start and end dates of spring and fall migrations for female Stone's sheep classified as geographic migrants in 2018 or 2019 (*n* =12) in the Cassiar Mountains, BC, Canada. Summary information includes minimum, median, maximum dates and 33rd and 66th percentiles for spring and fall migrations.

Migration dates	**Min**	**33%**	**Median**	**66%**	**Max**
Spring start	16-May	06-Jun	12-Jun	22-Jun	10-Jul
Spring end	18-May	14-Jun	19-Jun	26-Jun	05-Aug
Fall start	16-Aug	26-Aug	20-Sep	03-Oct	11-Dec
Fall end	23-Aug	21-Sep	07-Oct	11-Oct	07-Jan

Table 3.2. Summaries of percent of overlap (%), area of overlap (km^2), Euclidean distance (km), and elevation change (Δ elevation; m) between summer and winter ranges delineated with 95% Brownian bridge utilization distributions of 16 female Stone's sheep classified as a geographic migrant (*n* =12) and resident (*n* =4) in the Cassiar Mountains, BC, Canada, 2018 - 2019.

Parameter	Migration Tactic	$\bar{x}$	SE	Range
overlap (%)	migrant	2.9	1.3	0 - 10.6
	resident	48.6	10.5	25.6 - 74.8
area overlap (km2)	migrant	2.1	0.9	0 - 14.9
	resident	28.8	3.6	16.3 - 47.3
Euclidean distance (km)	migrant	17.5	3.4	6.2 - 45.9
	resident	2.1	0.3	0.3 - 7.6
Δ elevation	migrant	100.3	25.6	3.5 – 281.9
	resident	66.8	12.8	41.3 - 106.1

FIGURES

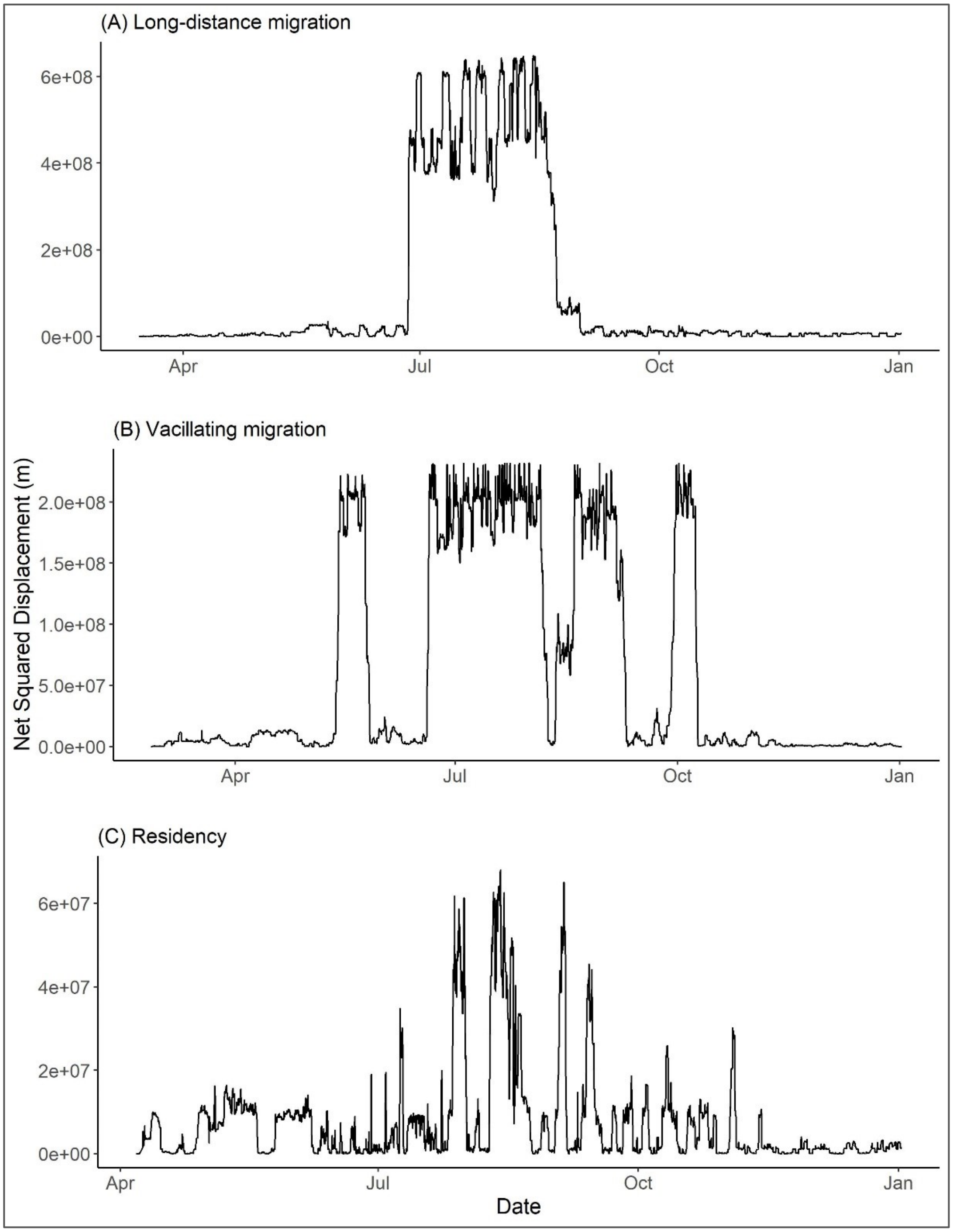

Figure 3.1. Examples of net squared displacement (m) from the winter range of collared female Stone's sheep in the Cassiar Mountains, Canada from March 2019 – January 2020; (A) long-distance migration, (B) vacillating migration, and (C) residency.

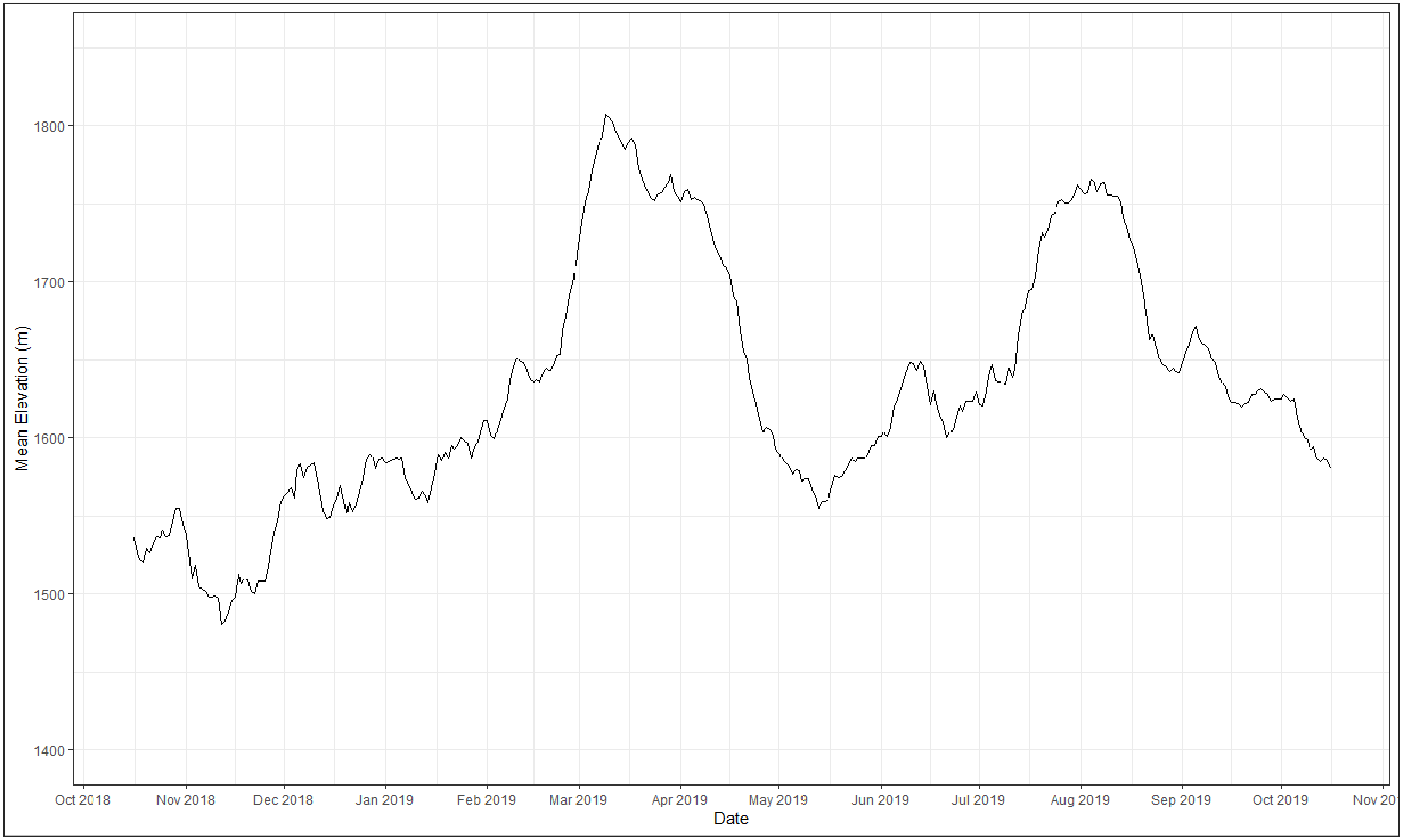

Figure 3.2. Mean daily elevations calculated with a 14-day moving window of collared female Stone's sheep (*n*=16) in the Cassiar Mountains, British Columbia, Canada, Oct 2018 – Oct 2019.

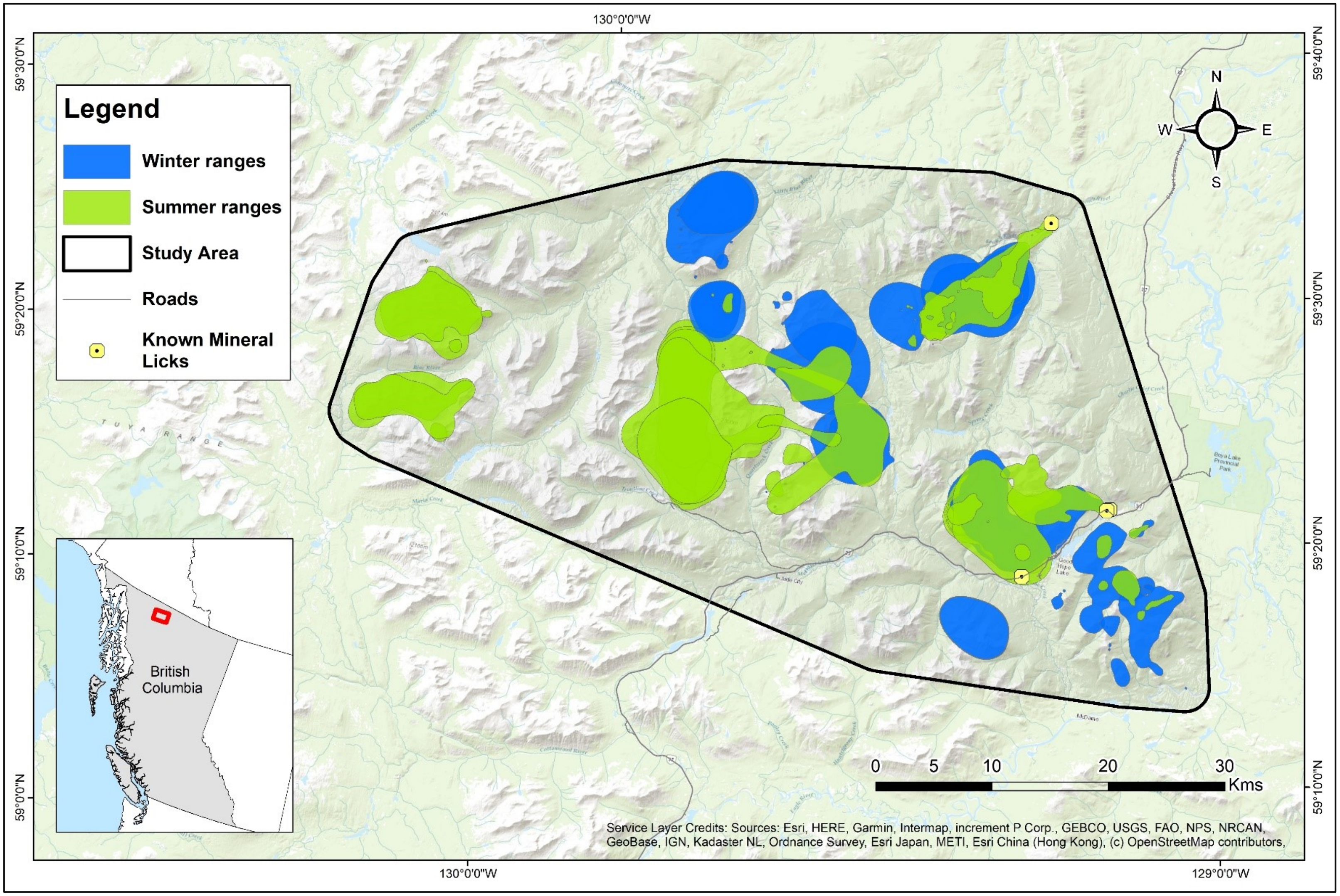

Figure 3.3. Summer and winter ranges of collared female Stone's sheep (*n*=16) in the Cassiar Mountains study area, British Columbia, Canada, 2018 – 2019. Summer ranges are shown in green and winter ranges in blue.

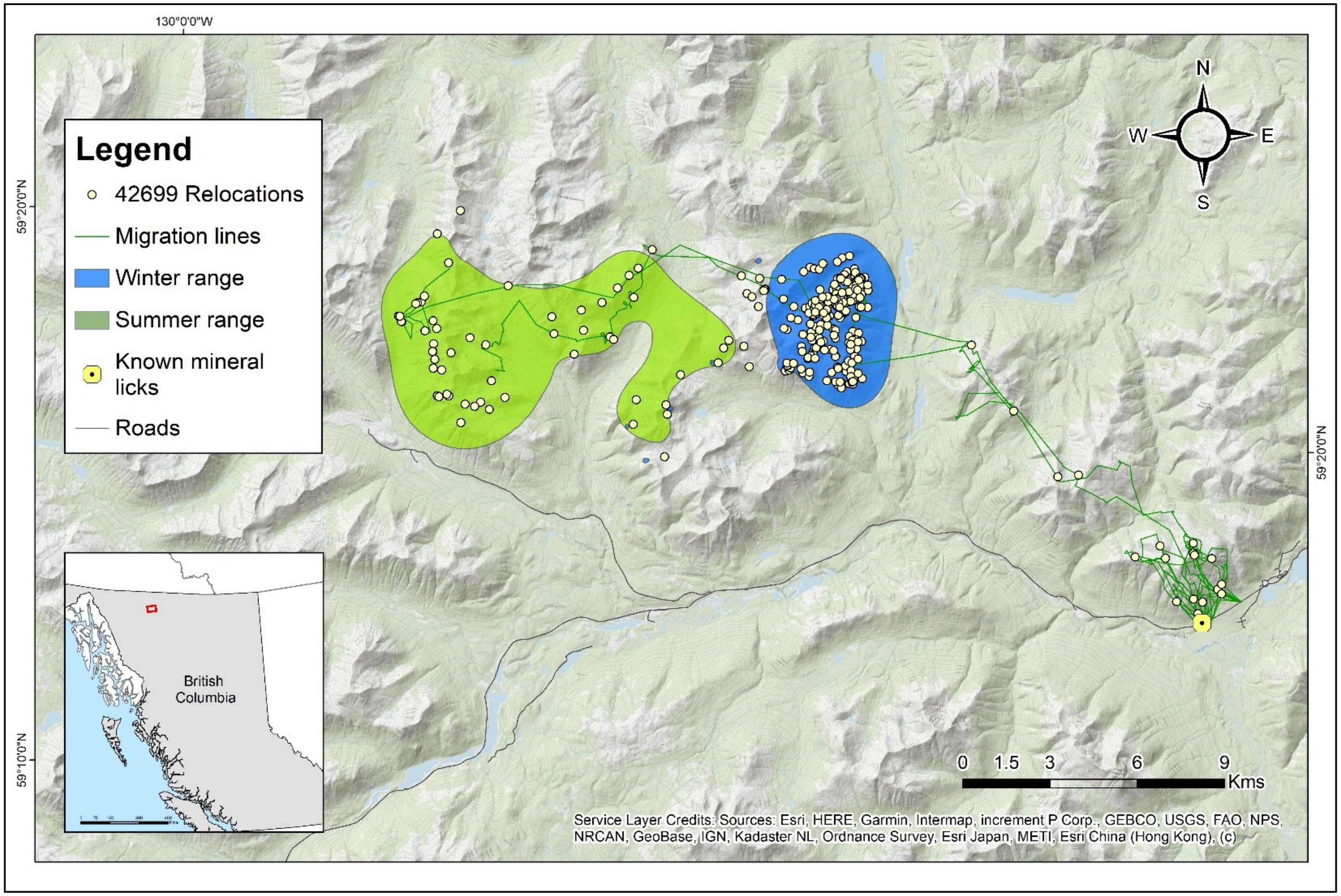

Figure 3.4. Mapped spring migration route of collared female Stone's sheep #42696 in the Cassiar Mountains, British Columbia, Canada, from May 2019 – April 2020. This map depicts the female's daily GPS relocations, winter range, summer range, and spring migration route line. A known mineral lick is depicted with a yellow marker, and Highway 37 and other roads are displayed with a grey line. The spring stopover site is located at the spatial cluster of GPS relocations located near the mineral lick located close to Highway 37.

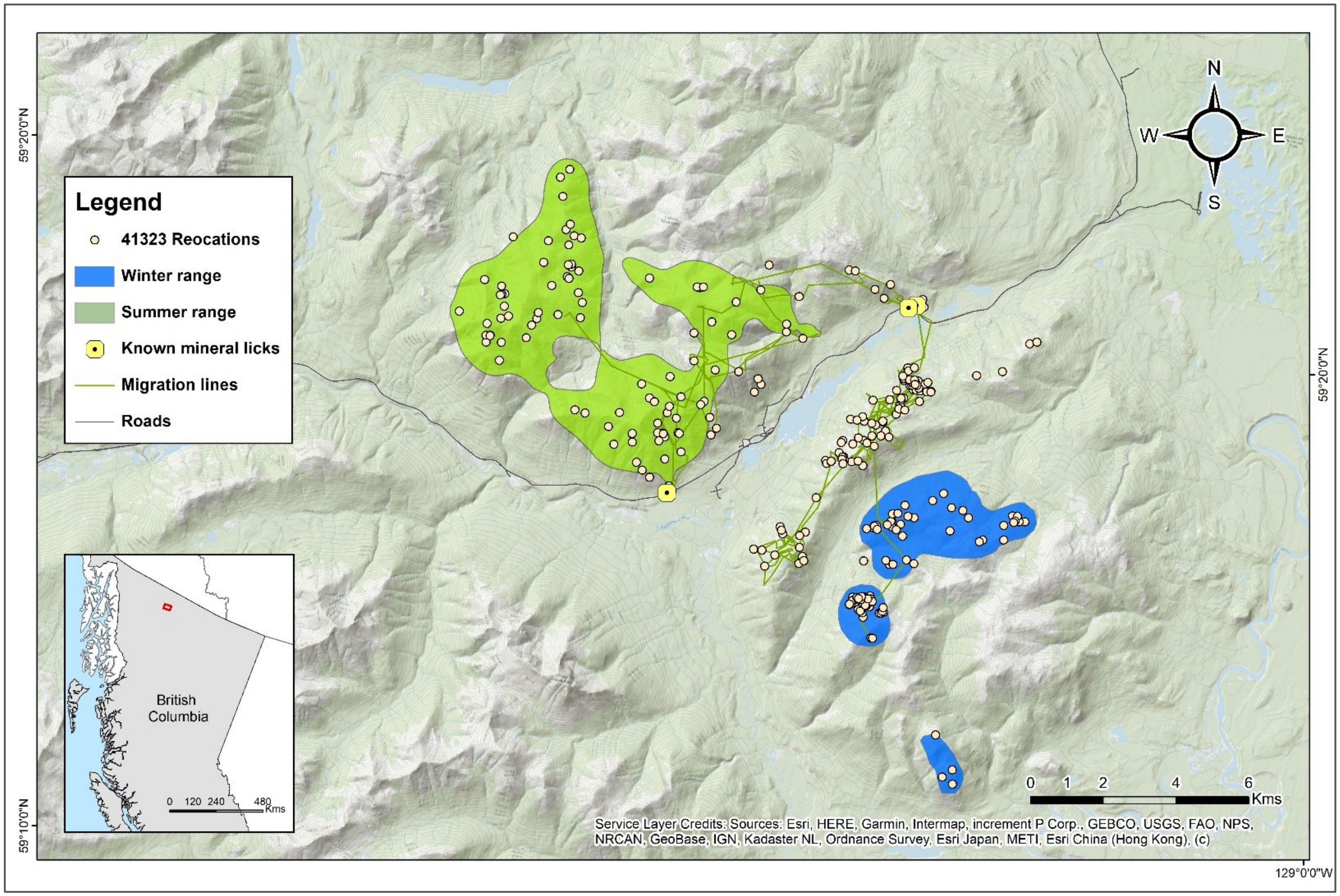

Figure 3.5. Mapped spring and fall migration routes of a collared female Stone's sheep (id: 41323) in the Cassiar Mountains, British Columbia, Canada, from May 2018 – April 2019. This map depicts the female's daily GPS relocations, winter range, summer range, and spring migration route line. Known mineral licks are depicted with yellow markers, and Highway 37 and other roads are displayed in grey. The spring/fall/rut stopover site is located at the spatial cluster of relocations located between winter range and Highway 37.

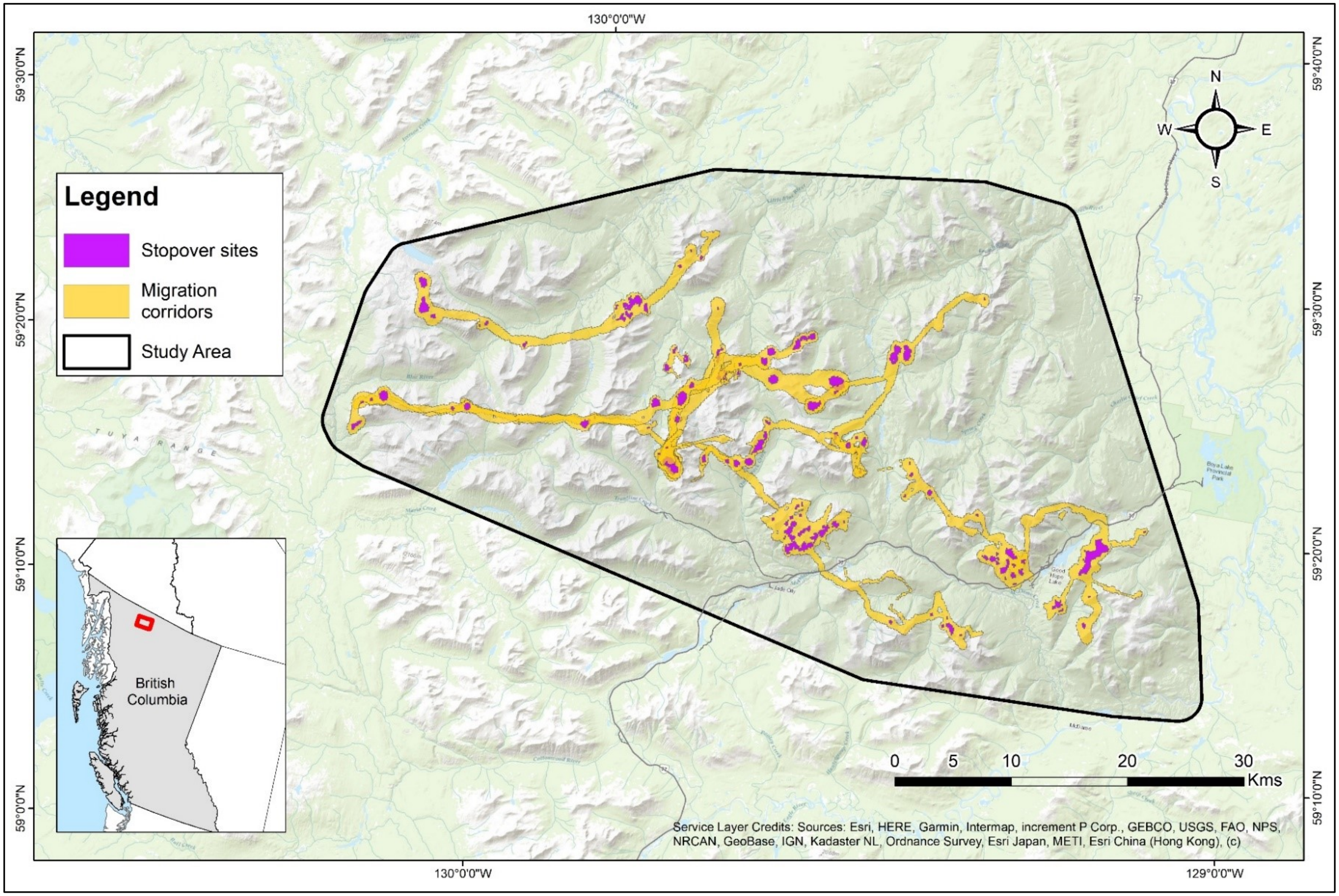

Figure 3.1. Migration corridors and stopover sites used during spring and fall migrations by female Stone's sheep migrants (*n*=12) in the Cassiar Mountains, British Columbia, Canada, 2018 – 2019.

Chapter 4 – Conclusion

A major objective of the Cassiar Stone's Sheep Study was to evaluate seasonal movements and habitat use of Stone's sheep to provide information that could help the Province of British Columbia, regional biologists, and local First Nations Governments making land-use and management decisions. In this thesis, I met this overall objective by evaluating critical lambing and nursery habitat selection (Chapter 2), and examining seasonal migration and habitat use patterns (Chapter 3).

In Chapter 2, I first delineated the timing and locations of lambing events in the Cassiar population, which occurred within the expected lambing season of mountain sheep at northern latitudes (Festa-Bianchet 1988*c*, Rachlow and Bowyer 1991). Next, I estimated resource selection models during the lambing and nursery periods, and found habitat selection was influenced by elevation, slope, ruggedness, NDVI, aspect, and distance to roads, similar to other work on bighorn sheep and Dall's sheep (Rachlow and Bowyer 1998, Smith et al. 2015, Robinson et al. 2020). I found females avoided roads during the lambing period, but selected habitats near roads during the nursery period. I suspect this occurred because females were attracted to the clusters of mineral licks located along Highway 37. Incorporating known mineral lick sites as a covariate in RSFs and ISSAs on mountain sheep may be important to account for the influence of mineral licks on habitat selection. I found females generally exhibited consistent patterns of selection across home range and fine spatial scales. However, I found some variations in the relative selection of elevation and NDVI across scales. I suggested the variations in relative selection of elevation occurred due to limited heterogeneity in elevation at fine scales, and in NDVI because foraging occurs at a fine, localized spatial scale (Boyce 2006) and thus NDVI at the home range scale was too variable compared to their local landscape. Resultingly, this study demonstrated the importance of considering scale when evaluating and interpreting individual or population level resource selection. Our study provides the first resource selection functions and integrated step selection analyses for Stone's sheep during lambing and nursery periods. Additionally, I developed predictive maps of relative habitat suitability during lambing and nursery periods across the Cassiar Mountain study area, which I hope will be beneficial for management and land-planning in the region.

In Chapter 3, I evaluated seasonal space-use of females in the Cassiar Mountains by examining home ranges, migration corridors, stopover sites, and classifying individual migrations strategies. I found diverse migration strategies exhibited across bands, including long-distance, short-distance and vacillating migration and resident behaviour. I also found diversity amongst bands in the timing and length of migrations, stopover site use, and number of seasonal ranges used. This provides evidence that diversity in migratory behaviours in spatially structured populations may be driven in response to local distributions and availability of resources, topography, and predation pressures. I found little evidence of individual variation within bands base don the migration behaviours exhibited by collared females in this study. In this chapter, I provided maps of the seasonal ranges, stopover sites, and migration corridors used by the Cassiar population. Berger et al. (2004) identified that preserving migrations of large mammals will likely be one of the greatest challenges for biologists in the 21st century. Harris et al. (2009) noted that the migration routes and seasonal ranges used by many ungulate populations are unknown, and emphasized the importance of identifying seasonal ranges and migration routes to implement effective conservation actions. My study provides the first delineation of migration routes, seasonal ranges and stopover sites used by Stone's sheep in the Cassiar Mountains, which can help identify areas of high conservation priority.

I hope the information provided in this thesis can be used in future management and land-planning initiatives in the Cassiar Mountains. I recommended implementing closures around predicted suitable lambing and nursery ranges provided in Chapter 2, as well as the seasonal ranges and migratory corridors presented in Chapter 3, to prevent possible disturbances, habitat loss or fragmentation from future commercial or recreational activities. I found the migratory routes of 2 bands intersected with Highway 37, and multiple nursing females used habitats close to the edge of Highway 37 to access mineral licks. To mitigate the risk of road strikes, and to help sustain the migrations of these 2 bands, I suggest installing road signage and speed reductions on short segments of Highway 37 near the known highway crossings. Lastly, I hope the findings from this thesis can be incorporated into future iterations of the Dease-Liard Sustainable Resource Management Plan (SRMP) and future land-planning initiatives in the Cassiar Mountains.

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Appendix 2.1. Resource Selection Function Candidate Model Set

Table 2.1.1. Candidate model set of 17 resource selection functions (RSF) used to estimate the habitat selection of 23 maternal female Stone's sheep during lambing and nursery periods in the Cassiar Mountains, 2018-2020.

Model Name	Variables[a]
Model 1 (Global)	Base + NDVI + N + E + R + RDS
Model 2	Base + NDVI + N + E + R
Model 3	Base + NDVI + N + E + RDS
Model 4	Base + N + E+ R + RDS
Model 5	Base + NDVI + N + E
Model 6	Base + N + E + R
Model 7	Base + N + E + RDS
Model 8	Base + NDVI + R + RDS
Model 9	Base + N + E
Model 10	Base + NDVI + R
Model 11	Base + R + RDS
Model 12	Base + NDVI + RDS
Model 13	Base + NDVI
Model 14	Base + R
Model 15	Base + RDS
Model 16 (Base)	$EL + EL^2 + S + S^2$
Model 17	Null

[a] EL = elevation, S = slope, N = northness, E = eastness, R= vector ruggedness measure, RDS = exponential decay function of Euclidean distance to roads, NDVI = total averaged maximum normalized vegetation index ($NDVI_{total\_max}$) across 2018-2020.

Appendix 2.2. Timing and synchronicity of lambing events across study years

The median birthdate during this study was May 14th, and ranged from May 4th to June 14th across study years. Although our birthdate estimates fall within the lambing seasons observed in other thinhorn and bighorn populations at northern latitudes (Bunnell 1980, Thompson and Turner 1982, Festa-Bianchet 1988*c*, Rachlow and Bowyer 1991, Grigg et al. 2017), we were able to detect and observe some annual variation in the timing and synchronicity of lambing events. Parturition in ungulate populations living in northern environments is known to coincide with the onset of the growing season (Berger 1979, Bunnell 1982, Festa-Bianchet 1988*a*). A lamb's birthdate can have impacts to their fitness and survival, with neonatal ungulates born after peak-parturition dates found to have reduced survival to 5 months old and yearling age (Clutton-Brock et al. 1987, Festa-Bianchet 1988*c*, Keech et al. 2000). Late-born lambs are more likely to enter fall and winter in poorer body condition than early-born lambs, and may be less adept to survive harsh winter conditions when forage is sparse and thermoregulation demands are high (Bunnell 1982, Festa-Bianchet 1988*c*, Festa-Bianchet et al. 2000). The body conditions of late-born lambs are often worse at the end of the summer, first because they likely receive less milk from their mother and of lower quality, since their mother must produce milk from older, less nutritious forage. Furthermore, late-born lambs may be born too late to beneficially graze on the highly nutritious forage that emerges earlier in the growing season (Berger 1979, Festa-Bianchet 1988*c*, Rachlow and Bowyer 1991). Because of this, we expected parturient Stone's sheep to give birth early in the lambing season for that to be synchronized with other mothers to exploit the nutritious forage growth occurring at the beginning of the growing season.

Birthdates in 2019 occurred earliest with the median birthdate of May 15th and were more synchronized over 30 days, in comparison to the birthdates in 2018 and 2020 that occurred later both with a median birthdate of May 30th, and less synchronized over 41 and 39 days, respectively (Figure B-1). The timing of parturition is likely related to environmental conditions during fall and winter seasons that can influence the timing of conception by impeding movements during the rut, and can influence the length of gestation and fetus development impacted by resource availability in winter (Millar 1977, Kiltie 1982, Skogland 1984). The annual variation in birthdates observed in this study could also be affected by low sample sizes in

2018 (*n* =4) and 2020 (*n* =6), compared to 2019 (*n* =13), which may have incorrectly represented the range of birthdates at the population level during these years. As anticipated with a species such as Stone's sheep, environmental conditions likely play a significant role in influencing the timing of lambing events that we documented for the collared Stone's sheep in this study. Future research on the influence environmental factors, such as snowfall amount and duration, and temperatures have on the timing of parturition in Stone's sheep would be very informative to land and resource managers, and offer improved understanding of the timing of critical life-stage periods.

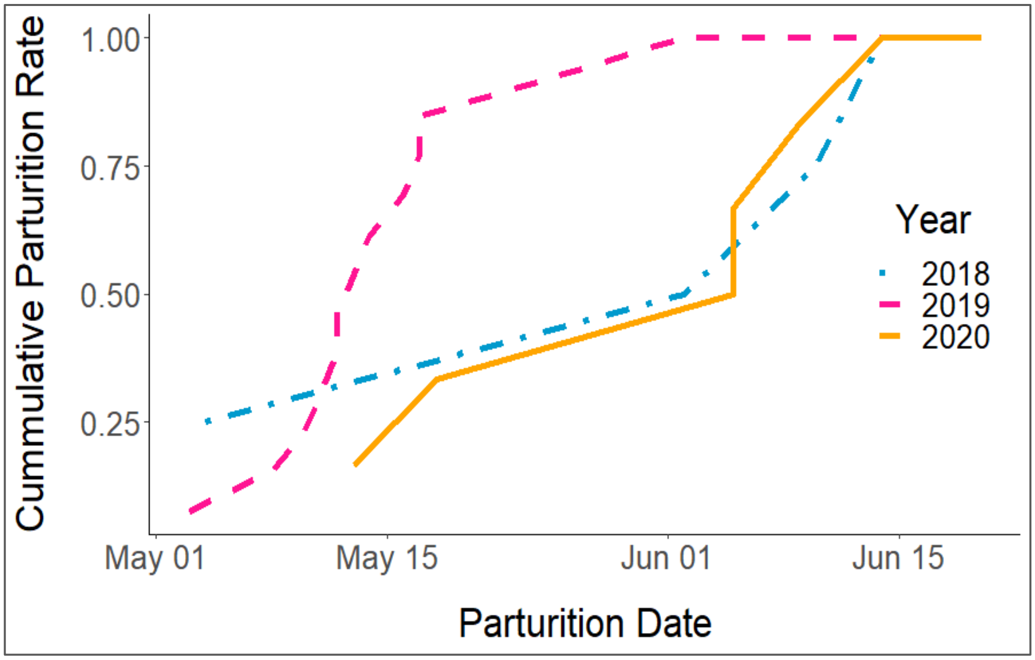

Figure 2.2.1. Cumulative proportion of parturition dates of Stone's sheep female-years in 2018 (*n* =4), 2019 (*n* =13), and 2020 (*n* =6) in the Cassiar Mountains, British Columbia, estimated by evaluating for abrupt changes in movement patterns exhibited by collared female Stone's sheep during the lambing season.

Appendix 2.3. Ranked resource selection functions for lambing and nursery periods

Table 2.3.1. Ranked resource selection models for the lambing period, variables included in each model, Akaike's Information Criterion corrected for small sample size (AICc), and difference in AICc scores (Δ AICc) between consecutive models estimated using GPS relocation data collected from female Stone's sheep (*n* =23) in the Cassiar Mountains from 2018-2020.

Model	**Variables** [a]	**AICc**	**Δ AICc**
Model3	EL + EL^2 + S + N + E + R + RDS	7713.39	0.00
Global	EL + EL^2 + S + NDVI + N + E + R + RDS	7715.11	1.71
Model1	EL + EL^2 + S + NDVI + N + E + R	7911.55	198.16
Model5	EL + EL^2 + S + N + E + R	7912.89	199.50
Model6	EL + EL^2 + S + N + E + R + RDS	8124.98	411.59
Model2	EL + EL^2 + S + NDVI + N + E + RDS	8126.82	413.43
Model7	EL + EL^2 + S + NDVI + R + RDS	8146.78	433.39
Model10	EL + EL^2 + S + R + RDS	8147.55	434.15
Model9	EL + EL^2 + S + NDVI + R	8274.03	560.64
Model13	EL + EL^2 + S + R	8283.68	570.29
Model4	EL + EL^2 + S + NDVI + N + E	8323.02	609.63
Model8	EL + EL^2 + S + N + E	8324.88	611.49
Model11	EL + EL^2 + S + NDVI + RDS	8509.21	795.82
Model14	EL + EL^2 + S + RDS	8510.05	796.66
Model12	EL + EL^2 + S + NDVI	8642.67	929.27
Model15	EL + EL^2 + S	8652.98	939.59
Null	Null	10888.04	3174.65

[a] EL = elevation, S = slope, N = northness, E = eastness, R= vector ruggedness measure, RDS = exponential decay function of Euclidean distance to roads, NDVI = total averaged maximum normalized vegetation index ($NDVI_{total\_max}$) across 2018-2020.

Table 2.3.2. Ranked resource selection models for the nursery period, variables included in each model, Akaike's Information Criterion corrected for small sample sizes (AICc), and difference in AICc scores (Δ AICc) between consecutive models estimated using GPS relocation data collected from female Stone's sheep (*n* =23) in the Cassiar Mountains from 2018-2020.

Model	**Variables** [a]	**AICc**	**Δ AICc**
Global	$EL + EL^2 + S + NDVI + N + E + R + RDS$	135408.7	0
Model1	$EL + EL^2 + S + NDVI + N + E + R$	136230.3	821.6111
Model7	$EL + EL^2 + S + NDVI + R + RDS$	136399.3	990.5805
Model3	$EL + EL^2 + S + N + E + R + RDS$	136409.6	1000.845
Model10	$EL + EL^2 + S + vrm5 + R + RDS$	137253.5	1844.803
Model5	$EL + EL^2 + S + N + E + R$	137328.1	1919.364
Model9	$EL + EL^2 + S + NDVI + R$	137337.8	1929.089
Model13	$EL + EL^2 + S + R$	138286.1	2877.35
Model2	$EL + EL^2 + S + NDVI + N + E + RDS$	138895.4	3486.705
Model4	$EL + EL^2 + S + NDVI + N + E$	139530.6	4121.906
Model11	$EL + EL^2 + S + NDVI + RDS$	139763.4	4354.622
Model6	$EL + EL^2 + S + N + E + RDS$	139794.9	4386.172
Model12	$EL + EL^2 + S + NDVI$	140497.9	5089.166
Model8	$EL + EL^2 + S + N + E$	140525.2	5116.439
Model14	$EL + EL^2 + S + RDS$	140529.8	5121.034
Model15	$EL + EL^2 + S$	141356.3	5947.558
Null	Null	163367.2	27958.43

[a] EL = elevation, S = slope, N = northness, E = eastness, R= vector ruggedness measure, RDS = exponential decay function of Euclidean distance to roads, NDVI = total averaged maximum normalized vegetation index ($NDVI_{total\_max}$) across 2018-2020.

Appendix 2.4. Additional parturition information by female-year

Table 2.4.1. Parturition dates, days spent at parturition site, and number of GPS relocations in parturition seasons of 2018- 2020, mean values across entire study period, and parturition rate across years, estimated for individual female Stone’s sheep and the total population in the Cassiar Mountains, British Columbia, Canada in 2018-2020 (*n* =23). Females that were alive, but were not estimated to be parturient and females that were dead or not collared during the parturition season are indicated with no text.

		2018			**2019**			**2020**	
Female	**Age at capture**	**Parturition date**	**Days of parturition**	**VIT expulsion date**	**Parturition date**	**Days of parturition**	**VIT expulsion date**	**Parturition date**	**Days of parturition**
41316	4								
41318	4				13-May	3.63		18-May	9.92
41319	6								
41320	4	02-Jun	7.0	28-May	22-May	1.67		06-May	11.29
41321	6								
41322	5	04-May	5.63	4-May	11-May	8.63		05-Jun	2.67
41323	4	10-Jun	9.71	8-June					
41324	6	14-Jun	4.09	14-June	03-May	4.17			
42695	8				16-May	5.79	17-May	14-Jun	6.75
42696	4				17-May	3.79	17-May		
42697	4				16-May	6.08	16-May	05-Jun	6.88
42698	7								
42699	5				12-May	5.54	13-May		
42700	8				08-May	3.46	08-May	09-Jun	1.5
42701	3				02-Jun	7.79	02-Jun		
42702	6				26-May	4.79	25-May		
42703	6				14-May	5.42	14-May		
42704	7				12-May	2.92	12-May		

Appendix 2.4. continued. Additional parturition information by female-year

	Total study years		
Female	**Parturition date ($\bar{x}$)**	**Days of parturition ($\bar{x}$)**	**Parturition rate**
41316			
41318	15-May	6.77	0.67
41319			
41320	20-May	6.65	1
41321			
41322	17-May	5.64	1
41323	10-Jun	9.71	1
41324	24-May	4.13	0.67
42695	16-May	6.27	1
42696	17-May	3.79	0.5
42697	16-May	6.48	1
42698			0
42699	12-May	5.54	0.5
42700	24-May	2.48	1
42701	02-Jun	7.79	0.5
42702	26-May	4.79	0.5
42703	14-May	5.42	0.5
42704	12-May	2.92	0.5
$\bar{x}$	22-May	5.62	0.72
Median	17-May	5.63	0.67

Appendix 2.5. K-fold cross validation results from population-level home range RSFs

Table 2.5.1. Spearman-rank correlations (r_s) for individual and average folds from 5-fold cross-validations of top lambing and nursery habitat selection models. Spearman-rank correlations and p-values of each fold and mean ($\bar{r}_s$) are provided.

	Lambing period		**Nursery period**	
Fold	r_s	p	r_s	p
1	0.96	< 0.0001	0.90	< 0.001
2	0.92	< 0.002	0.87	< 0.01
3	0.98	< 0.0001	0.81	< 0.01
4	0.99	< 0.0001	0.84	< 0.01
5	0.98	< 0.0001	0.87	< 0.01
$\bar{r}_s$	0.97	< 0.0001	0.86	< 0.01

Appendix 2.6. Exploring resource selection for individual female-years during the lambing and nursery period

We observed little variation in habitat selection across individual female-years throughout the lambing period, and some variation among female-years throughout the nursery period (Table 2.6.1). All female-years (*n* =23) selected for intermediate elevation, intermediate slopes, and rugged terrain. As we expected, most females-years selected southwest slopes, while 3 of 23 (13%) female-years selected northeast-facing slopes during lambing periods. In this study, 7 females gave birth multiple times, and we found almost all repeat mothers (6 of 7) selected the same habitat features as the previous year, possibly indicating fidelity to specific habitat features. All female-years that had roads within or near their available locations at 200m or less (*n* =11) expressed significant avoidance of roads during the lambing period.

During the nursing period there was some variation in habitat features selected among female-years related to the slope, aspect and ruggedness. We found all females selected intermediate elevations and most selected for high slopes (17 of 23); all female-years that had roads within or near their domain of availability (< 200m; *n* =11) surprisingly selected for habitats closer to roads (however this may be a function of the proximity of roads to the location of important mineral licks used by the ewes). Variation in ruggedness occurred between female-years with 16 of 23 individuals selected for ruggedness, meanwhile, 7 of 23 females avoided rugged terrain. The aspects selected during the nursery period also varied between individuals with 13 of 23 selecting southwest faces, and 10 of 23 selecting northeast faces. The selection of greenness varied between individuals with 13 of 23 individuals avoiding high greenness (this may be a function of the availability of preferred forage types rather than a true reflection of NDVI) and

10 of 23 selecting for habitats with high maximum NDVI. Overall, more variation was observed between female-years during the nursery period than the lambing period.

Table 2.6.1. Variable estimates (β_i), standard error, and sign or shape of β_i from the top-ranking lambing and nursery resource selection models for individual female Stone's sheep in the Cassiar Mountains, British Columbia, Canada 2018-2020.

	Lambing			**Nursery**		
Variable	**(β)**	**(SE)**	**β_i sign or shape**[a]	**(β)**	**(SE)**	**β_i sign or shape**[a]
Elevation	3.05	0.48	23 (∩)	4.01	0.12	23 (∩)
Elevation^2	-2.45	0.43		-2.96	0.10	
Slope	1.39	0.05	23(+), 0(-)	0.41	0.01	17(+), 6(-)
NDVI$_{max}$				-0.31	0.01	10(+), 13(-)
Northness	-0.57	0.03	4(+), 19(-)	-0.16	0.01	10(+), 13(-)
Eastness	-0.36	0.03	4(+), 19(-)	-0.17	0.01	10(+), 13(-)
Ruggedness	0.46	0.02	21(+), 2(-)	0.29	0.01	16(+), 7(-)
Exponential decay distance to roads	3.94	0.38	11(+), 0(-)	-0.49	0.02	0(+), 12(-)

[a] ∩ indicates selection for intermediate values of a variable with a positive β_i for linear variable and a negative β_i for the squared variable.

Appendix 2.7. Trail camera photos of Stone's sheep mineral lick use

Figure 2.7.1. Captured trail camera photos of Stone's sheep licking soils at the Mud Lake mineral lick in the Cassiar Mountains, British Columbia, Canada. (A) A captured photo of a collared female (id:42700) and yearling licking salts on May 7, 2019. (B) Two Stone's sheep rams licking salts on June 5, 2020. Numerous Stone's have been observed licking soils at the Mud Lake mineral lick during this study, 2018-2020.

Figure 2.7.2. Collared female Stone’s sheep (id: 41322) and her lamb licking soils at a roadside mineral lick located less approximately 5m from Highway 37 near Mud Lake in the Cassiar Mountains, British Columbia, Canada in September 2019. Photo credit: Cat Lee.

Figure 2.7.3. Photo of a Stone’s sheep ewe licking salts off of Highway 37 near Mud Lake in the Cassiar Mountains, British Columbia, Canada that were manually added during the winter of 2003 to prevent freezing on the highway. Photo credit: Bill Jex.

Appendix 3.1. Summary of geographic and altitudinal migration strategies by individuals and bands

Table 3.1.1. Band number (No.; 1-9) order by descending Euclidean distances (km), number of females in each band (*n*), study year, percent overlap (%), area (km2) of overlap, Euclidean distance (km) between summer and winter ranges, change in mean elevations (Δ elevation) in meters in winter and summer seasons, and the classified geographic and altitudinal migration strategies for each collared female Stone's sheep (*n* = 16) in the Cassiar Mountains, British Columbia, Canada, 2018-2020.

Band No.	*n*	Female ID	Year	Overlap (%)	Area of overlap (km2)	Euclidean distance (km)	Δ elevation (m)	Geographic migration strategy[a]	Altitudinal migrations strategy[b]
1	1	42696	2019	0	0.00	45.87	116.99	LDM	ABR
2	1	42703	2019	0	0.00	31.56	43.56	LDM	ABR
3	2	42701	2019	0	0.00	22.34	201.51	LDM	ABR
		42704	2019	0	0.00	23.25	281.90	LDM	TRAD
4	3	42698	2019	0	0.00	17.82	166.59	LDM	ABR
		41320	2019	32.54	16.32	1.02	106.13	RES	ABR
		42702	2019	48.12	23.28	1.66	58.80	RES	ABR
5	1	41324	2019	0	0.00	15.01	3.45	LDM	ABR
6	2	41318	2019	2.33	2.24	11.21	39.54	LDM	ABR
		42699	2019	1.02	0.80	10.51	120.81	LDM	ABR
7	2	41321	2018	10.48	7.10	9.66	65.06	V-SDM	ABR
		41323	2018	0	0.00	9.43	152.30	V-SDM	ABR
8	2	42695	2019	10.64	7.69	6.19	7.71	SDM	ABR
		42697	2019	10.54	7.68	6.85	4.00	SDM	RES
9	2	41322	2019	28.17	20.18	1.40	48.53	RES	ABR
		42700	2019	74.78	33.31	0.34	61.71	RES	ABR

[a] Geographic migration strategies include, long-distance migration (LDM), short-distance migration (SDM), vacillating short-distance migration (V-SDM), and residency (RES).

[b] Altitudinal migration strategies include, abbreviated altitudinal migration (ABR), traditional altitudinal migration (TRAD), and residency (RES).

Appendix 3.2. Start and end dates of seasonal migrations

Table 3.2.1. Start and end dates of spring and fall migrations and length of migration in days for each collared female Stone's sheep classified as a geographical migrant (n = 12), and mean duration in days across all collared migrants in the Cassiar Mountains, British Columbia, Canada, 2018-2020.

	Spring migration			**Fall migration**		
Female	Start date	End date	Duration (days)	Start date	End date	Duration (days)
41318	2019-06-05	2019-06-17	12	2019-08-21	2019-08-24	3
41321	2018-05-20	2018-06-14	25	2018-08-21	2018-08-23	2
41323	2018-06-26	2018-07-05	9	2018-09-27	2018-10-31	34
41324	2019-05-25	2019-05-28	3	2019-10-08	2019-10-11	3
42695	2019-06-12	2019-06-13	1	2019-12-11	2020-01-07	27
42696	2019-06-25	2019-07-04	9	2019-08-16	2019-10-14	59
42697	2019-06-10	2019-06-11	1	2019-12-11	2020-01-07	27
42698	2019-07-10	2019-08-05	26	2019-09-19	2019-10-03	14
42699	2019-06-05	2019-06-26	21	2019-08-17	2019-08-23	6
42701	2019-06-29	2019-07-01	2	2019-09-09	2019-09-21	12
42703	2019-06-12	2019-06-17	5	2019-09-21	2019-09-24	3
42704	2019-06-26	2019-06-27	1	2019-08-20	2019-09-01	12
$\bar{x}$			**8.5 days**			**14.9 days**

Appendix 3.3. Evaluating elevation use by collared female Stone's Sheep

Table 3.3.1. Summary of elevation use including the minimum (min), maximum (max), mean ($\bar{x}$), and standard error (SE) for all collared female Stone's sheep (n =16) in the Cassiar Mountains, British Columbia, Canada, 2018-2020.

	Elevation (m)			
Female	**min**	**max**	**$\bar{x}$**	**SE**
41318	817.3	2089.2	1719.8	5.4
41320	850.6	1853.2	1476.3	6.2
41321	788.9	1941.7	1601.6	14.3
41322	788.3	1953.1	1550.4	8.1
41323	772.0	1913.0	1437.3	10.3
41324	1395.0	2263.6	1777.8	4.2
42695	1398.4	2124.8	1756.9	5.3
42696	1215.9	2094.7	1713.8	6.0
42697	1398.1	2134.2	1754.6	5.2
42698	814.7	2047.5	1543.3	8.3
42699	817.3	2164.8	1711.1	9.9
42700	805.3	1980.3	1590.5	9.0
42701	1241.8	2106.3	1739.6	9.6
42702	842.4	1840.8	1516.6	6.6
42703	1336.5	2135.4	1709.1	7.6
42704	1250.5	2133.5	1687.3	8.9
$\bar{x}$	**772.0**	**2263.6**	**1642.9**	**7.8**

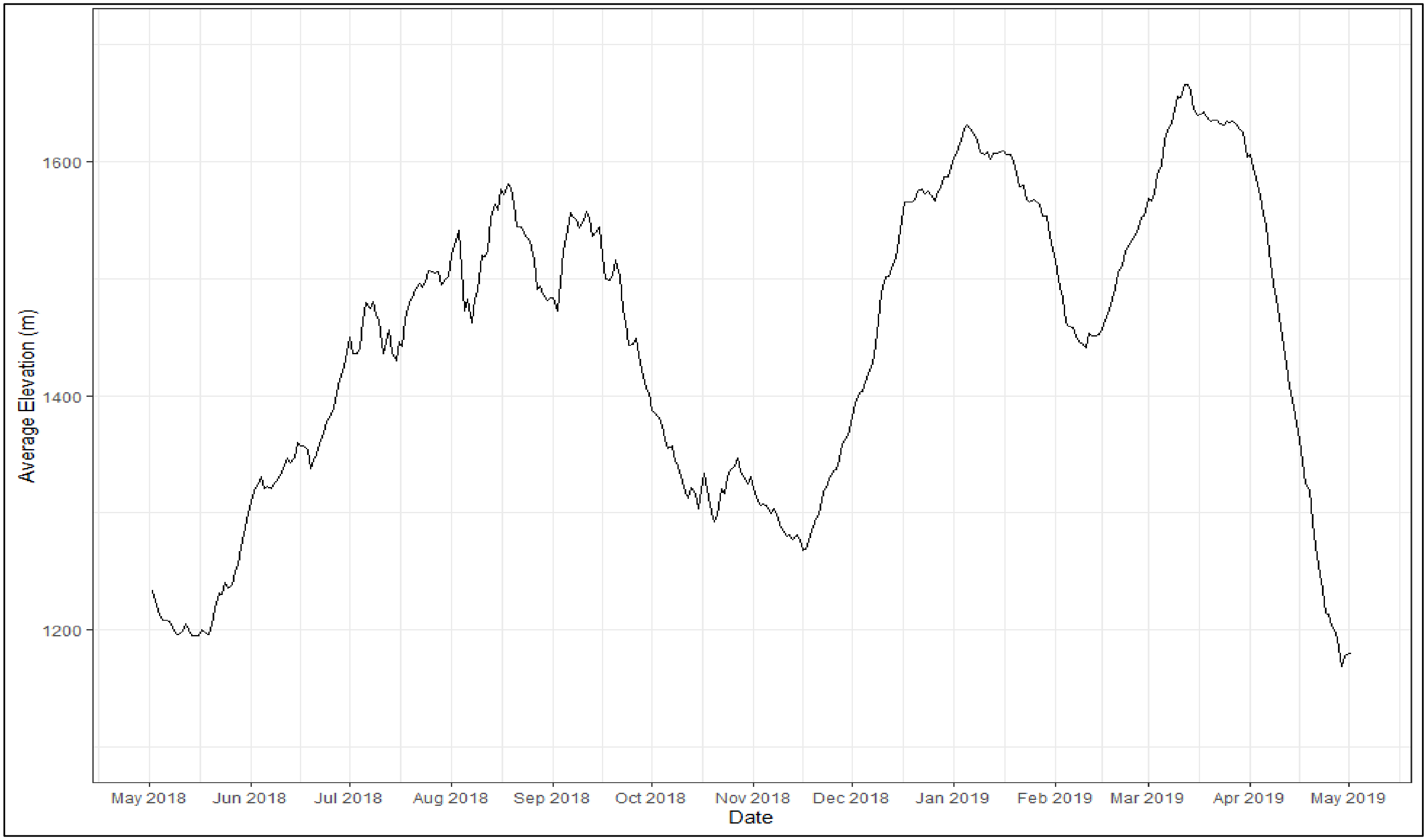

Figure 3.3.1. Mean daily elevation calculated with a 14-day moving window of collared female Stone's sheep #41323 in the Cassiar Mountains, British Columbia, Canada, March 2018 – April 2019.

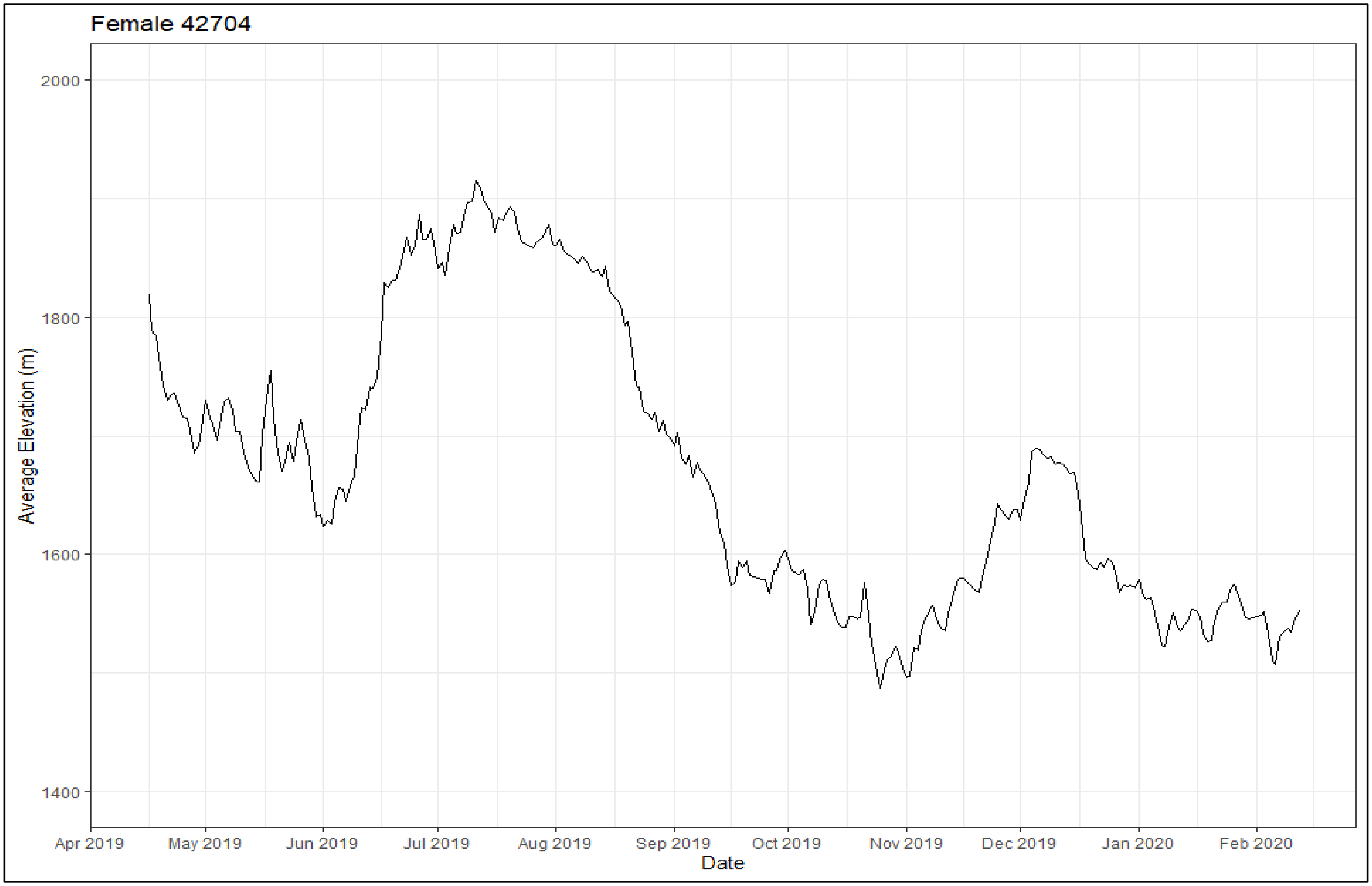

Figure 3.3.2. Mean daily elevations calculated with a 14-day moving-window for collared female Stone's sheep #42704 in the Cassiar Mountains, British Columbia, Canada from April 2019 – February 2020.

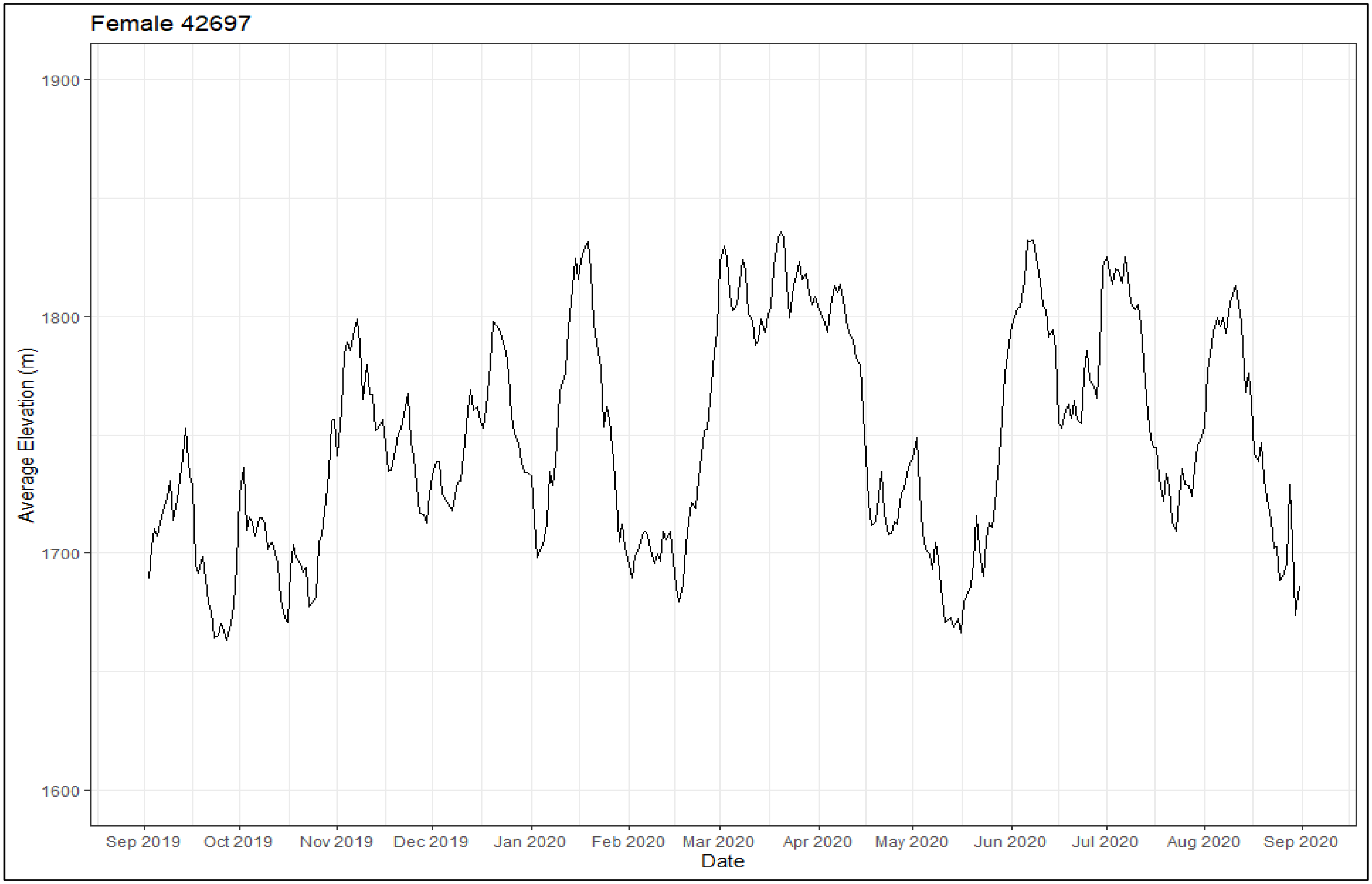

Figure 3.3.3. Mean daily elevations calculated with a 14-day moving-window for collared female Stone's sheep #42697 in the Cassiar Mountains, British Columbia, Canada from Sept 2019 – 2020.