Temporal patterns and behavioural states of mountain goat (*Oreamnos americanus*) movements to hotspots in the Rocky Mountains

by

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Abstract

Concentrated resources, or hotspots, can influence movement behaviour of many species. I studied the movement ecology of two groups of mountain goats (*Oreamnos americanus)* and their relationship with hotspots in the Canadian Rocky Mountains. First, I investigated fidelity to two roadside mineral licks. Movement patterns to mineral licks were documented over several temporal scales and I found that mountain goats have strong trans-generational, seasonal and daily movements to these mineral licks. Second, I investigated movements to foraging, travelling, and bedding areas in summer ranges, using hidden Markov models (HMMs) and predicted behavioural states. These behavioural states were ground validated and the results showed that HMMs can be used as a proxy for habitat hotspots. Understanding how animals adjust their movement behaviour to hotspots can provide valuable information for the management of these critical habitat features and the wider conservation of mountain goats.

Keywords: Mountain goats, *Oreamnos americanus*, habitat hotspot, mineral lick, temporal patterns, hidden Markov models, Rocky Mountains

This thesis is dedicated to the mountains and all the creatures who make a living amongst the rock and ice.

"Mountains are the closest our planet reaches towards the heavens. The purest air, the purest water, and the purest light on earth are found amidst these uplifted forms. They are the source of awesome natural power, shaping winds, weather and the rivers that flow across the land. And they are the home of very special living creatures… one large animal that belongs almost entirely to the realm of towering rock and unmelting snow. Pressing hard against the upper limit of life's possibilities, it exists higher and steeper through the year than any other big beast. It is possibly the best and most complete mountaineer that ever existed on any continent: the mountain goat."
Douglas H. Chadwick – A beast the color of winter 2002

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Chapter 1.

General Introduction

1.1. Habitat hotspots

Concentrated resources, or hotspots, outside and within an animal's usual home range can influence movement and investigating how animals modify their movement patterns to access these natural features can provide insight into animal behaviour (Freymann, de Visser, and Olff 2010; Xue et al. 2018; Montalvo et al. 2019). In ecology the word hotspot was first used to describe leks, places where males congregate to display to prospective mates (Bradbury, Gibson, and Tsai 1986). The term hotspot was then popularized by Norman Myers in the late 1980s, by defining a biodiversity hotspot as a place where "exceptional concentrations of endemic species that face exceptional degrees of threat" (Myers 1990).

More recently the term hotspot has been used to described key habitat features that play an outsized ecological role in determining habitat use and behaviour within an individual's usual home range (Grant and Scholes 2006; Bestley et al. 2010; Lai, Bêty, and Berteaux 2015). Hotspot is often used to describe patches in the landscape which disproportionately contribute to the support of herbivore populations and function differently than surrounding areas (Anderson et al. 2009). For species with large or complex ranges within heterogeneous terrestrial landscapes, the hotspot concept has been applied to describe animal movements towards key resources, such as watering holes (Montalvo et al. 2019), termite mounds (Davies et al. 2014) and grazing lawns (Winnie, Cross, and Getz 2008; Yoganand and Owen-Smith 2014). In terrestrial landscapes, herbivore species often select places that expose them to lower predation risk and provide access to high quality forage (Winnie, Cross, and Getz 2008; Yoganand and Owen-Smith 2014; Davies et al. 2014). These locations are frequently assigned as different classifications of hotspots within scientific literature such as, nutrient (Grant and Scholes 2006), foraging (Arcos et al. 2012), resource (Churski et al. 2017) and habitat hotspots (Yoganand and Owen-Smith 2014). My thesis explores resource and habitat hotspots and the management implications for both.

Mineral licks as resource hotspots

Resource hotspots are areas where high levels of nutrients important to herbivores are present within the soil (Grant and Scholes 2006). Resource types include bomas/kraals (Huruba et al. 2018), termite mounds (Freymann, de Visser, and Olff 2010), sodic patches (Craine et al. 2009), bird guano (Natusch et al. 2017), dung beetle middens (Veldhuis et al. 2018), concentrated herbivore dung (Veldhuis et al. 2018) and mineral licks (Kroesen, Hik, and Cherry 2020). Resource hotspots, such as mineral licks, may be rare within an animal's home range. North American ungulate species travel long distances, often at the risk of increased predation, outside their usual home range to visit these sites (Poole and Heard 2003; Ayotte et al. 2006; Slabach et al. 2015).

All ungulate species deliberately ingest soil from mineral licks to obtain nutrients they cannot acquire from regular forage (Slabach et al. 2015; Harris, Rice, and Wells 2017). For ungulates, mineral licks provide a necessary function that is distinct from foraging areas. Mineral licks are concentrated in a patch and are found atop outcrops of 'edible' soils (Panichev et al. 2013). Although mineral lick sites are considered an essential part of the landscape used by herbivores, they are rare (Dormaar and Walker 1996). Mineral licks are preferentially used by herbivores over extended periods of time and are characterized by high quality nutrient availability. They are a critical, limited resource for ungulates and the nutrients they provide have a large impact on fecundity, population dynamics and survival (Ayotte, Parker, and Gillingham 2008; Rice 2010). Mineral licks are functionally different from surrounding areas as they are most often used by ungulates within ecosystems that have low nutrient availability (Poole, Bachmann, and Teske 2010).

High-value features as habitat hotspots

Habitat hotspots have high quality habitat disproportionate to the surrounding landscape that minimizes energetic costs of foraging, travelling and predation risk (Anderson et al. 2010). Areas where animals spend a disproportional amount of time could be considered habitat hotspots such as foraging areas, movement corridors and bedding sites. The identification of hotspots can provide critical information for wildlife managers to identify important areas for species that live in large and complex ranges such as mountain goats. By examining the fine temporal time series locations of GPS collared animals, movement patterns of individuals can be inferred to high value habitat. Characterising movement patterns can uncover unique movements to places that have high value. Furthermore, studying animal movements to hotspots in areas that are large, complex, and difficult to access can provide insight to an animal's behavioural states and habitat usage in areas where it is logistically challenging for a researcher to visit (Grant and Scholes 2006). Studies encompassing a long time series of movements using methods that will not influence animals' behaviour, are necessary given that animals may only move to hotspots under specific conditions, such as time of day or foraging distance from safe terrain.

1.2. Mountain Goats

Mountain goats are one of the least studied ungulates in North America because of their affinity for high elevations and steep terrain (Smith 1988; Festa-Bianchet, and Côté 2008). Mountain goats are elusive high alpine ungulates that are sensitive to human presence and often flee when humans approach, making them difficult to observe (St-Louis et al. 2013; Richard and Côté 2016). Advances in technology have made it easier to track mountain goats with GPS collars that provide fine-scale spatial and temporal data on their movements that allow us to infer behaviour.

Figure 1.1 The distribution of the Rocky Mountain goat (*Oreamnos americanus*), as indicated in Shackleton, D. M. [Editor] and the IUCN/SSC Caprinae Specialist Group. 1997. "Wild Sheep and Goats and their Relatives." Status Survey and Action Plan for Caprinae. IUCN: Gland, Switzerland and Cambridge, UK. Blue square indicates the study area.
Adapted from Ninjataco (CC-BY SA)

Mountain goats are widely distributed throughout the western mountain ranges of North America (Figure 1.1). Their populations are considered globally secure, yet they are a species of management concern because they have characteristics that make them vulnerable to environmental change caused by human activities or natural events (Hamel et al. 2006). Conservation managers stress the importance of understanding mountain goat behaviour and habitat use (Mountain Goat Management Team 2010) but due to the remote and complex environment in which they reside there are few studies that focus on their behaviour. Mountain goats live in mountainous terrain within the alpine and sub-alpine zone in a wide variety of habitats from cliffsides to open meadows to subalpine forests (Lowrey et al. 2017). They are generalist herbivores and are considered intermediate browsers that forage on grasses, sedges and forbs (Festa-Bianchet, and Côté 2008). All ungulates, including mountain goats, are known to visit mineral licks to obtain supplemental minerals not found in their regular forage (Hebert and Cowan 1971; Ayotte et al. 2006).

Study area

This study was conducted in Yoho and Banff National Parks in the Canadian Rocky Mountains (Figure 1.1). We examined two groups of mountain goats occurring on either side of the Continental Divide. The home ranges of each study group are separated by the upper Bow River valley. Both areas contain steep and rugged mountains with high summits over 3000 m, and valley bottoms at 1500 m. However, the topographical characteristics of the mountains differ across the Continental Divide. In the Sherbrooke lake area of the Waputik Range on the west side of the Continental Divide, thicker ice on western slopes during previous glacial periods resulted in heavier glaciation, creating more moderate summits (Bobrowsky and Rutter 2007; Figure 1.2). In the Slate Range, on the east side of the Continental Divide, summits are characteristically “castle-like” because the folds of different layers of rock lay flat, creating flat-topped summits with plummeting cliffs (Baird 1962). Glaciers and other agents erode horizontal rock layers slowly, which explains the steep summits and the broad, shallow U-shaped valleys characteristic of the Slate range (Figure 1.2). The Sherbrooke study group on the west side of the Continental Divide is situated around Sherbrooke Lake in Yoho National Park, but also includes a major valley-bottom transportation corridor for the Trans-Canada Highway (TCH) and the main Canadian Pacific Railway line. The Slate study group on the east side of the Continental Divide occurs in the Slate Range northeast of Lake Louise, and while there are numerous popular hiking trails and a ski resort on the periphery of their range these mountain goats are not exposed to vehicle traffic. Individuals in both areas typically inhabit elevations between 2440 m and 1940 m.

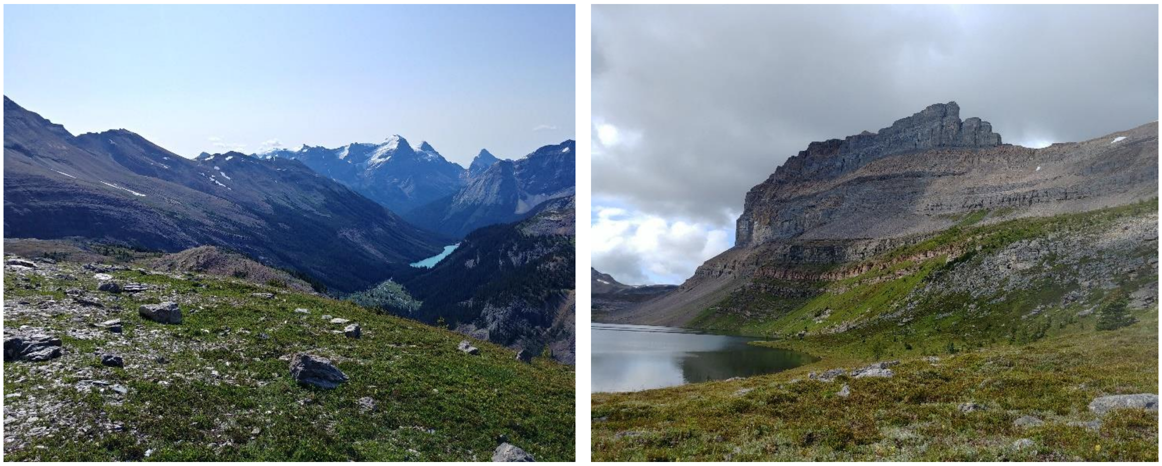

Figure 1.2 Typical habitat in Sherbrooke (left) and Slate (right) study areas in Yoho (British Columbia) and Banff (Alberta) National Parks, Canada. The Sherbrooke study area illustrates the moderately sloped ridges and the Slate study area shows Mount Redoubt with "castle like" appearance typical of the Slate range.

Mineral licks and mountain goats

Mineral licks are preferentially used by herbivores over extended periods of time and North American ungulate species travel long distances to access these resources (Ayotte et al. 2006, Slabach et al. 2015). Mineral licks are highly localized resources that generally persist over many years and contribute disproportionately to the overall health of herbivores compared with other locations within their home range (Giotto et al. 2015; Thaker et al. 2019). The benefits of geophagy are still uncertain, but may include (1) detoxification of secondary plant compounds; (2) alleviation of gastrointestinal stress; and (3) nutrient supplementation to meet metabolic demands (Jones and Hanson 1985; Kreulen 1985; Ayotte et al. 2006; Ayotte, Parker, and Gillingham 2008; Slabach et al. 2015). Consequently, some groups of mountain goats are attracted to mineral licks.

Mountain goats are attracted to locations adjacent to the Trans-Canada Highway (TCH) in Yoho National Park because of the presence of several mineral licks within 30 m of the highway (Figure 1.3). The TCH is under review for expansion and the proposed construction comes within a few meters of these mineral licks, or may even entirely remove them. It is unclear how important these areas are for mountain goats and how long-term effects of soil disruption, associated with the realignment of the highway will affect these areas. Information regarding the potential effects of highway construction activities is required to determine appropriate mitigation measures and effectiveness of monitoring techniques applicable to mountain goats.

Figure 1.3 Trans-Canada Highway mineral lick with two people for scale (left); mountain goats, nannie and young consuming soil at night (right).

1.3. Overview of thesis chapters

My thesis explores resource and habitat hotspots and how mountain goats move to certain habitat features within the landscape. My first data chapter (Chapter 2) explores the temporal patterns of movement to a resource hotspot, a mineral lick, over decadal, seasonal and daily patterns. My second data chapter (Chapter 3) examines the behavioural states of mountain goats within their home range and the habitat hotspots they choose. Together these chapters provide insights on the temporal patterns and behavioural states of mountain goat movements to hotspots.

Chapter 2 examines the temporal patterns of a group of mountain goats that consistently travel outside of their normal home range to mineral licks with fidelity. A key objective of Chapter 2 is to provide scientific baselines of age classes, frequency and duration of time spent at mineral licks. Little is known about what elements attract mountain goats to roadside mineral licks and what elements within the soil they are consuming. I describe the historical use of this roadside mineral lick using dendrochronology techniques. I use fine spatial and temporal data from GPS-collared mountain goats and trail cameras to examine mountain goat movements to mineral licks over the seasonal and daily scales. This chapter contributes understanding of how and why animals, particularly ungulates, visit mineral licks and provides science-based advice on the management actions to conserve mineral licks that mountain goats utilize.

Chapter 3 assesses hourly locations of 20 GPS-collared mountain goats to predict underlying behavioural states using a hidden Markov model (HMM) as a proxy to predict habitat hotspots. Given the complexities of mountain goat habitat, I applied HMMs to predict common ungulate behavioural states such as foraging, travelling, bedding, and possible mineral lick excursions to locate habitat hotspots. The objective of Chapter 3 is to identify key habitat hotspots for mountain goats and movement corridors used to reach them. I use environmental co-variates to see if behaviour changes over time of day and distance to escape terrain.

I conclude with a brief chapter (Chapter 4) reviewing my key findings, resource management implications and future directions of this research. Overall, I identify the need to reduce the attractive chemical components of the road abrasives used along the highway, and that could ultimately reduce vehicle collisions with mountain goats. This thesis provides baseline data for habitat management in areas where anthropogenic disturbances exist and are increasing. It is critical to assess all high value habitat for mountain goats. Research often focuses on areas where mountain goats spend most of their time like foraging and bedding areas. Yet, I found places where mountain goats spend proportionally less time like mineral licks and movement corridors have high-value and should be considered when managing mountain goat populations.

Chapter 2.

Patterns of decadal, seasonal and daily visitation to mineral licks a critical resource hotspot for mountain goats (*Oreamnos americanus*) in the Rocky Mountains

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2.1. Abstract

Concentrated resources, or hotspots, within an individual's usual home range may be strong determinates of movement behaviour. We evaluated the patterns of mineral lick use by a population of mountain goats (*Oreamnos americanus)* displaying high site fidelity at two mineral licks along the Trans-Canada Highway in the Rocky Mountains, British Columbia, Canada. Access to these mineral licks was characterized by deliberate and repetitive movements into marginal habitat. We describe the patterns of mineral lick use over decadal, seasonal and daily periods by using dendrochronological analysis of trampling scars along mountain goat trails, movements determined from GPS collar locations, and camera traps placed along trails and at mineral licks, respectively. Our findings suggest that mountain goats have strong trans-generational behavioural traditions and that they predictably access mineral licks using the same trails, seasons, and daily patterns. Differences in the patterns of mineral lick visitation between males and females may be related to reproductive and nutritional status, while their nocturnal use appears to be a response to disturbance at the mineral licks. Understanding how animals adjust their behaviour in response to highly localized resource hotspots outside their usual home range can provide valuable information for the management of these critical habitat features and the wider conservation of mountain goat populations.

Keywords

Mineral lick, hotspot, temporal patterns, sex-specific patterns, mountain goats, *Oreamnos americanus*

2.2. Introduction

Resources are not equally distributed across landscapes and constraints on access to specialized and limiting resources may determine movement patterns for many species (Myers 1990; Reid 1998). Concentrated resources, or hotspots, are key habitat features that play an outsized ecological role in determining habitat use and behaviour within an individual's usual home range (Scoones 1995; Reid 1998; Hunter 2017). These resource hotspots are uncommon habitat features that disproportionately provide essential nutrient resources. Resource hotspots are often described as concentrated patches that are preferentially used by wildlife over extended periods of time, and characterized by high resource availability such that they differ functionally from surrounding areas (Anderson et al. 2010; Muvengwi, Mbiba, and Nyenda 2013; Stokes et al. 2015; Urmy and Warren 2018). For species with large or complex ranges within heterogeneous terrestrial landscapes, the hotspot concept has been applied to describe animal movements towards key resources, such as watering holes, termite mounds and grazing lawns (Winnie, Cross, and Getz 2008; Yoganand and Owen-Smith 2014; Davies et al. 2016; Montalvo et al. 2019). Some hotspots are fixed in space but only accessible or necessary at certain times of the year, and may disproportionately influence an animal's behaviour (Davies et al. 2016; Montalvo et al. 2019).

Mineral licks are highly localized resources that generally persist over many years and contribute to the overall health of herbivores compared with other locations within an animal's normal home range (Kreulen 1985; Matsubayashi et al. 2007; Blake et al. 2010; Panichev et al. 2013; Panichev et al. 2016; Hunter 2017). Geophagia, the intentional consumption of soil, is a behaviour that is frequently observed in many animals within tropical and temperate regions, including bats, parrots, primates, and ungulates (Ayotte, Parker, and Gillingham 2008; Krishnamani and Mahaney 2000; Ghanem et al. 2013; Lee et al. 2014). Animals often travel long distances outside their usual habitat to visit specific mineral licks (Rice 2010; Link et al. 2011). The benefits of geophagy are still uncertain, but may include (1) detoxification of secondary plant compounds; (2) alleviation of gastrointestinal stress; and (3) nutrient supplementation to meet metabolic demands (Jones and Hanson 1985; Kreulen 1985; Ayotte et al. 2006; Ayotte, Parker, and Gillingham 2008; Slabach et al. 2015).

Mineral licks are used by all North American ungulates and geophagy is observed most often for herbivores within ecosystems that have low nutrient availability (Atwood and Weeks 2002; Jones and Hanson 1985). Three types of mineral licks exist: rockface licks are solid rock that animals directly lick, wet licks are associated with mineral rich mud or ground water and dry licks contain dry mineral soil exposed by erosion (Dormaar and Walker 1996; Ayotte et al. 2006). Studies have documented different species of ungulates visiting the different types of mineral licks. For example, moose (*Alces alces)* and elk (*Cervus elaphus*) prefer wet licks and Stone's sheep (*Ovis dalli stonei*) and mountain goats (*Oreamnos americanus)* target dry licks (Ayotte et al. 2006).

Mountain goats live in steep mountainous environments, where essential resources are seasonally and spatially heterogeneous, and they have been observed to make deliberate and long-distance movements to access certain dry mineral licks (Rice 2008). Mountain goats travel to specific mineral licks, visiting in large groups over certain times of the snow-free season (Hebert and Cowan 1971). Researchers have documented mountain goat movements to mineral licks describing the seasonality (Poole, Bachmann, and Teske 2010), spatial fidelity (Jokinen et al. 2014), licking intensity (Ayotte, Parker, and Gillingham 2008) and trade-offs between distance travelled and length of stay at the mineral lick (Rice 2010). These studies and many others have documented mineral lick utilization by mountain goats and have recorded variations of timing, duration and frequency of visits (Hebert and Cowan 1971; Jones and Hanson 1985; Poole and Heard 2003). The importance of mineral licks for mountain goats is often recognized, yet, there are fewer empirical studies focused on how these features may disproportionately influence animal behaviour over different time scales.

Our research objectives are to characterize the soils consumed by mountain goats, create an assessment of long term philopatry to these licks and define frequencies of male and female visits over a decadal, seasonal and daily time periods. Mountain goats are exposed to significant risks when using these sites, indicative of the importance of these mineral resources. We predict that the soils consumed at the mineral licks will be high in minerals mountain goats have been shown to seek at other mineral lick study areas such as sodium (Na), calcium (Ca), phosphorus (P) and magnesium (Mg) (Kreulen 1985; Ayotte et al. 2006; Ayotte, Parker, and Gillingham 2008; Slabach et al. 2015).

Our study population of mountain goats accesses mineral licks adjacent to an area of high anthropogenic disturbance, the Trans-Canada Highway (TCH), experiencing potential for vehicle collisions, high traffic volumes and predation. It is currently unknown if these mineral licks are human-caused or existed prior to highway construction in the 1950's. Anecdotal accounts report that these mineral licks have been used over decades, but this long-term philopatry of mineral lick use outside of mountain goat alpine habitat is poorly documented. We determined if mountain goat use of these mineral licks was established before or after highway construction and predicted that mountain goats have taken advantage of exposed soil on highway cut banks created during highway construction to access mineral licks, and that they are also attracted to the soils within the highway ditches that contain gravel and sand abrasives and de-icing road salt.

We hypothesize that male and female mountain goats will arrive during different times of the season and have different durations and frequencies of visits. Males will be driven by the need to alleviate gastro-intestinal distress caused by the switch of winter to spring forage; however, female visitation to mineral licks may be hindered in early spring by the demands associated with parturition (Kreulen 1985; Dormaar and Walker 1996; Ayotte et al. 2006). We predict that females will have larger group sizes and more diverse group compositions when visiting the mineral licks.

Advances in technology have made it easier to document detailed behavioural strategies of individual mountain goats and how they travel from their usual high alpine habitat to low elevation mineral licks. Mountain goat vehicle collisions often occur at roadside mineral licks and identifying the elements that attract mountain goats to these areas will help identify solutions to preventing further mortalities. Consequently, determining the seasonality, timing, duration and group composition of mountain goat visits can assist in management of human disturbances in the areas. Finally, understanding how animals adjust their behaviour in response to scarce but constant resource hotspots outside their usual home range will provide relevant information for conservation and management of these highly localized but essential habitat features.

2.3. Methods

Study Area

We conducted our study in Yoho National Park in the Rocky Mountains, British Columbia, Canada (Figure 2.1a; 116° 21' 56.84" W, 51° 27' 3.95" N) during 2017 - 2019. Yoho National Park is bisected by transportation corridors, including the Trans-Canada Highway (TCH) and Canadian Pacific Railway (CPR) lines running through a narrow valley surrounded by ranges with high summits over 3000 m. The TCH was constructed between the years 1950 and 1958. During spring and summer, mountain goats periodically leave their usual high elevation habitat to visit two mineral licks located along the TCH (~1550 m). They travel from sparsely vegetated talus fields and alpine meadows, down through mixed forest cover of lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*) and Douglas-fir (*Pseudotsuga menziesii*) to access valley bottom mineral licks. Approximately 100 mountain goats inhabit the mountain complex adjacent to the licks and typically use habitat in elevations between 2440 m and 1940 m (Parks Canada, unpublished data; Figure 2.1a). Two narrow, distinct, and well-travelled mountain goat trails, both approximately 1500 m in length and 700 m in elevation difference, connect their high alpine habitats with their respective lower elevation mineral licks. These trails extend into the alpine to a larger network of mountain goat trails connecting main foraging and bedding areas up to 10 km away.

Characteristics of Mineral Licks

Two mineral lick sites, Ogden (West) and Bosworth (East), are located adjacent to the TCH, along an eroded soil bank created during highway construction and are situated less than 10 m from the roadside at their closest points (Figure 2.1b). These are dry mineral licks which are remnants of alluvial deposits and usually occur from the deposition of elements that concentrated above impermeable soil layers and then became exposed by erosion (Panichev et al. 2016). The mineral licks are separated by 3.5 km, accessed from different mountain ridges and located over 1 km away from the nearest suitable escape terrain (slopes of > 40 degrees; DeVoe et al. 2015). At each mineral lick mountain goats have excavated soil under large-diameter trees (Figure 2.1c), primarily Douglas-fir, very similar to typical mineral licks in the Rocky and Purcell Mountains (Poole, Bachmann, and Teske 2010). Mountain goats have been observed consuming soil both underneath the tree caverns (Figure 2.1d) and along highway ditches in-between the TCH and the mineral licks. The highway ditches contain gravel and sand abrasives remaining from the winter snow removal and ice control. It is unknown what ratio of soils mountain goats consume from the mineral licks compared to the highway ditch soils. Soils, tree roots and camera trap sampling were conducted at the Ogden mineral lick (hereafter referred to as the primary site).

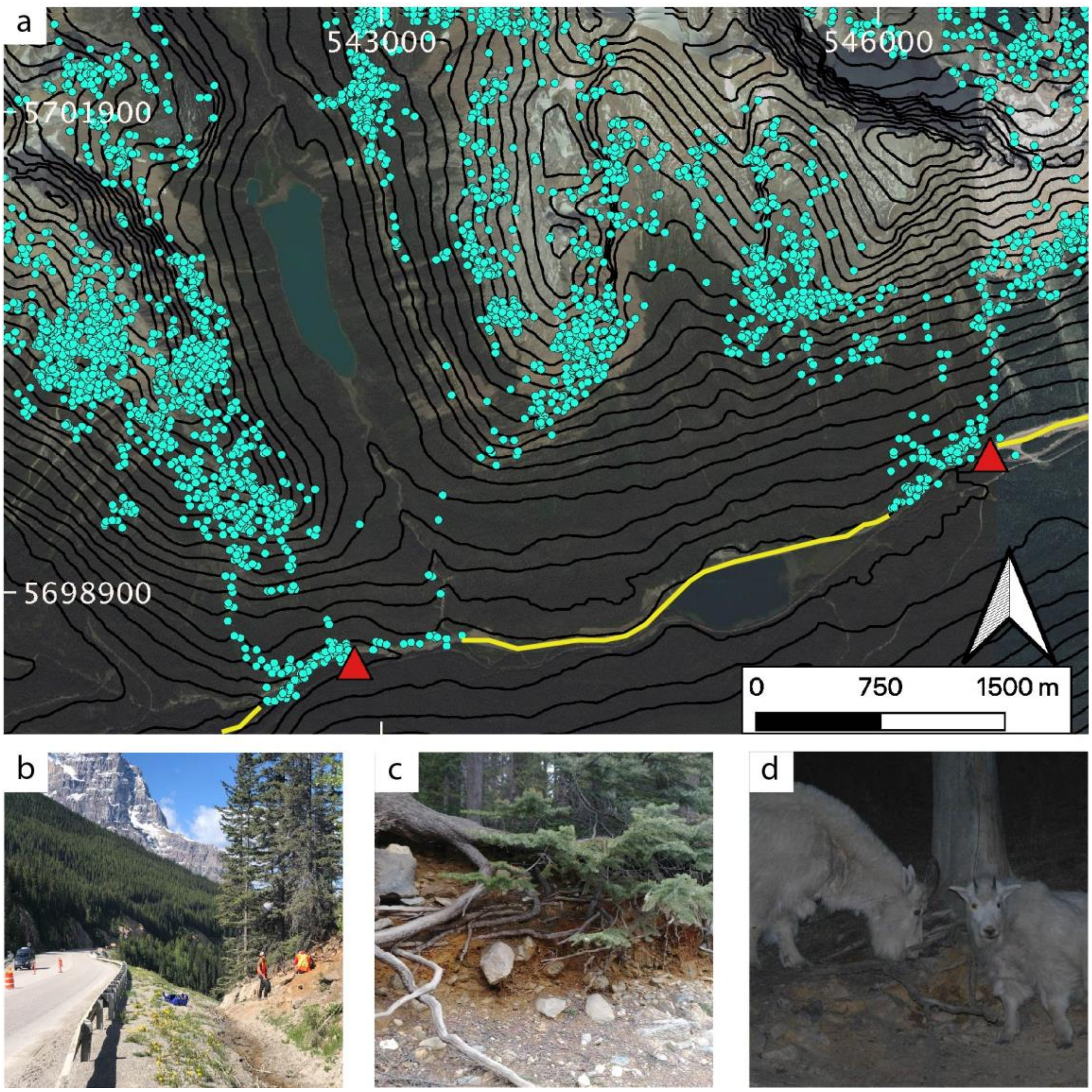


Figure 2.1 (a) Map of the Sherbrooke mountain goat range in Yoho National Park, British Columbia. The core area includes Sherbrooke Lake in the valley bottom and two mineral lick sites (red triangles) along the Trans-Canada Highway (yellow line). The blue points are individual mountain goat GPS collar observations (5 male, 4 female) from June and July 2018; (b) a roadside mineral lick with two people for scale; (c) a mineral lick with excavated soil under trees located < 10 m from roadside; (d) nannie and young consuming soil at night.

We collected soil samples (~ 350 g) around the primary mineral lick site from four different areas: (i) highway ditches, (ii) mineral licks excavated under tree roots, (iii) treeline, and (iv) within the forest. Mountain goats were observed consuming soil at both the highway ditches and mineral licks and were not observed to consume soils along the tree line and forest where soil is not exposed. We randomly collected 6 soil samples from each location. Mineral lick soil was collected where evidence of mountain goat digging, and consumption were obvious. Highway ditch samples were collected at the surface of the soil in areas where mountain goats were observed consuming soil. The treeline and forest soil pits were dug at the depth of 1.2 m to simulate the depth of mineral lick caverns. Samples were collected from the 'B' layer of soil with low organic matter and finer grained soils. The treeline sites were excavated and sampled from under the base of Douglas-fir trees, as all the observed mineral lick caverns were located under trees.

Soil samples were sent to A&L Laboratories, London, Ontario for analysis of pH; carbonate equivalent; cation exchange capacity (CEC); available macro-elements (Ca, Mg, Na, K, S, P) and trace elements (Fe, Mn, Zn, Cu). All soil samples were analyzed using the Mehlich III procedure (Sen Tran and Simard 1993). A subset of mineral lick, highway ditches and forest samples were also tested for selenium and sand, silt and clay ratios.

We used principal component analysis (PCA) to summarize and visualize the differences between the highway ditches, mineral lick, treeline and forest. A one-way nested analysis of variance (ANOVA) was used to test for significant differences in concentrations of macro and trace elements, pH and CEC between the highway ditches, mineral lick, treeline and forest. The Tukey's test was used for *post hoc* comparisons (Sokal and Rohlf 2012). All analyses were performed in R 1.1.563 (R Core Team, 2019).

Long-term evidence for use of mineral licks

Dendrochronological techniques were used to detect evidence of trampling scars on tree roots to determine the age of the mountain goat trails (Speer 2012). These techniques have been used in other studies to re-construct abundance patterns of barren-ground caribou (*Rangifer tarandus groenlandicus*) herds in the sub-Arctic (Morneau and Payette 1998; 2000; Zalatan, Gunn, and Henry 2006). Trail cameras record mountain goats primarily using these trails but other sharp hoofed ungulates such as mule deer (*Odocoileus hemionus)* and white-tailed deer (*Odocoileus virginianus*) have been recorded using these trails to a lesser extent. We collected 44 live roots (diameter: mean 3.0 cm, range 1.0 – 6.0 cm) that displayed visible signs of trampling scars that were greater than 1 cm in diameter along two distinct mountain goat trails leading from the alpine to the primary mineral lick (Figure 2.2). The trails were distinct and narrow, varying from 0.5 m to 1.5 m wide. Trees with large-exposed roots crossing the trails included lodgepole pine, Engelmann spruce, and Douglas-fir. We collected samples from < 25-degree terrain and within thickly covered forests to avoid the possibility of mechanical damage caused by avalanches. Trampling damage occurs over the snow-free period (May – October) to the upper sections of exposed roots along well-travelled trails. Trampling scars were characterized by damage to the xylem as an elongated or oval scar with neat margins (Morneau and Payette 1998; 2000). We pooled ages into 5-year classes, which accounted for the possibility of missing annual growth rings.

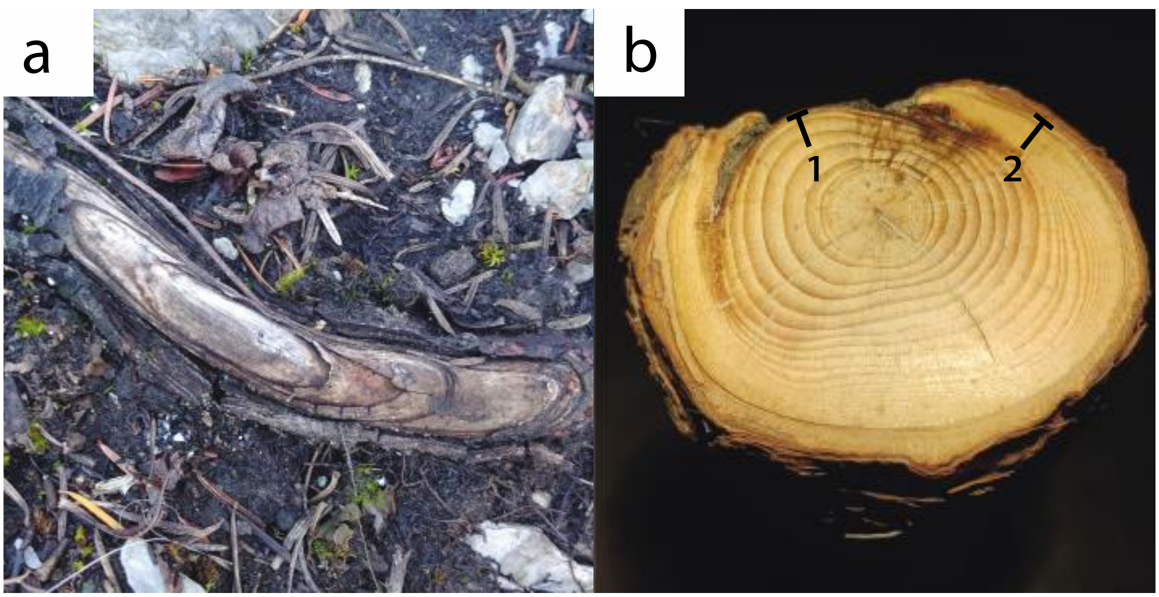


Figure 2.2 Photographs of (a) a trampled root along a mountain goat trail and (b) a cross-section of a root with trampling damange to the exposed xylem. We determined the age of the scar by counting from the damage (1) to the edge of the cambium (2).

We cut the roots into cross-sections where the oldest damage was present. We identified the scars based on the exposed damage of the xylem and resin accumulation on the damaged part of the root. We finely sanded the cross-sections to enhance the visual separation of annual growth rings. We determined the age of the scarring by counting the rings between the scar and the cambium to determine minimum age and determined the age of the roots by counting from the pith to the edge of the cambium. Counting annual growth rings may produce errors due to absent or false rings, so we calculated only a minimum age and assumed the age classes of ± 5 years (Speer 2012).

Seasonal Use of Mineral Licks

Ten adult mountain goats, five male and five females, were captured and fitted with Vectronic Vertex Lite 3-D Iridium global positioning system (GPS) collars (Vectronic Aerospace GmbH, Berlin, Germany). One male and one female were captured and chemically immobilized in modified Clover traps near the primary low elevation mineral lick in July – August 2017 using the methods of Cadsand et al. (2010). The rest of the collared mountain goats were physically immobilized via standard helicopter net-gun techniques in October 2017 (Barrett, Nolan, and Roy 1982). Helicopter captures occurred in high elevation habitat on the mountains immediately above the mineral licks. All captures followed the Canadian Council of Animal Care guidelines for the safe handling of wildlife (Parks Canada Agency Animal Care Task Force # 30681, Research Permit #30681 and #YNP-2019-32338, and Simon Fraser Animal Care Committee #: 1302B-19). During the two-year analysis period from 1 November 2017 – 1 November 2019 the collars on two males stopped functioning and three female mortalities occurred: two from apparent grizzly bear predation and one following a vehicle collision. Consequently, our analysis of 2018 data were based on four female and five male mountain goats, and for 2019 we used the remaining three female and three male collared mountain goats. On 31 July 2019 one female mountain goat was hit by a vehicle, leaving three male and two female collars for the last three months of the study.

Each GPS collar was programmed to upload hourly spatial fixes for fine spatial (± 10 m) locations. Data were cleaned by filtering any non-3D validated GPS points and removing impossible speeds travelled between successive points (speed >10 km h^{-1}). We used a 750 m buffer around the mineral lick site including the trails to delineate which GPS collar locations represented a mineral lick visit using ArcGIS 10.6 (ESRI, Redlands, California, USA). We used both Ogden and Bosworth mineral lick sites to determine the frequency, duration and timing of mineral lick visits (Appendix A, Figure A1). The duration of mineral lick visits was calculated by the number of consecutive hourly fixes within the 750 m buffer. If only one fix occurred it was counted as 1 hour, so an error of ±1 h is possible for duration of time spent travelling to the mineral lick. We used a single sample t-test to determine if male and female visits to mineral licks differed significantly in their frequency or duration of visits to mineral licks.

Daily Use of Mineral Licks

Eight remote camera traps were deployed along two primary mountain goat trails to capture mountain goat groups moving downslope to visit the mineral lick. We used motion-trigger cameras (Hf2x Hyperfire 2 Covert Ir, Reconyx Inc., Holmen, Wisconsin) set approximately 1.2 m off the ground on the trunks of trees with the cameras tilted upslope and directed towards the trails. We chose areas where the trails were in an open location, with little understory and where the trail was not braided. These trails run from the top of a ridgeline to the valley (from elevations of 2205 – 1550 m) over a distance of 1.2 km. These trails lead to the TCH mineral licks and highway ditches.

Remote camera traps operated continuously between 14 May and 13 August 2019. Cameras were programmed to capture images during a 24 h period. Two out of eight camera traps were chosen to calculate daily mountain goat visitation. Both were on two main trails leading to the same mineral lick, and on average, had the highest number of mountain goats recorded each week. Each camera was equipped with infrared motion sensors and was set up to take 5 “RapidFire” images when triggered and would continue taking pictures until no motion or heat was detected. We counted and classified all animals that triggered the cameras and recorded total numbers of animals in distinct groups within the last photo frame triggered. A distinct group were those that were separated by more than two minutes.

All images were classified using Timelapse (Version 2.2.2.9). We counted only mountain goats moving toward mineral licks. All mountain goats moving away from mineral licks were removed to avoid double counting. Mountain goats were classified by sex and age by using three criteria: observation of genitals, urination posture, and horn morphology. Only adults > 2 years were classified as male or female because the sex of kids and yearlings cannot be easily identified using visual clues in the field (Smith 1988). Kids (0 - 12 months) and yearlings (12 - 24 months) were identified by comparing relative body size and horn length. To analyze the diel activity patterns, we divided a 24 h period into hour-long segments, and each independent record was classified within those intervals. These methods minimized potential observer bias as data were collected remotely and analyzed using *a priori* criteria to classify individuals. The datasets generated and/or analyzed during the current study are available at Data Dryad Digital Repository: https://doi.org/10.5061/dryad.44j0zpcb4.

2.4. Results

Soil Characteristics

The PCA of element concentrations showed an overall association between the mineral lick, treeline and forest areas, but were different from the highway samples (Figure 2.3). The first four principal components explained 90% of the variance using the Kaiser criterion with eigenvalues > 1.

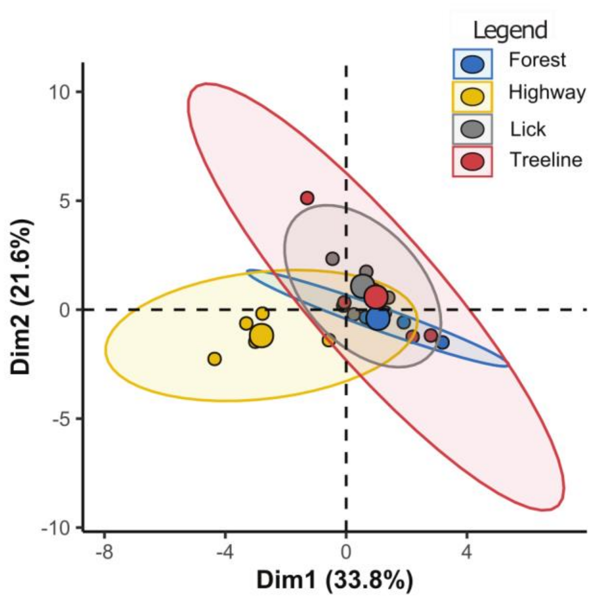


Figure 2.3 Principal Component Analysis of macro and trace elements in soil samples from the forest, highway ditches, mineral lick and treeline sites in Yoho National Park.

The mineral lick and highway samples had significantly higher concentrations of Na than the forest and treeline samples (Figure 2.4). The mineral lick was significantly higher in Mg compared with highway, treeline and forest soil samples but was not significantly different in any other concentrations of macro or trace elements. Highway soils had significantly higher values for Ca, P and Zn but were lower for Mg. Other elements known to be important to mountain goats at mineral licks, including Ca, P, Zn and Cu (Jones and Hanson 1985; Kreulen 1985; Ayotte et al. 2006) were relatively similar between the mineral lick, forest and treeline (Appendix A, Figure A2). There was no difference in the concentration of the elements K, S, Mn and Fe at the four sample areas. There were no detectible levels of selenium in any of the soil samples tested.

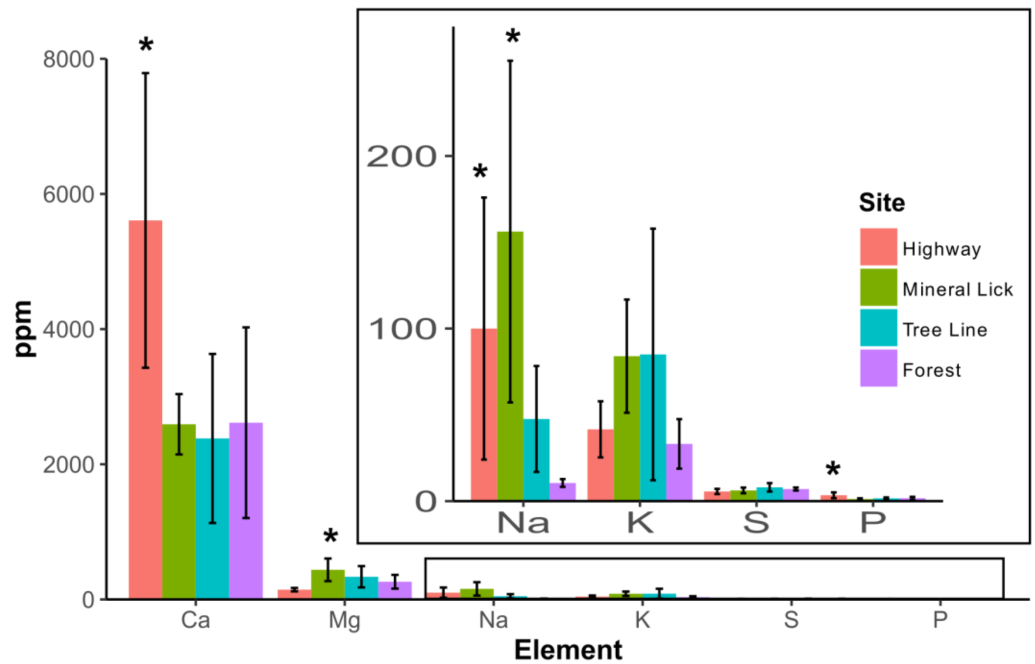


Figure 2.4 **Concentrations (mean +/- SE) of macro elements (ppm) of soil samples collected from the forest, highway ditches, mineral lick and treeline. Significant differences (* $p < 0.05$) between sites were tested using a one-way ANOVA.**

Long-term evidence for the use of mineral licks

The 44 roots collected were aged from 15 years to 105 years, with the dating of trampling scars ranging from < 5 to 65-70 years ago (Figure 2.5). The oldest recorded scar was dated from the early 1950’s with the highest frequency of scars observed between 2010 and 2018.

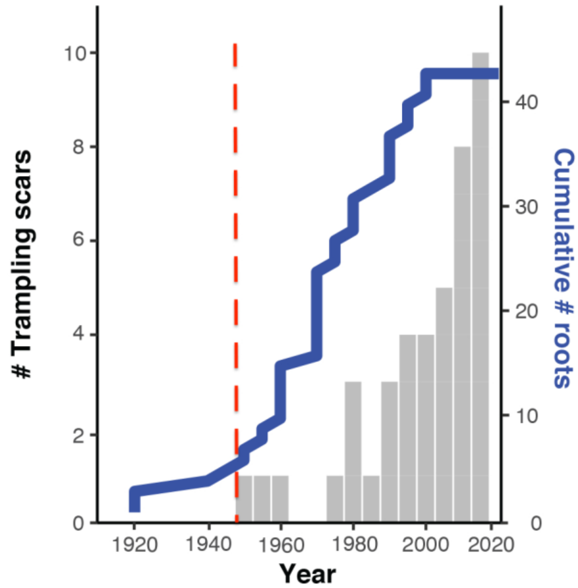


Figure 2.5 **Age of trampling scars on conifer roots (grey bars) pooled into 5-year classes and cumulative number of roots included in the sample for each year class (blue line). Roots were collected along trails leading to mineral licks frequently used by mountain**

Seasonal Use of Mineral Licks

The phenology of seasonal visits to the mineral licks was consistent over both years with the majority of mountain goats accessing mineral licks between May and the end of July (Figure 2.6a). All GPS collared mountain goats visited a mineral lick, either Ogden or Bosworth, at least once per year during the two years they were tracked. Males arrived at the mineral lick first starting in May, one month earlier than the females in mid-June. Both males and females overlapped for the months of June and July and females continued to visit the mineral licks in August (Appendix A, Figure A3). No GPS collared mountain goats visited the mineral lick between December and mid-March.

Females generally spent more time at mineral lick sites than males ($t = -3.49$, $df = 110.55$, $p\text{-value} < .001$). During each visit to the mineral lick, females spent 7.3 h (range = 2.0 – 18.0, no outliers) and males spent 5.3 h (range = 1.0 – 9.0, one outlier of 88 h; Figure 2.6b). The observed frequency and duration of visitation for each sex was consistent between years. Males visited more frequently than females (11.3 ±0.97 SE vs 7.4 ±0.48 SE: $t = -3.13$, $df = 9.96$, $p\text{-value} < 0.01$; Figure 2.6c). However, there was some variation, with a single female visiting a mineral lick 17 times in 2018 but only 6 times during 2019.

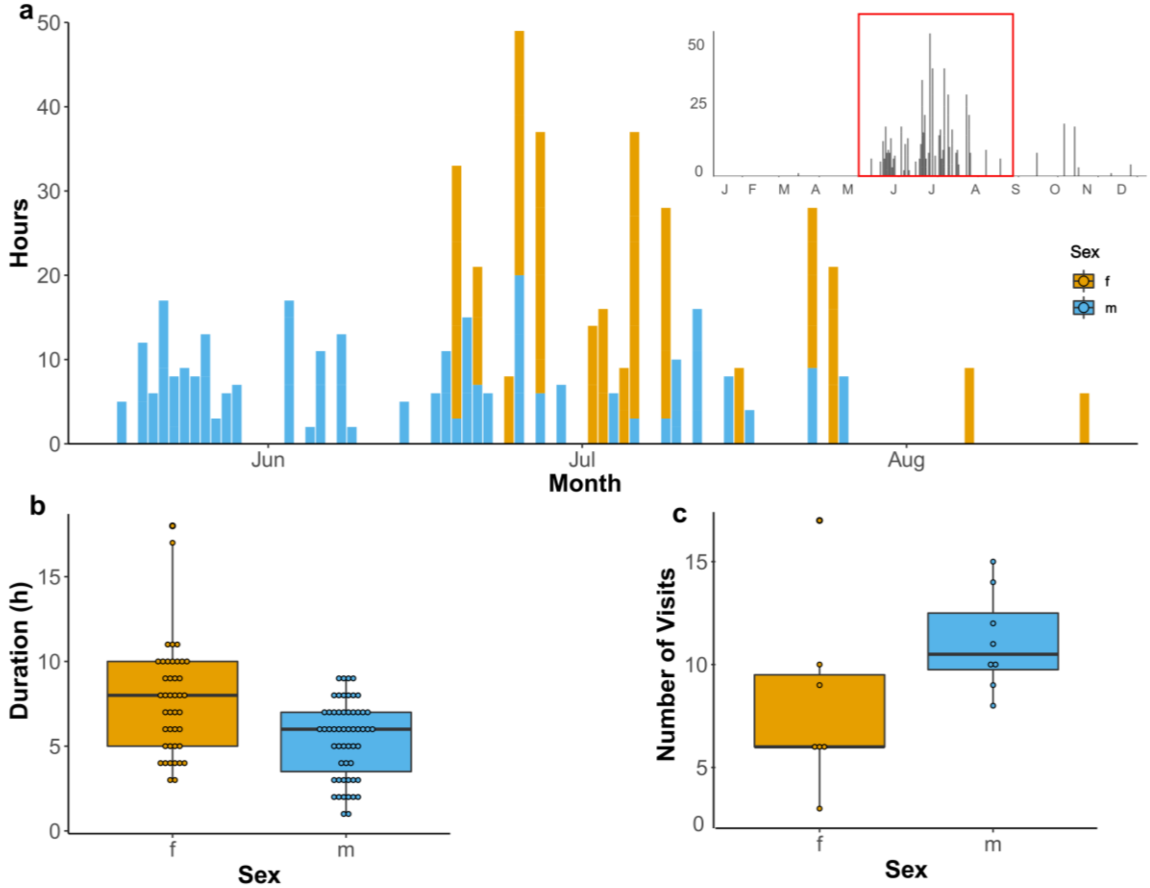


Figure 2.6 **(a) Time spent by GPS collared mountain goats at mineral licks adjacent to the Trans-Canada Highway during May to August 2018 (5 male, 4 female). Top right inset shows mineral lick use during the entire year (2018). (b) The duration and (c) number of female and male mountain goat visits for 2018 and 2019 (combined), with the lower and upper box boundary of 25th and 75th percentiles respectively and the line inside the box median, lower and upper error lines 10th and 90th percentiles respectively. Dots indicate the (b) duration of a single visit and (c) the number of visits per year from individual GPS collared mountain goats. There was one outlier, a male, who visited for 88 hours (not shown).**

Daily Use of Mineral Licks

Camera traps detected 501 independent instances of mountain goats travelling along trails to the TCH mineral licks, including 147 males, 193 females, 85 kids and 55 yearlings (Appendix A, Figure A3). We were unable to classify the age and sex of 21 mountain goats. The group size and composition and the seasonal timing of males and females was similar to the pattern observed with the individual GPS collar locations. The first date a male triggered a camera trap was 19 May; the first visit of a female was 14

June; and the first visit of a female with a kid was 17 June. In only 24 instances out of 394 (6%), males travelled in groups with females. Female-only groups were larger (mean size = 4.0, SE +/- 0.68, range = 1 - 16) compared with male groups (mean size = 1.5, SE = ± 0.28, range = 1 - 9). The largest group was a mixed group of 24 individuals, including all ages and sexes, on 8 August. Visits to the mineral lick generally occurred between 22:00 and 04:00 (Figure 2.7). Other animal species were recorded travelling along the trails at various times throughout the summer including four grizzly bears (*Ursus arctos)*, four black bears (*Ursus americanus)*, one coyote (*Canis latrans*), 44 mule deer, three white-tail deer, 56 rabbits (*Lepus spp.)*, three porcupines (*Erethizon dorsatum*), and seven humans (*Homo sapiens*).

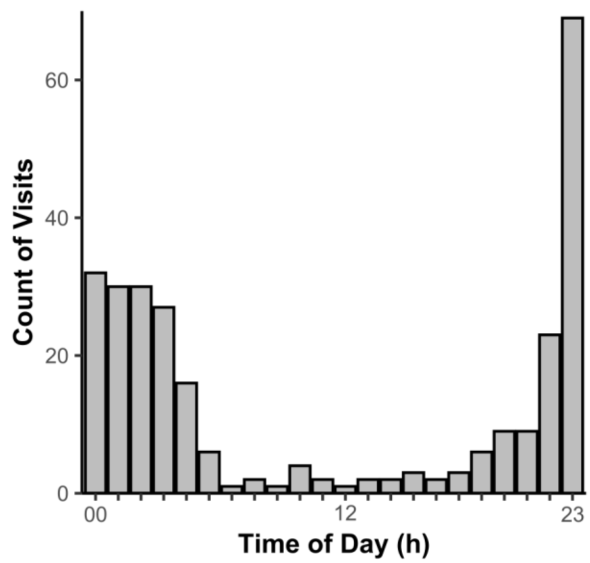


Figure 2.7 Time of day that mountain goat groups triggered camera traps as they moved down the trails to mineral licks along the TCH during summer 2019.

2.5. Discussion

Our findings provide a detailed description of the deliberate and regular behaviour of seasonal visits to a resource hotspot and suggest that this behaviour has persisted over long periods. We found the soils consumed at the mineral lick and highway ditches were high in elements mountain goats are suspected to search for (Kreulen 1985; Ayotte et al. 2006; Slabach et al. 2015). We showed that mountain goats display extreme site fidelity over many decades to this mineral lick with root trampling scars providing supporting evidence of the long-term use of trails leading towards mineral licks along the TCH over the past 65 years. The evidence suggests that mountain goats did not visit the primary mineral lick before the TCH was built. Mountain goats visited mineral licks frequently over the snow-free period, with males starting during snow melt in May, followed by females with newborn kids in mid-June. Mountain goats have developed strong behavioural traditions visiting this mineral lick over many decades, and within a season males and females have different seasonal patterns of visitation while travelling in distinct group sizes. The unique nocturnal pattern may be caused by proximate anthropogenic factors such as highway disturbance. The temporal patterns of mineral lick use by male and female mountain goats and the behavioural adaptions they display highlight the importance of these mineral licks for this population.

Soil Characteristics

We found high elemental concentrations of Na and Mg at the mineral lick and Na, Ca, P, Zn and Cu in the highway ditches along the TCH, common elements mountain goats are known to seek out (White 1983; Poole, Bachmann, and Teske 2010; Slabach et al. 2015). The requirements for these minerals may prompt mountain goats to visit mineral licks and the roadside ditches in the spring. Sub-alpine spring forage is commonly Na deficient and high in K (Hebert and Cowan 1971; Kreulen 1985; Atwood and Weeks 2002; Ayotte et al. 2006). Na and Mg are thought to offset increased K which is found in high elevation spring forage, and can interfere with the absorption and retention of other elements (Hebert and Cowan 1971; Kreulen 1985; Atwood and Weeks 2002; Ayotte et al. 2006). The spring timing of the mineral lick visits coincides with increased requirements for Ca and P during late pregnancy and lactation and female mountain goats may seek out high levels of Ca and P that are found within the highway ditches (Dormaar and Walker 1996; Ayotte et al. 2006). The gravel and sand abrasives remaining in the roadside ditches from the winter snow removal and ice control can best explain the extreme differences in mineral content among the highway ditch, mineral lick, treeline and forest soils (Figure 2.3). Consequently, highway ditches may be a major attractant to this roadside area for lactating females. Interestingly, the mineral lick, treeline and forest were similar in composition, except for the differences in Na and Mg (Figure 2.4).

The primary mineral lick in our study is most likely caused by a combination of factors including easy access and proximity to mountain goat habitat, as well as presence of the eroded cut banks adjacent to the highway maintenance ditches that concentrate abrasives. Consequently, mountain goats target the eroded banks of the TCH because of easily accessed soils. Trees concentrate fine-textured soils and minerals under their roots, which can explain the behaviour of excavating under trees as documented by other research studies in the Kootenay and Rocky Mountain regions (Hebert and Cowan 1971; Poole, Bachmann, and Teske 2010).

Long-term evidence of the use of mineral licks

We found no trampling scars that predate the construction and completion of the TCH. We suspect mountain goats started using this mineral lick after the TCH completion in 1958 given the soil sample and dendrochronology evidence. Trampling scars on the exposed roots of trees across mountain goat trails showed evidence of long-term use leading to mineral licks for over 65 years. This is consistent with other observations of extended mineral lick use in the Rocky Mountains by National Park wardens and from reports of mountain goat highway mortalities in the area dating back to 1975. Yoho National Park was surveyed for mineral licks in 1949, prior to the construction of the TCH, and there was no mention of this specific mineral lick being used by mountain goats (McTaggart Cowan and Brink 1949). Mineral lick use is determined by the geographical and physical features of the area (Panichev et al. 2016) and either this population of mountain goats had an alternative mineral source or did not have access to mineral resources at the primary mineral lick until after the TCH was constructed.

The long-term use of the primary mineral lick by mountain goats is supported by root scar evidence. We observed that females with young routinely visit the mineral licks every spring facilitating inter-generational learning such that this behaviour is passed from females to their offspring. In other species, foraging site locations are learned from their parents such as young black bear cubs that learn to forage in specific locations and target specific foods (Mazur and Seher 2008).

Natural root mortality may bias our counts and could limit our detection of past mountain goat use along the trails or decrease the detectability of trampling scars. The use of trampling scars to reconstruct mountain goat use over time is based on scar production and scar loss. Scar production occurs with damage to the xylem by mechanical damage and scar loss will occur with a death and decay of a tree-root. While the chance of detecting older scars was reduced because we collected fewer old roots, our results show trampling scars only appeared in the 1950s and increased over time.

Seasonal use of mineral licks

GPS collared mountain goats accessed mineral licks during the first days of the snow-free season, with most visits in May, June and July, followed by less frequent individual visits between early August and December (Figure 2.6a). No visits occurred between the months of December and March, most likely because access to the mineral lick required moving through deep snow in the forest. These patterns are also consistent with previous studies within the Rocky Mountain region (Hebert and Cowan 1971; Singer 1978; Ayotte, Parker, and Gillingham 2008; Poole, Bachmann, and Teske 2010; Jokinen et al. 2014).

GPS collared mountain goats made frequent trips over the spring and summer seasons and the high frequency of short-term visits can best be explained by their proximity to the mineral licks. We found mountain goats travelled a maximum of 10 km and visited the mineral licks repeatedly over the season while other studies have found if a mountain goat’s range was far from a mineral lick then the visits were less frequent but for a longer duration (Rice 2010). Short (< 1 day) and frequent trips may be evidence of a trade-off between the benefits of nutritional value of the mineral lick and the increased exposure to predation risk (Kreulen 1985; Rice 2010). Our findings suggest that mountain goats in our study area visit for shorter trips possibly to limit the exposure to predators as time spent away from escape terrain while still accessing minerals. Mountain goats are most often reported within 500 m of escape terrain (DeVoe et al. 2015) while the mineral lick is over 1 km away from cliffs. Indeed, two GPS collared mountain goats were killed due to predation near the mineral lick, and similarly, Poole et al. (2010) suspected two predation mortalities at mineral lick sites. Balancing resource access and safety have been reported for numerous other species including bison (*Bison bison)*, elk and pygmy rabbits (*Brachylagus idahoensis)* (Hebblewhite and Merrill 2009; Fortin and Fortin 2009; Camp et al. 2017).

Males arrived earlier in the spring, spent less time at mineral licks than females and visited more frequently (Figure 2.6b, c). The later timing of female visits may coincide with the lambing period and the ability of newborn kids to travel longer distances (Hebert and Cowan 1971). Females travelled to mineral licks in larger groups than males. Mountain goats are highly gregarious and like many ungulates they are sexually segregated during the summer (Festa-Bianchet, and Côté 2008). Female groups consist of kids and yearlings, so the group size was expected to be bigger. Male groups were much smaller consisting of one to three individuals. Males, unhindered by parturition and shepherding newborn kids down steep trails, can visit earlier, more frequently and spend less time at the mineral licks. Males visit earlier due to the abrupted switch from a low quality winter diet to a lush spring forage and with higher mobility than females they can access elements that ease the indigestion that comes from the diet switch earlier than females (Kreulen 1985). The higher frequency of male visits could be explained by the difference in either nutrient demands or their willingness to accept greater risk (Festa-Bianchet and Côté 2008). Male mountain goats may accept a higher risk of predation because their large body size makes them less vulnerable and they do not have to account for the predation risk of juveniles (Conradt 1998; Ruckstuhl and Neuhaus 2002).

Daily use of mineral licks

We found that this population of mountain goats tended to visit at the same times over a 24-hour period, displayed a nocturnal pattern to access mineral licks and spent the duration of the night at these sites (Figure 2.7). There was little activity between the daylight hours of 05:00 and 21:00. This pattern was the same for both sexes, GPS collared individuals and camera trap group visits. In the alpine, away from human disturbance, this population of mountain goats follows a crepuscular pattern, forging during the daylight hours, travelling during the crepuscular periods and bedding at night and in the afternoon (See Chapter 3). Similarly, mountain goats in Glacier National Park (USA) that visit highway licks have a nocturnal pattern, while another study population with no highway disturbance followed a crepuscular pattern (Pedevillano and Wright 1987; Singer 1978). In contrast, the Caw Ridge (Alberta) mountain goat population, with no highway disturbance, has activity levels that peak in the early morning, midday and late afternoon while decreasing during late morning and evening (Romeo and Lovari 1996). The recursion of movements within the same 24-hour periodicity is a widespread phenomenon among large herbivores and large scale studies suggest that increased familiarity with the area increases effectiveness of acquiring resources (Wolf et al. 2009). Humans have a strong effect on the daily patterns of wildlife, which has led to increased nocturnality in numerous mammals (Gaynor et al. 2018). Traffic volume on the TCH is greatest during the day (Parks Canada, unpublished data) and mountain goats may have adapted their behaviour to visit road-side mineral licks during periods of lowest traffic. Mountain goats have been recorded to react negatively to human disturbance from hikers, all-terrain vehicles and helicopters (Côté et al. 2013; St-Louis et al. 2013; Richard and Côté 2016). Avoidance of high traffic volume may be an important factor influencing the visitation of mineral lick areas along busy transportation corridors. We suspect that these specific movements are probably related to the tendency to return to familiar areas at familiar times with reduced traffic volume.

Hotspots as a critical landscape feature determining movement behaviour

Our study provides long-term insights spanning many decades combined with high-resolution contemporary data to analyze how behavioural strategies evolved in animals to access resource hotspots outside of their usual home range. We attempted to assess the trade-offs between geophagy and human disturbance, predation risk exposure, and parturition for mountain goats accessing these mineral lick sites. Environmental factors such as the phenology of spring green up and predator activity may influence the frequency and duration of mineral lick visits for both male and female mountain goats. The strategic nocturnal visits of this population of mountain goats may be an adaption to high traffic volumes along the TCH. Mountain goats have likely adapted to significant risks by using different behavioural strategies to access mineral licks that are then passed between generations.

Our finding that mountain goats alter their behaviour to visit a site that is most likely human caused has implications for management. This information can help find ways to reduce the attractive chemical components of the road abrasives used along the highway and could ultimately reduce vehicle collisions with mountain goats. Road construction that results in newly exposed soils and cut banks may result in increased mountain goat presence, particularly in areas mountain goats are already known to frequent. In these situations, highway exclusion fencing may prevent mountain goats from being killed in collisions with vehicles. However, simultaneous creation of similar mineral rich features using a combination of terrain alterations (e.g. cut banks and depressions) and mineral rich soil in alternative locations would ensure long-term mineral requirements are fulfilled. Quantifying and monitoring the seasonality, timing, duration and group composition of mountain goat visits to human-influenced resource hotspots can assist in measuring the success of managing these areas

Resource hotspots have outsized ecological functions, and investigating the temporal patterns of how animals modify their behaviour to access these critical resources can provide insight to the behavioural rhythms associated with accessing scarce resources (Freymann, de Visser, and Olff 2010; Xue et al. 2018; Montalvo et al. 2019). Mineral licks are preferentially used by herbivores over extended periods of time and North American ungulate species travel long distances, often with increased predation risk outside of their usual home range to visit these sites (Ayotte et al. 2006; Slabach et al. 2015). Dependencies on scarce resource hotspots can introduce patterns in movement strategies and high site fidelity to dependable resources (Giotto et al. 2015; Thaker et al. 2019). Within the broader context of behavioural ecology our study demonstrates the larger implications of geophagy on mountain goat movement, energetics, predation risk exposure, and seasonal habitat use. Finally, understanding how animals adjust their behaviour in response to scarce but constant resource hotspots outside their usual home range may also provide relevant conservation and management opportunities. Mineral licks may be overlooked when accounting for wildlife conservation, and our findings provide a detailed example that can inform and assess other hotspots used by mountain ungulates.

Chapter 3.

Behavioural states of mountain goats *(Oreamnos americanus)* as a proxy for habitat hotspots using hidden Markov models

3.1. Abstract

Understanding where, why, and how individual animals move is a fundamental biological question, but directly observing an animal's behaviour and the habitat they utilize is logistically challenging. Mountain goats (*Oreamnos americanus*) are elusive high alpine ungulates that live in steep and mountainous environments where it is difficult to directly observe and record behaviour. Hidden Markov models (HMMs) are emerging as a useful method for predicting the behaviour of animals over space and time. We used HMMs to identify hidden behavioural states and predict habitat hotspots of mountain goats. We evaluated how these inferred states can serve as a proxy to identify habitat hotspots. We explored associated environmental covariates, time of day and distance from escape terrain, to explain these behaviours. We visited field sites that were selected by mapping fast to slow movements of mountain goats to look for physical evidence of several behaviours, including foraging, travelling, and bedding. We found mountain goats are most likely to forage during daylight hours away from escape terrain, travel within and away from escape terrain during the crepuscular periods and bed nearest to escape terrain in the night-time and afternoon. The inferred behavioural states were validated against the field sites and in 64% of the cases the model predicted the habitat characteristics recorded in the field. Our method is best at "uncovering" foraging areas, then bedding sites and lastly travel. Our results illustrate that HMMs have the power to predict the relationship between behavioural states and habitat hotspots and this approach may assist wildlife managers in assessing why goats use certain hotspots and how they travel between them.

3.2. Introduction

Understanding where, why, and how individual animals move is a fundamental biological question (Nathan et al. 2008; Dingle 2014), but directly observing animal behaviour and the habitat they utilize is logistically challenging (Cagnacci et al. 2010). Advances in technology using global positioning systems (GPS) have provided improved spatial and temporal resolution for determining animal behaviour and habitat use without the confounding effects of disturbance from the researcher. These indirect observations from GPS collars can be used to gain insights on animal behaviour and habitat, particularly in home ranges that are often inaccessible (Seidel et al. 2018). Animal behaviour has been inferred by characterizing patterns of time series movement from GPS collars using measures such as step length (distance from last point), or tortuosity (turning angle from last point) (Morales et al. 2004; Owen-Smith, Fryxell, and Merrill 2010).

Common techniques for assessing animal habitat use within their home range such as Resource Selection Functions (RSFs) or Step Selection Functions (SSFs) do not consider an individual's behavioural state at each step (Seidel et al. 2018). RSFs calculate the habitat "used" versus "available" using a logistic regression framework (Boyce et al. 2002), while SSFs use a time-series of "available" points using a set of randomly drawn steps from each time series of points as a whole (Thurfjell, Ciuti, and Boyce 2014). RSFs and SSFs use recorded locations to examine habitat in broader terms (Hebblewhite and Merrill 2008) but other studies have emphasized the importance of considering the behavioural context in which animal movements occur (Beyer et al. 2010; Wilson, Gilbert-Norton, and Gese 2012).

More recently, state-space models, such as hidden Markov models (HMMs), have been used to identify different modes of animal movement and behavioural state switching (Zucchini, MacDonald, and Langrock 2016). In the past decade published studies using HMMs have successfully predicted the movement patterns of California brown pelicans (*Pelecanus occidentalis californicus;* Dean et al. 2012), the diving behaviour of Blainville's beaked whale (*Mesoplodon densirostris;* Langrock et al 2014) and the winter movements of swift foxes (*Vulpes velox*; Butler et al. 2019), among many other applications (Mor, Garhwal, and Kumar 2020; McClintock et al. 2020). HMMs allow researchers to examine animal behaviour within the framework of a time series of discrete observations of movements. Animal movement is a natural framework for HMMs because it contains a time series of discrete finite observations from GPS locations using step length and tortuosity to infer the hidden behavioural states of animals (Michelot, Langrock, and Patterson 2016; Zucchini, MacDonald, and Langrock

2016). HMMs assume a time series and a finite number of GPS tracking locations (observed states) that are produced by the underlying sequence of unobserved “hidden” behaviour that depends on the state of the proceeding step (Patterson et al. 2008). At each time step a discrete observation in the form of a location point is available to interpolate the hidden behaviours. Broadly, HMMs predict the future behavioural state of an animal given its current state, an assumption known as the Markov process (Patterson et al. 2008). In each timestep the behavioural state can switch to a new behaviour or stay the same.

HMMs have been used to study elusive animals that are difficult to observe, including black bears (*Ursus americanus*; Karelus et al. 2019), elephants (*Loxodonta Africana*; Vogel et al. 2020) and caribou (*Rangifer tarandus*; Franke et al. 2004). Nevertheless, few studies have confirmed predicted behavioural states through on-the-ground observation of habitat at GPS locations, with the exception of carnivore hunting and caching behaviour in wolves (*Canis lupus*; Franke et al. 2006), lions (*Panthera leo;* Goodall et al. 2019*)* and snow leopards (*Panthera pardus saxicolor;* Farhadinia et al. 2020).

Mountain goats are elusive high alpine ungulates that live in steep and mountainous environments where it is difficult to directly observe and record behaviour. Conservation managers stress the importance of understanding mountain goat behaviour and habitat use (Mountain Goat Management Team 2010) but due to the remote and complex environment they reside there are few studies that focus on their behaviour. Mountain goats are sensitive to human presence and often flee the area when humans approach making them difficult to observe (St-Louis et al. 2013; Richard and Côté 2016) but advances in technology have made it easier to track mountain goats with GPS collars. Given the complexities of mountain goat habitat, we chose to apply HMMs to predict common ungulate behavioural states such as, foraging, travelling, bedding and mineral lick excursions. We predicted that different patterns of step lengths and turning angles would allow us to uncover different behavioural states.

Mountain goat research often focuses on winter habitat (Poole, Stuart-Smith, and Teske 2009; Richard, Wilmshurst, and Côté 2014), summer habitat (DeVoe et al. 2015; Sarmento, Biel, and Berger 2019) or both (Rice 2008; White et al. 2011; Lowrey et al. 2017), but less is known about the spring season when large phenological changes happen quickly in high-elevation mountain environments. In the spring, receding snow increases forage availably from low quality winter browse to fresh spring forage (Ayotte et al. 2006), mountain goats increase their localized winter movements to wider ranging ones (Rice 2008; Lowrey et al. 2017), parturition occurs (Festa-Bianchet, and Côté 2008), and visits to known mineral licks peak (Kroesen, Hik, and Cherry 2020). During the spring and early summer, it is unknown how mountain goats utilize certain types of habitat during different times of the day and away from escape terrain.

Our research objectives were to predict mountain goat hidden behavioural states, identify if behaviours change over time of day or distance to escape terrain and evaluate if states can serve as a proxy for habitat hotspots using field classification. First, we hypothesized that fast to slow mountain goat movements during June and July may be indicative of high alpine mineral licks and other habitat hotspots such as high-quality foraging areas, the end of movement corridors or bedding areas. Second, we used HMMs to identify the hidden behavioural states of a mountain goat. Given that ungulates often have more than two states (Schmidt et al. 2016) we predict that we will find three or more behavioural states based on step lengths and turning angles. We then investigated the relationships between predicted behavioural states and time of day and distance from escape terrain and determined if these associations differed between two study groups separated by the Continental Divide. Many terrestrial ungulates have been shown to have diurnal patterns (Ager et al. 2003) and escape terrain has been shown as a primary factor in habitat choice for mountain ungulates (DeVoe et al. 2015). Lastly, we used habitat characteristics collected during field site visits to test if the predicted behavioural states could serve as a proxy for different types of habitat hotspots. Our HMM framework provides an opportunity to uncover how elusive mountain herbivores utilize habitat hotspots in different behavioural states, and consider wider applications for the management of mountain goat populations (Fraser et al. 2018).

3.3. Methods

Study area

Our study was conducted in Yoho and Banff National Parks in the Canadian Rocky Mountains (Figure 3.1). We studied two groups of mountain goats occurring on either side of the Continental Divide, between Alberta and British Columbia. The home ranges of each study group are separated by 15 km and the upper Bow River valley. Both areas contain steep and rugged mountains with high summits over 3000 m, and valley bottoms at 1500 m. However, the physio-geographic characteristics of the mountains differ across the Continental Divide. In the Slate Range, on the east side of the Continental Divide, summits are characteristically “castle like” because the folds of the geomorphic rock lay flat creating flat topped summits with plummeting cliffs (Baird 1962). Glaciers and other agents erode horizontal rock layers slowly, which explains the steep summits and the broad shallow U-shaped valleys characteristic of the Slate range. Within the Sherbrooke study area in the Waputik Range, on the west side of the Continental Divide, valleys are noticeably V-shaped due to the steep streams containing fast moving water with erosive power. This, combined with the thicker ice on the western slopes during previous glacial periods resulted in heavier glaciation creating more moderate summits (Bobrowsky and Rutter 2007). The Sherbrooke study group on the west side of the Continental Divide is situated around Sherbrooke Lake in Yoho National Park, but also includes a major valley-bottom transportation corridor for the Trans-Canada Highway (TCH) and the main Canadian Pacific Railway line. The Slate study group on the east side of the Continental Divide occurs in the Slate Range north-east of Lake Louise in Banff National Park, and while there are numerous popular hiking trails, and a ski resort on the periphery of their range, these mountain goats are not exposed to vehicle traffic. Individuals in both study groups typically inhabit elevations between 2440 m and 1940 m.

Mountain goats live in the alpine and sub-alpine in a wide variety of mountainous habitats from cliffsides, to open meadows to subalpine forests (Lowrey et al. 2017). Mountain goats are often found near or on steep slopes or cliff bands called “escape terrain” to evade most mammalian predators that would be unable to access these slopes (Poole and Heard 2003; DeVoe et al. 2015). Mountain goats are generalist herbivores and considered intermediate browsers and generally forage on grasses and forbs (Festa-Bianchet, and Côté 2008). Alpine vegetation contains low sodium and high potassium content, and mountain goats often travel long distances outside their normal alpine habitat to visit mineral licks to obtain supplemental minerals (Hebert and Cowan 1971; Ayotte et al. 2006; Kroesen, Hik, and Cherry 2020).

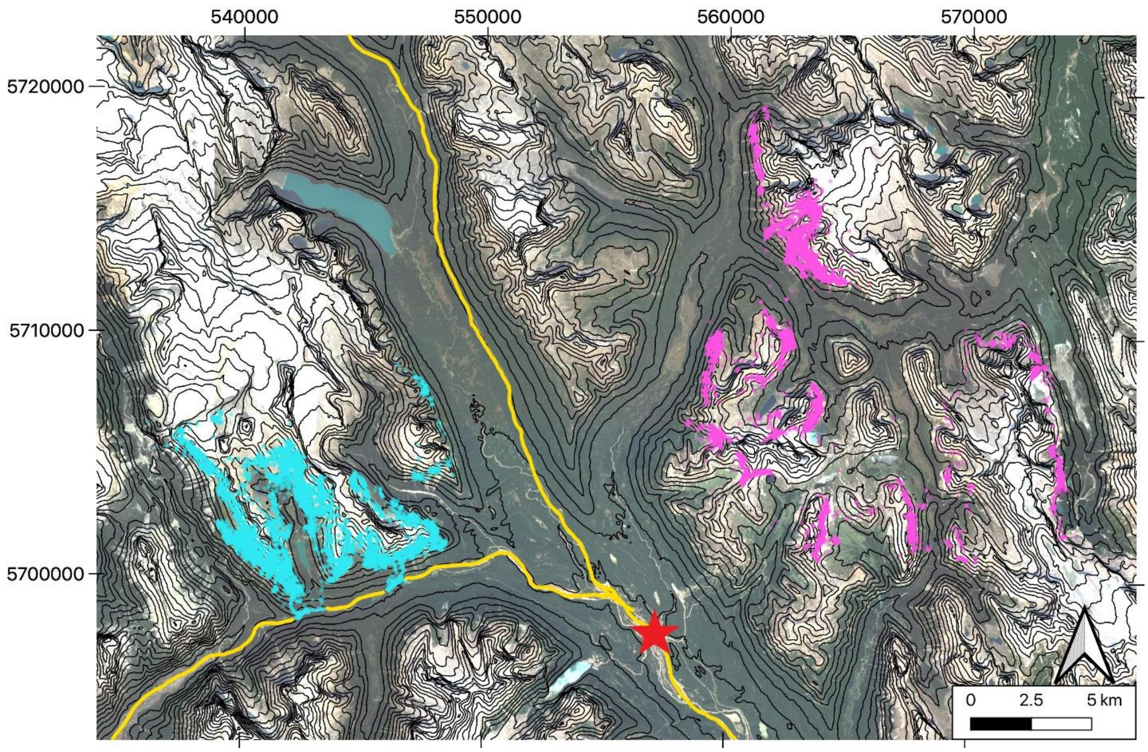


Figure 3.1 Map of the Sherbrooke (blue, n = 9 individuals) and Slate (pink, n = 10 individuals) mountain goat ranges based on nearly 35,000 GPS collar locations between 1 June and 15 July 2018 in Yoho (British Columbia) and Banff (Alberta) National Parks, Canada. The red star is the village of Lake Louise and the yellow line depicts the Trans-Canada Highway running east to south and the Icefields Parkway branching off to the north. The Continental Divide runs from North to South, and effectively separates the Sherbrooke and Slate goats from each other.

GPS Collars

Twenty mountain goats were collared, ten in both the Sherbrooke (5M, 5F) and Slate (6M, 4F) ranges and fitted with Vectronic Vertex Lite 3-D Iridium global positioning system collars (Vectronic Aerospace GmbH, Berlin, Germany) (Parks Canada Agency Animal Care Task Force # 30681, Research Permit #30681 and #YNP-2019-32338, and Simon Fraser Animal Care Committee #: 1302B-19). We captured 18 adult mountain goats by helicopter net-gun in October 2017. One male and one female were captured and chemically immobilized in modified clover traps as described in Cadsand et al. (2010) in the Sherbrooke study area during July and August 2017.

Each GPS collar was programmed to record a location (+/- 0.01 km) every hour. Data was cleaned by removing any non-3D validated GPS points and movements greater than 10 km/hour between successive fixes. All data was examined to identify movements or locations associated with impossible distances or across impassible terrain. We focused on the spring season from June 1st to July 15th because at this time of year mountain goats display increased movement to ecologically relevant hotspots such as mineral licks, which are often areas of management interest (Poole and Heard 2003; Kroesen, Hik, and Cherry 2020).

During the two-year analysis period the Sherbrooke study area had two male defective GPS collars and three female mortalities occurred, two from apparent grizzly bear predation and one wildlife-vehicle collision. The Sherbrooke 2018 season analysis was based on four female and five male mountain goats, and the 2019 season used the remaining three female and three male collared mountain goats. In the Slate range all GPS collared mountain goats survived for the 2018 season. In 2019, one female and two male collars ceased transmitting.

Analysis

HMMs assume data is regularly sampled over time and measurement error is negligible (Patterson et al. 2009). We used the R package MomentuHMM (McClintock and Michelot 2018) to predict missing locations using an average movement rate between irregularly spaced observations. The interpolated points were processed using the crawlWrap function that fits a continuous time correlated random walk model (Johnson et al. 2008) and predicts the temporally-regular locations using the crawlWrap package in R (McClintock and Michelot 2018). The interpolated points filled in the missing data and allowed us to assume temporally regular dataset of hour-hour fixes per individual. We calculated the step-lengths and turning angles for each step between two consecutive locations.

Hidden Markov Model Analysis

HMMs are state-space models designed using a two Markov processes with hidden and observed states (Zucchini, MacDonald, and Langrock 2016). HMMs are comprised of two probabilistic processes: the unobserved Markov chain which is the “hidden” state of the animal and the observed locations collected from GPS collars. The R package “momentuHMM” (McClintock and Michelot 2018) was used for fitting the

HMM to the movement tracks. The initial parameters inputted were chosen values based on biological and literature reviews common for ungulates. The initial values for each behavioural state were the mean around the gamma (step length) and von Mises (turning angle) distributions for which all the observed behaviours were categorized. We modeled the step lengths which were positive and continuous, with gamma distributions, and the turning angles, circular-values, with von Mises distributions (Langrock et al. 2012; Zucchini, MacDonald, and Langrock 2016). Common behavioural states of large ungulates we included were resting, foraging and travelling (Owen-Smith 2002). We did not assume that an animal will remain in a single state for one hour, however, the dominant behaviour will be predicted by the model. For example, in foraging areas ungulate species tend to move slowly, turn frequently and take shorter steps and while traveling they move directly with long steps, and at rest they take no steps (Patterson et al. 2008).

We assigned behavioural states, characterized by different distributions of step lengths and turning angles. We chose these initial parameters based on the accuracy of the GPS collars (+/- 10 m), step length and turning angle histograms and based on prior biological movements on other foraging ungulates such as elk (Cervus canadensis; Michelot et al. 2016), African buffalo (Syncerus caffer; Hooten et al. 2019), caribou (Rangifer tarandus; Franke et al. 2004), suggesting the step lengths and turning angles for these animals are biologically interpretable. We chose initial parameters of moderate step lengths (10 m - 100 m) and moderate turning angles ($\pi/2$) for foraging, large steps (> 500 m) and large turning angles (π) for travelling, and shortest steps (< 10 m) and moderate turning angles ($\pi/2$) for bedding. The models fitted used a fixed distribution for turning angles and step lengths, have a fixed set of transition probabilities and do not vary with environmental co-variates. We explored an in-between state, foraging*bedding, where a mountain goat would be moving slowly or intermittently rest in-between foraging bouts, by imputing short step lengths (10 m – 50 m) and small turning angles ($\pi/4$). We tested these initial parameters by imputing extreme parameters and did not change the confidence intervals (Table 3.1).

We compared three candidate HMMs, 2-state (foraging and travelling), 3-state (foraging, travelling and bedding) and 4-state (foraging, travelling, bedding and foraging*bedding) and with Akaike information criteria (AIC). Based on the AIC we chose to run the 3-state model for analysis. We used the Viterbi algorithm (Viterbi 1967) to globally decode the most likely sequence of the probability of observing the behavioural state under the fitted model and assigned a state to each observed step (Langrock et al. 2012). We checked the pseudo residuals for goodness-of-fit. The pseudo-residuals should follow a normal distribution if the fitted model is estimating the density of step lengths and turning angles (Patterson et al. 2009; Zucchini, MacDonald, and Langrock 2016). We combined the hidden behavioural state classifications to the corresponding GPS locations. We used the moveHMM (Michelot, Langrock, and Patterson 2016) and momentuHMM packages (McClintock and Michelot 2018) for the program R (R Core Team 2017) to perform all HMM analysis.

We established how behavioural states changed over time of day and distance from escape terrain. Daylight hours were defined as 5:00 to 22:00 and nocturnal times were defined from 22:30 – 5:00, during our study period the sunset time and sunrise times only changed by 15 minutes. Distance from escape terrain was defined as a specific threshold of slopes greater than 40 degrees (DeVoe et al. 2015). Distance from escape terrain, steep and rugged terrain in which mountain goats use to escape and avoid predators, has been associated as an important covariate in mountain goat habitat (Poole and Heard 2003; DeVoe et al. 2015). We calculated distance from escape terrain using a 30 m digital elevation model for the study area which was calculated by comparing the height of a cell to the height surrounding cells using QGIS (version 3.12.3). Output values ranging from 1 – 90 degrees indicating the slope steepness. We used the threshold of 40 degrees to define escape terrain. We then calculated the Euclidian distance of each GPS fix from the escape terrain.

Field Site Selection and Validation

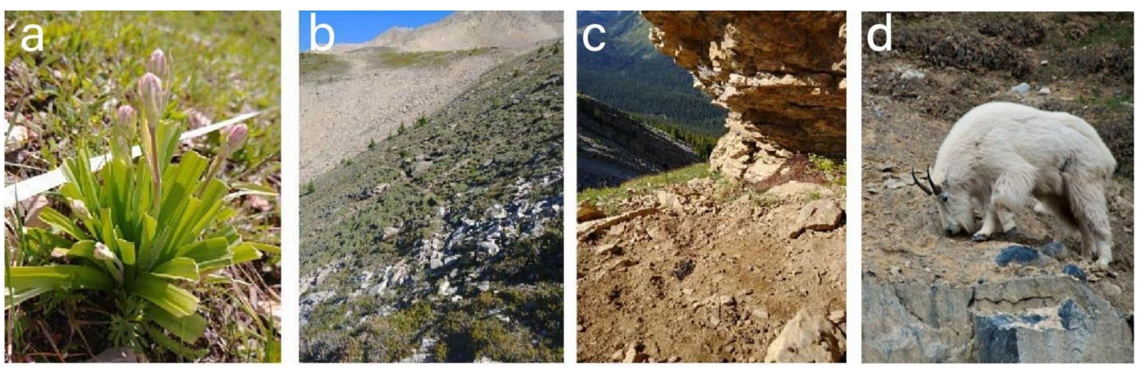
We selected and visited field sites prior to our HMM analysis. Our field site selection was based on the distance between hourly GPS collar locations. Distances between locations were calculated from UTM coordinates using the package “amt” in R version 1.1.563 (R Core Team, 2019). We prioritized sites where mountain goats changed their behaviour from fast (> 1km/hour) to slow (< 0.1 km/hour) movements. We considered movement between hourly locations > 1 km to be travelling behaviour. Distances between hourly locations < 0.01 km and equal to zero were considered stopped. A mountain goat moving <0.01 km/ hour could be stationary and thus bedded because the error of the GPS track is up to < 0.01 km. Movements between fast and slow (i.e., 0.01 km/hour – 1 km/hour) were considered foraging.

We walked to the defined sites guided with handheld GPS (+/- 10 m). We did not visit any sites that were considered over class 3 terrain (Rose 2013), which may involve the use of hands to climb over or around large rocks, and steep slopes. If possible, we initially examined sites from lower elevations or with Google Earth (version 7.3.3.7699) and did not visit the site if it appeared dangerous to approach or exposed to hazards.

At all sites, we conducted pellet and herbivory surveys as evidence of mountain goat presence and foraging intensity, respectively. Both pellet and herbivory surveys were 10 min in duration and were initiated at the center of the site and then moved in concentric circles outward, if possible. If the site was very steep, we started above the center point and zig-zagged downslope. The herbivory and pellet surveys were conducted at the same time using teams of two observers, and each team member was assigned the same survey (herbivory, pellet) for consistency. The pellet surveys counted distinct pellet piles and were used as a general measure for absence (0), low (≤ 5) or high (> 6) usage in the area. An individual pellet was counted as one pile when only one pellet was found in the area. The herbivory surveys counted clumps of sedges, grasses or forbs bitten horizontally and the number of each that we observed. We defined herbivory classes as, (1) no evidence (2) trace (one or two plants grazed), (3) moderate (¼ or less plants grazed) or (4) high (more than ¼ plants grazed). We recorded any signs of other large ungulates or small mammal dwellings near the area, to account for other signs of herbivory. We counted herbivory based on the characteristics of large pieces of plants missing, not irregular nibbling typical of small mammals or invertebrates. We recorded only one instance where we observed another ungulate, bighorn sheep (*Ovis canadensis),* grazing in a valley below the elevation where mountain goats are normally found.

We recorded and classified physical evidence of common ungulate behaviours as of foraging, travelling, bedding, or mineral lick use (Figure 3.2). Foraging states were classified based on evidence of herbivory, forage availability and observations of mountain goat grazing. Travelling states were classified with either evidence of well-worn linear paths or lack of mountain goat signs (i.e. low pellet count, no foraging, no bedding evidence), as a mountain goat was assumed to have moved quickly through the area. Bedding states were classified with evidence of bedding which included ovals dug into the ground or compressed vegetation and high pellet counts. We searched for mineral licks within a $100m^2$ area by looking for digging, teeth marks or excavations under tree roots (Poole, Bachmann, and Teske 2010).

When evidence of more than one behaviour was observed in the field, we used hierarchical rules to classify each field site. If signs of bedding were present, we considered this a bedding site even if there were also some signs of foraging. A foraging site was an area with moderate to high herbivory and contained no bedding areas. A travelling site was considered when there was a game trail or trace signs of foraging and no bedding signs as a mountain goat was assumed to have quickly moved through the area. There were no signs of mineral licks located during site visits and therefore no need to consider them within this hierarchical analytical approach.



Moderate to high herbivory Mountain goats grazing | Trails, no bedding signs or trace herbivory | Bedding signs & pellet piles | Digging or excavations under tree roots

Figure 3.2 Photographs of typical evidence used to classify ground validation locations classified as (a) foraging, (b) travel, (c) bedding and (d) mineral lick.

To summarize, we validated the model using the field-site visits and thus determined the probability of the hidden states being correctly identified with HMMs. We compared the predicted behavioural state vs. “observed” habitat classification using QGIS. We mapped the predicted and the observed states of the animal to determine if these states aligned. These field observations were compared with the model of predicted hidden behavioural states.

3.4. Results

We used 16,122 and 18,604 GPS locations for Sherbrooke and Slate groups, respectively. The mean number of locations collected for each individual mountain goat in Sherbrooke was 1075 (2018) and 1074 (2019), and in Slate was 1064 (2018) and 1066 (2019). We removed and then interpolated < 0.1% (109 and 283 Sherbrooke and Slate Range, respectively) errant GPS points during the cleaning process.

HMM Analysis

We found the most support for the three-state model based on AIC and fit of the pseudo-residuals, termed each hidden state as foraging, travelling and resting movement states. The candidate models suggest that mountain goats have three behavioural states, described by the fitted distribution curves and state allocation (Figure 3.3). The first behaviour was consistent with local movement we termed foraging, characterized by moderate step lengths and large turning angles. The second behaviour was consistent with long distance travelling. The movements were faster than the mean speed of a mountain goat and the tortuosity was low, implying they were following a direct path and not returning to the same spot. The third behaviour was consistent with convoluted, tortuous, and short tracks of stationary or bedding, as GPS tracks. A visual example of each behavioural state, step characteristics, mean step lengths and turning angles are indicated in Table 3.1.

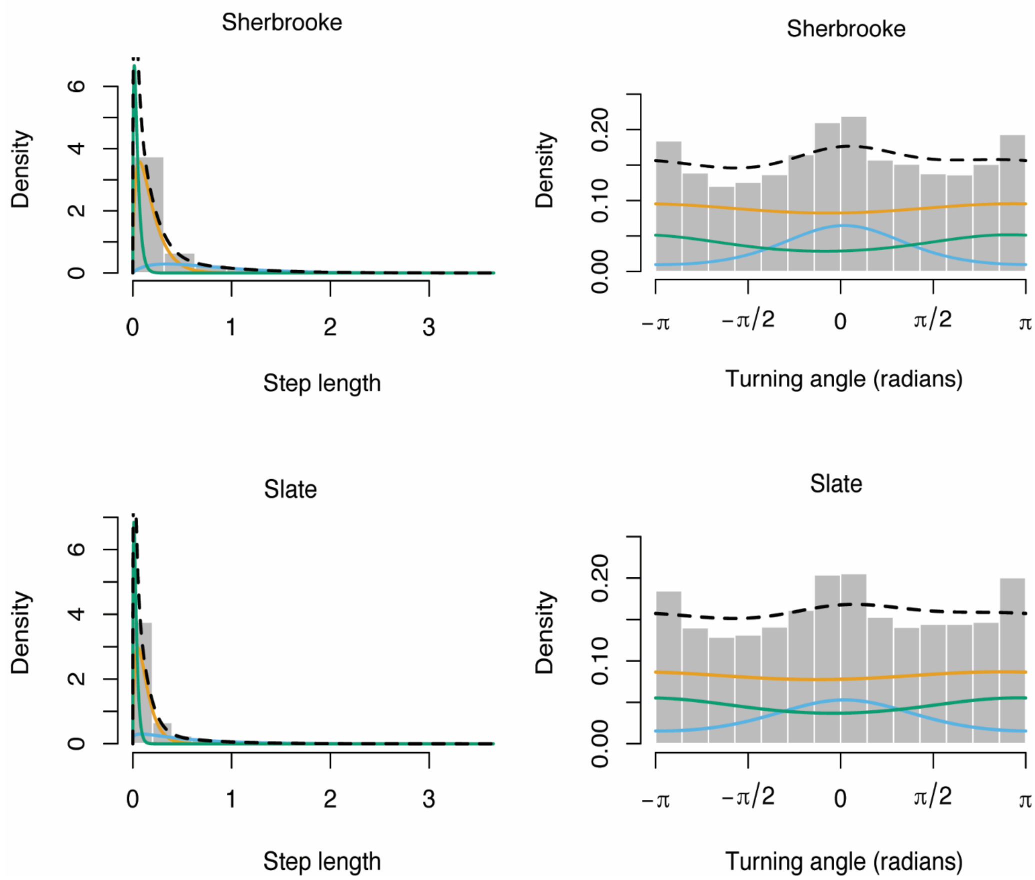
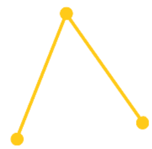
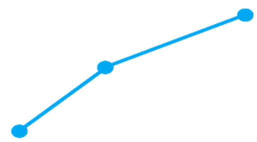


Figure 3.3 **Histograms of observed step lengths (left) and turning angles (right) for the Sherbrooke (upper) and Slate (lower) mountain goats. The coloured lines are the estimated densities in each state, foraging (orange), travelling (blue) and bedding (green), and the dotted black line is their sum.**

Table 3.1 Classification criteria for each behavioural state, foraging, travelling and bedding. Typical step characteristics are listed, along with estimates and 95% confidence intervals for movement parameters determined by the 3-state models. The step lengths are modeled with a gamma distribution, and the turning angles with a von Mises distribution, based on 1-h location movements for the Sherbrooke and Slate collared mountain goats.

State	Foraging	Travelling	Bedding
State Diagram			
Step Characteristics	moderate steps moderate turning angles	large steps large turning angles	small steps moderate turning angles
Step mean (km)	0.11 (0.10, 0.13)	0.49 (0.43, 0.56)	0.03 (0.02, 0.03)
Angle mean (radians)	2.93 (0.72, 4.57)	0.06 (-0.73, 0.14)	2.87 (2.61, 3.12)

When using the Viterbi algorithm to identify the most likely state of each location under the three-state model, the highest number of locations were identified as foraging (58% Sherbrooke, 51% Slate), then bedding (23% Sherbrooke, 29% Slate), and lastly travelling (19% Sherbrooke, 20% Slate). Maps of individual mountain goats' tracks classified by the HMM (Figure 3.4) reveal the spatial distribution and sequential patterns of activity and the transitions between each state. The transition probability matrix provides the probabilities of transitioning from one state to another (Appendix B, Table B1). When in a foraging state, the highest probability is to remain in a foraging state, with an equal probability of shifting from foraging to resting and travelling in Sherbrooke and a higher probability from shifting to foraging to bedding in the Slate Range. From the travelling state, the most likely transition is to remain in the same state. Once in a bedding state, the highest probability is to remain in a bedding state with a smaller probability of transitioning to a foraging state. This suggests that the observed behavioural state tends to persist for longer than one period of observation, for all three states. Mountain goats are more likely to enter the travelling state from the foraging state than after a bedding state. On spatial scales, the foraging state occurs in large clusters, the travelling state is associated with dispersed points, and the bedding state is characteristically a tight cluster of points (Appendix B, Figure B1).

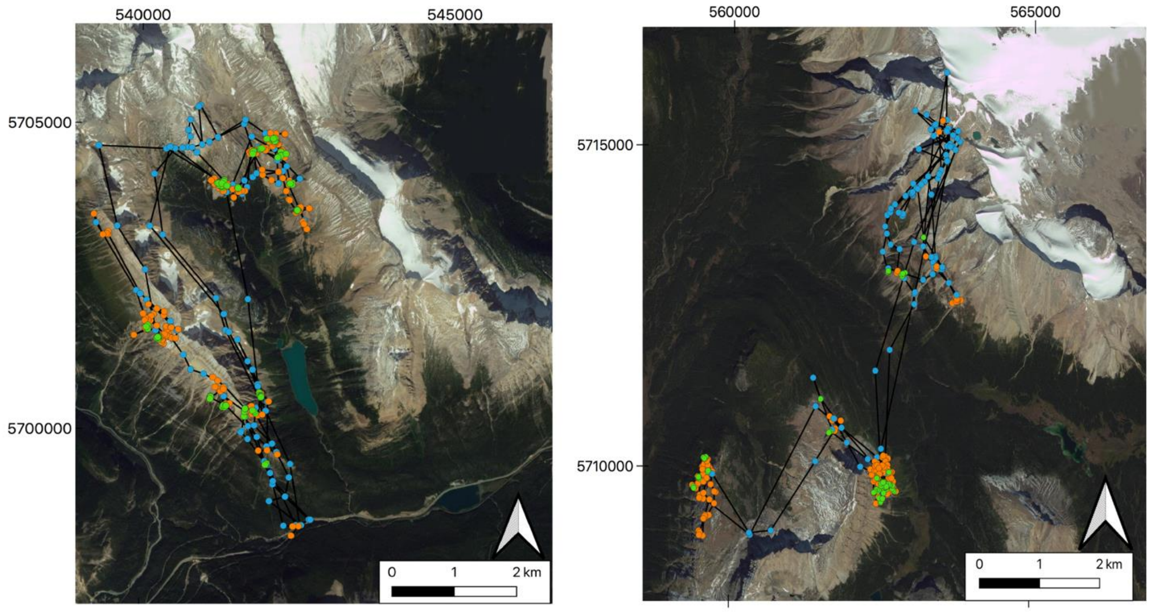


Figure 3.4 **Location of behavioural states, foraging (orange), travelling (blue) and bedding (green), for two representative individual mountain goats in the Sherbrooke (left) and Slate (right) range for the period 15-29 June 2018, based on hidden Markov model probabilities. Similar patterns were observed for all individuals included in the study.**

Environmental Covariates

There were clear differences to how the behavioural states related to diurnal patterns and distance from escape terrain (Figure 3.5). Time of day had a strong effect for both study groups on the state probabilities. Foraging was most likely to occur during the daylight hours, travelling in the crepuscular periods, and bedding during the night and during the mid-afternoon. The Sherbrooke and Slate groups responded similarly, with foraging being the most likely to occur away from escape terrain and bedding to occur closer to within escape terrain. The Sherbrooke group was likely to travel away from escape terrain, while the Slate group travel occurred closer to escape terrain.

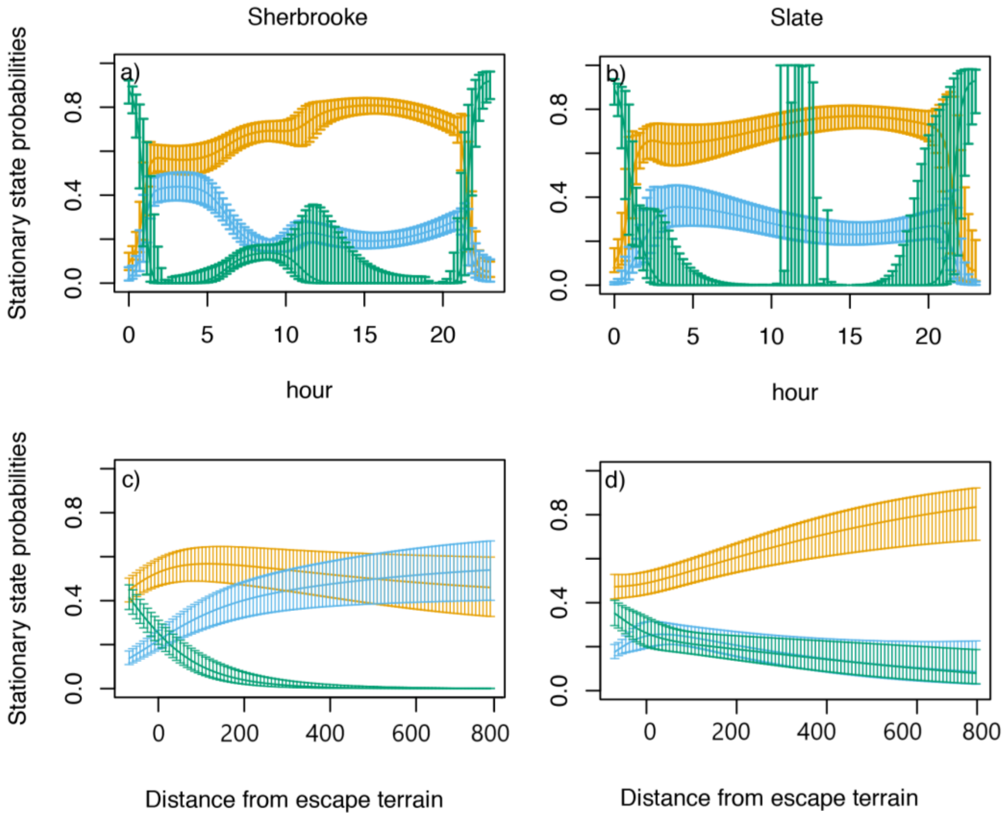


Figure 3.5 Stationary state probabilities for the Sherbrooke (left) and Slate (right) mountain goats as functions of two covariates: time of day (upper; a,b) and distance from escape terrain in meters (lower; c.d). The coloured lines represent each state, foraging (orange), travelling (blue) and bedding (green). The vertical lines provide pointwise 95% confidence intervals.

Field site selection and validation

We selected a total of 230 (92 Sherbrooke and 171 in Slate range) points to ground validate. We visited 92 sites which included 41 sites in Sherbrooke and 51 sites in the Slate Range. Out of 92 field sites investigated we found evidence of the hidden behaviour within the habitat in 59 sites (64%). Overall, we ground validated foraging 74% (20/27), bedding 63% (31/49) and travelling 50% (8/16) states. The behavioural state predictions from the HMMs for Sherbrooke and Slate Range were validated correct 60% and 66% respectively. In the Sherbrooke study area, we validated foraging 100% (11/11) and travelling 50% (8/16) followed by the bedding 42% (6/14) states. In the Slate range we validated bedding 71% (25/35) then foraging 56% (9/16). We could not validate any travelling states in the Slate Range as all sites were over class 3 terrain. All three behavioural states were found to some degree at 22 sites, with 44 sites having evidence of two states and 26 sites having evidence of only one state.

3.5. Discussion

We applied a hidden Markov state-space model to classify mountain goat behaviours as a proxy for habitat hotspots based on fine GPS-collar location data in two separate mountain goat groups over two years. Contrary to our expectations we did not find any high alpine mineral licks. However, in the field we were successful in recording evidence of many foraging areas, heavily used movement corridors and bedding sites. Using GPS collar locations, we used HMMs to predict three behavioural states in both the Sherbrooke and Slate ranges and interpreted the behaviours as foraging, travelling, and bedding. We were able to validate these behaviours using our field habitat classifications, using hierarchical rules, 64% of the time. Time of day influences the probability of detecting specific behavioural states, where foraging activity occurs in the daylight hours, travel in the crepuscular periods and bed at night and afternoon. Mountain goats in the Sherbrooke study area forage and travel away from escape terrain while the Slate range mountain goats only forage away from escape terrain.

We calculated the probability of state persistence and state switching and found that behaviour occurs in bouts. Transitions between each state were unlikely, especially if a mountain goat was bedding. This pattern is likely because we measured behavioural states in hourly intervals and goats appear to spend consecutive hours in one state. When transitions between states do occur, a bedding mountain goat would be more likely shift to forage before travelling. A foraging mountain goat was more likely to shift to bedding than to travelling. Both foraging and bedding reflects the places where mountain goats spend most of their time as these behaviours involve short step-lengths in the same location for long periods. Foraging and bedding locations would be considered a habitat hotspot, characterized by high resource availability, by wildlife and conservation managers because of the time spent accessing necessary resources for survival (Anderson et al. 2010).

The travelling state is the widest ranging and least concentrated state, and HMMs may be useful in helping conservation managers detect important movement corridors with no foraging or bedding habitat. Movement corridors may be missed in other types of habitat use analyses such as RSFs or SSFs because how much time and space an animal takes up within the landscape defines their habitat utilization. Yet features that mountain goats move quickly through, such as movement corridors, may be just as critical for their survival (Hebert and Cowan 1971). Abrahams et al. (2016) employed a SSF with different sampling frequencies, depending on the movement patterns of GPS collared African wild dogs (*Lycaon pictus*), including foraging, resting and commuting, and demonstrated that the response of selecting roads varied significantly depending on the behavioural state in which roads were encountered. If an African wild dog was commuting, they were more likely to use a road than if they were foraging or resting. These findings indicate that including behavioural information into an animal movement study is critical for understanding how wildlife respond to certain features within the landscape (Abrahms et al. 2016). Additionally, mountain goats travel quickly through these areas during crepuscular periods, which reduces the likelihood of them being detected in these habitats during aerial surveys (Gonzalez-Voyer, Festa-Bianchet, and Smith 2001; Rice, Jenkins, and Chang 2009) or through opportunistic observations. It is ecologically relevant to define areas animals use frequently, yet, move quickly through and may not have traditional habitat features that can be defined through remote sensing including vegetation classification or slope angle (DeVoe et al. 2015; Lowrey et al. 2017).

Mountain goats in both the Sherbrooke and Slate study areas exhibited similar patterns over the time of day. Similar to previous studies mountain goats forage more during the daylight hours, travel during the crepuscular periods and sleep in the night and afternoon (Romeo and Lovari 1996). We observed that mountain goats in both study groups were in the foraging state during daylight hours. Travelling occurred during the crepuscular periods which is presumed to maximize thermoregulation and minimize predation in other ungulates, including white-tailed deer (Singer 1978; Pedevillano and Wright 1987; Ager et al. 2003; Webb et al. 2010). Bedding occurs during the darkest hours of the night and in the mid-afternoon when the daytime heat would be the hottest and mountain goats cease travelling and foraging to avoid heat-stress (White et al. 2011; Sarmento, Biel, and Berger 2019).

We found evidence that mountain goat behavioural states are strongly linked to distance from escape terrain. Similar to other studies we observed that mountain goats are most likely to be in the foraging state when they are the farthest from escape terrain and bed in areas nearest to escape terrain (Poole and Heard 2003; DeVoe et al. 2015). The Sherbrooke group tended to travel away from escape terrain, while the Slate group stayed nearest to escape terrain. The physio-geological characteristics of the two mountain ranges could account for these differences. The Sherbrooke and Slate mountain ranges have different geology (Bobrowsky and Rutter 2007), with the Sherbrooke study area surrounded by mostly moderately sloped terrain containing large ridges in which the goat trails circumnavigate terrain along moderately sloped ridges. In contrast, the Slate mountain range is characterized by large summits and steep cliffs where mountain goats travel close to ledges.

Our HMM predicted behavioural states as a proxy of mountain goat habitat hotspots correctly 64% of the time for the Sherbrooke and the Slate ranges combined. Our method is best at “uncovering” foraging areas, then areas where goats bed, and lastly where they travel. Many field locations that we ground validated had evidence of high use, with bedding and foraging evidence as well as many trails leading to and from these areas. Interestingly, during our navigation to these field sites there was often no evidence of mountain goats along our chosen routes until we were near the sites. This suggests that a collared goat’s behaviour of moving “fast” to “slow” indicates a habitat hotspot for many mountain goats in the study population. Initially our study was designed to find alpine mineral licks, but we found no evidence of states that defined travel to mineral licks. Alpine mineral licks are difficult to locate and may not be as abundant as low elevation mineral licks, especially in the Rocky Mountains (Jokinen et al. 2014). We may not have found alpine mineral licks in either range because there were none available, or they were infrequently visited by GPS collared mountain goats.

Unexpectedly, we discovered many mountain goat trails during our fieldwork. The trails were clearly used as heavily trafficked movement corridors with many mountain goat tracks and pellet piles within areas with very little forage. Given this observation, the HMM appear to perform well at predicting movement corridors in the Sherbrooke study area. In contrast, the Slate range was too steep to validate any of the suspected travelling sites. Future work with drones may be useful to validate these potential travel sites that were not accessible by foot. Anecdotally, bedding sites often occurred near foraging sites, but in a more clustered manner, often with a wide view of the area on or near escape terrain.

Our state classification should only be considered as a proxy for the underlying 'true' animal behaviour. As we limited our classification to the three most common states for mountain goats, we may have missed other less common states, such as kidding, or evasion from predators, and this may partially explain our validation success. Other studies that "uncovered" the hidden behavioural states of African lions found 75% behaviours correct (Goodall et al. 2019), detected 86% wolf kill sites correctly (Franke et al. 2006) and found snow leopard prey caches 41% of the time (Farhadinia et al. 2020). Similarly, there were many sites that had evidence of all three behavioural states, and we chose to adopt a conservative approach with hierarchical rules to validate only one of the behavioural states present at the field sites. For example, we were interested in separating bedding sites, including those where foraging also occurred, from areas where only foraging occurred. Animal movement is usually driven by short term goals and internal states such as reproduction, maintenance, feeding, survival and escaping predators (Holyoak et al. 2008), and our study used individual GPS collars to draw broad conclusions about behavioural habitat selection of the population. Sex or age specific individual variation of the GPS collared mountain goats should be considered in future studies.

Our detectability may have been driven by fieldwork accessibility and our *a priori* design. Our field site selection was also biased towards foraging and bedding sites. First, we targeted places where mountain goats moved fast to slow, deliberately biasing towards sites away from trails because a mountain goat would move quickly on a trail and then slow down once it arrived at a foraging or bedding site. Second, mountain goats may forage on small grasses and sedges that were more available during the month prior to our field visits. In some cases, the foraging evidence on southerly aspects was limited or plants had already gone to seed in late August. Third, our study assumed that GPS collared mountain goats are independent of each other, and yet we know they are highly gregarious (Festa-Bianchet, and Côté 2008). Lastly, in the Slate Range we found more bedding sites than any other sites and it is possible travelling was mis-classified here as mountain goats may travel slower in complex terrain. As noted above, we were unable to validate these sites, especially travelling and bedding sites because they were located on very steep terrain.

We used HMMs to uncover different habitat is used by mountain goats in different ways depending on their behavioural state. We visited areas where mountain goats switched their behavioural state between moving fast to slow and almost all these areas had evidence of mountain goat foraging, travelling and bedding sites. Overall, we provide new insights into the behavioural states of mountain goats and how they move throughout the landscape during different times of the day and distance from escape terrain. We detected travelling areas even when the terrain is inaccessible. Our findings also provide insights into how different groups of mountain goats use their terrain differently but exhibit similar behavioural states over the time of day.

The lack of basic data for elusive animals, including habitat use, distributions or behaviour can be obstacles in management, planning and establishing conservation priorities (Parsons 2016). Our research can help inform conservation priorities and management decisions to determine foraging, bedding and travel areas without extensive travel into the field, which is often rugged, complex and dangerous to access (Fraser et al. 2018). Our data suggests that hidden Markov models can detect high use habitat areas and movement corridors that connect them. Behavioural state predictions can guide resource managers in identifying not only key foraging habitat and important bedding sites but also possible movement corridors. Remote data collection and modelling behaviour can uncover habitat hotspots and detect features that may be overlooked by habitat managers because animals may travel quickly through the area. Our results have the potential for wider application, including predicting habitat hotspots for elusive ungulates and herbivores that have large, cryptic and difficult to access home ranges.

Chapter 4.

General Discussion

4.1. Overview

I examined how resource hotspots can influence the movement behaviour of mountain goats over large and small temporal and spatial scales. I investigated the movement ecology of two groups of mountain goats and their relationship with two different kinds of hotspots in the Canadian Rocky Mountains. In Chapter 2, I investigated mountain goat movements to mineral licks, a concentrated resource hotspot, over different time periods from decadal to seasonal to diurnal. In Chapter 3, I examined behavioural states as a proxy for mountain goat habitat hotspots, specifically foraging, travelling and bedding areas. By examining movements over a variety of temporal and spatial scales we can gain a better understanding of how mountain goats access resources and habitat hotspots in complex terrestrial landscapes.

The temporal patterns of mountain goat movements to resource hotspots uncovered deliberate and regular seasonal visits to mineral licks and suggest this behaviour has persisted over decades (Chapter 2). Root trampling scars provide evidence of site fidelity with long-term use of trails leading towards mineral licks. Mountain goats visited mineral licks frequently over the snow-free period, with males beginning to visit during snow melt in May, followed by females with newborn kids in mid-June. Mountain goats have developed strong behavioural traditions visiting this mineral lick over many decades, and within a season males and females have different seasonal patterns of visitation while travelling in distinct group sizes. The temporal patterns of mineral lick use by male and female mountain goats and the behavioural adaptions they display highlight the importance of these mineral licks for this population.

HMMs were used to infer behavioural states as a proxy for habitat hotspots such as foraging, travelling and bedding based on high resolution GPS-collar location data in two separate mountain goat groups over two years (Chapter 3). I examined how behavioural states change in relation to two environmental co-variates, time of day and distance to escape terrain. We found foraging occurs in the daylight hours, travel in the crepuscular periods and bed at night and afternoon. Interestingly, it seems topography affects behaviour. For example, mountain goats in the Sherbrooke study area forage and travel away from escape terrain while the Slate range mountain goats forage away from escape terrain but will travel through escape terrain. I ground-validated physical evidence of behavioural states and recorded evidence of high-quality foraging areas, heavily used movement corridors and bedding sites. I was able to ground validate these using hierarchical rules and found foraging and bedding locations were found in clusters and travelling was the least dense state. Importantly, HMMs can detect movement corridors and may help land managers identify important areas where mountain goats spend less time but are important to habitat connectivity.

4.2. Management Implications

In this thesis I provide new baseline data for management planning within and outside a mountain goat population's normal home range. Mineral licks are important to mountain goats and understanding the use of these sites is necessary to create guidelines for mountain goat conservation plans. Analysis of soils uncovered high levels of salts along the roadside, likely stemming from chemical components in road abrasives used along the highway. I recommend reducing the use of these chemicals in highway maintenance to reduce attracting mountain goats onto the road and ultimately reducing vehicle collisions. I found other trace elements that are important for mountain goat fecundity at these mineral lick sites and if this area is impacted by highway construction access to these minerals may be limited. Soils at the mineral lick and forest were similar in composition according to our PCA analysis. If highway construction limits access to the mineral licks a possible solution would be to expose forest soils further upslope away from the highway, reducing vehicle collision exposure and creating access to mineral soils. Understanding the timing and intensity of mineral lick use over different time periods provides a baseline into how anthropogenic disturbances may influence critical resource access over time and will help target peak times when mountain goats will be most at risk to disturbance. As more data is gathered on the phenomenon of mineral lick utilization, we will be better able to expand our understanding of when and why mountain goats use mineral licks. Characterizing the differences between male and female mountain goat use of mineral licks can help wildlife conservation managers reduce the impact of stressors such as disturbances during the peak visiting times, which may be particularly important for lactating females.

My research can inform conservation priorities and management decisions by identifying foraging, bedding and travel areas without extensive travel into mountain goat habitat, which is often rugged, complex and dangerous to access. Understanding how mountain goats use the landscape can help land managers identify habitat conservation priorities. Information about seasonal range use can guide resource managers in identifying not only key foraging habitat and important bedding sites but also movement corridors that connect these sites. Remote data collection and modelling behaviour can uncover habitat hotspots and detect features that may be overlooked by habitat managers because animals do not spend large amounts of time there. Identifying movement corridors that mountain goats travel quickly through is important to maintain connectivity between habitat patches. My research indicates mountain passes, ridges and stopovers should be considered in land use planning. These results have the potential for wider applications, such as predicting habitat hotspots for elusive animals that have large, cryptic and difficult to access home ranges.

4.3. Future Directions

I examined the temporal and spatial scales of mountain goats accessing resource and habitat hotspots within and outside their normal home range. The results of this study provide detailed insights on an elusive alpine ungulate. The lack of basic data for elusive animals, including habitat use, distributions or behaviour can be obstacles in management, planning and establishing conservation priorities (Parsons 2016). The detailed temporal data I provided concerning mineral lick use along the TCH highlights a clear resource hotspot and I recommend continued monitoring at this mineral lick site. I recommend limiting disturbances such as highway construction in times of high use especially during times when females and kids are at the mineral lick. I also recommend that researchers adopt an HMM approach over different seasons to predict areas such as kidding sites and important wintering habitats. In addition, my results may provide a foundation for incorporating varying spatial scales, which could be used to infer continental scale behavioural patterns of mountain goats within different ranges.

Mountain goats are the least studied ungulate in North America, primarily because they live year-round in inhospitable and inaccessible mountain habitats. While they are not listed as a species at risk in Canada, mountain goats are sentinels of the effects of the climate change and are easily disturbed by human presence (Mountain

Goat Management Team 2010). My thesis provides detailed information about mountain goat behavioural states in protected areas, where they do not experience hunting pressures or anthropogenic disturbances such as heli-skiing, forestry, mining, or development. We can use this data to inform how mountain goats alter their movement patterns in response to environmental and anthropogenic changes.

References

Abrahms, B., N. R. Jordan, K. A. Golabek, J. W. McNutt, A. M. Wilson, and J. S. Brashares. 2016. “Lessons from Integrating Behaviour and Resource Selection: Activity-Specific Responses of African Wild Dogs to Roads.” *Animal Conservation* 19 (3): 247–55. https://doi.org/10.1111/acv.12235.

Ager, Alan A., Bruce K. Johnson, John W. Kern, and John G. Kie. 2003. “Daily and Seasonal Movements and Habitat Use by Female Rocky Mountain Elk and Mule Deer.” *Journal of Mammalogy* 84 (3): 1076–88. https://doi.org/10.1644/BBa-020.

Anderson, Paul R. Armsworth, Felix Eigenbrod, Chris D. Thomas, Simon Gillings, Andreas Heinemeyer, David B. Roy, and Kevin J. Gaston. 2009. “Spatial Covariance between Biodiversity and Other Ecosystem Service Priorities.” *Journal of Applied Ecology* 46 (4): 888–96. https://doi.org/10.1111/j.1365-2664.2009.01666.x.

Anderson, J. Grant C. Hopcraft, Stephanie Eby, Mark Ritchie, James B. Grace, and Han Olff. 2010. “Landscape-Scale Analyses Suggest Both Nutrient and Antipredator Advantages to Serengeti Herbivore Hotspots.” *Ecology* 91 (5): 1519–1529. https://doi.org/10.1890/09-0739.1.

Arcos, José Manuel, Juan Bécares, Dani Villero, Lluís Brotons, Beneharo Rodríguez, and Asunción Ruiz. 2012. “Assessing the Location and Stability of Foraging Hotspots for Pelagic Seabirds: An Approach to Identify Marine Important Bird Areas (IBAs) in Spain.” *Biological Conservation* 156: 30–42. https://doi.org/10.1016/j.biocon.2011.12.011.

Atwood, Todd C., and Harmon P. Weeks. 2002. “Sex- and Age-Specific Patterns of Mineral Lick Use by White-Tailed Deer (*Odocoileus Virginianus*).” *The American Midland Naturalist* 148 (2): 289–96. https://doi.org/10.1674/0003-0031(2002)148[0289:SAASPO]2.0.CO;2.

Ayotte, Jeremy B., Katherine L. Parker, Joselito M. Arocena, and Michael P. Gillingham. 2006. “Chemical Composition of Lick Soils: Functions of Soil Ingestion by Four Ungulate Species.” *Journal of Mammalogy* 87 (5): 878–888. https://doi.org/10.1644/06-mamm-a-055r1.1.

Ayotte, Jeremy B., Katherine L. Parker, and Michael P. Gillingham. 2008. “Use of Natural Licks by Four Species of Ungulates in Northern British Columbia.” *Journal of Mammalogy* 89 (4): 1041–50. https://doi.org/10.1644/07-mamm-a-345.1.

Baird, David. 1962. *Yoho National Park: The Mountains, the Rocks, the Scenery*. Vol. 4. Ottawa: Geological Survey of Canada.

Barrett, Morley W., J. W. Nolan, and Laurence D. Roy. 1982. “Evaluation of a Hand-Held Net-Gun to Capture Large Mammals.” *Wildlife Society Bulletin (1973-2006)* 10 (2): 108–14.

Bestley, Sophie, Toby A. Patterson, Mark A. Hindell, and John S. Gunn. 2010. “Predicting Feeding Success in a Migratory Predator: Integrating Telemetry, Environment, and Modeling Techniques.” *Ecology* 91 (8): 2373–84. https://doi.org/10.1890/08-2019.1.

Beyer, Hawthorne L., Daniel T. Haydon, Juan M. Morales, Jacqueline L. Frair, Mark Hebblewhite, Michael Mitchell, and Jason Matthiopoulos. 2010. “The Interpretation of Habitat Preference Metrics under Use–Availability Designs.” *Philosophical Transactions of the Royal Society B: Biological Sciences* 365 (1550): 2245–2254. https://doi.org/10.1098/rstb.2010.0083.

Blake, John G., Jaime Guerra, Diego Mosquera, Rene Torres, Bette A. Loiselle, and David Romo. 2010. “Use of Natural Licks by White-Bellied Spider Monkeys (*Ateles Belzebuth*) and Red Howler Monkeys (*Alouatta Seniculus*) in Eastern Ecuador.” *International Journal of Primatology* 31 (3): 471–83. https://doi.org/10.1007/s10764-010-9407-5.

Bobrowsky, Peter, and Nathaniel W. Rutter. 2007. “The Quaternary Geologic History of the Canadian Rocky Mountains.” *Géographie Physique et Quaternaire* 46 (1): 5–50. https://doi.org/10.7202/032887ar.

Boyce, Mark S, Pierre R Vernier, Scott E Nielsen, and Fiona K. A Schmiegelow. 2002. “Evaluating Resource Selection Functions.” *Ecological Modelling* 157 (2): 281–300. https://doi.org/10.1016/S0304-3800(02)00200-4.

Bradbury, J., R. Gibson, and I.M. Tsai. 1986. “Hotspots and the Dispersion of Leks.” *Animal Behaviour* 34 (6): 1694–1709. https://doi.org/10.1016/S0003-3472(86)80257-3.

Butler, Andrew R., Kristy L.S. Bly, Heather Harris, Robert M. Inman, Axel Moehrenschlager, Donelle Schwalm, and David S. Jachowski. 2019. “Winter Movement Behavior by Swift Foxes (*Vulpes Velox*) at the Northern Edge of Their Range.” *Canadian Journal of Zoology* 97 (10): 922–30. https://doi.org/10.1139/cjz-2018-0272.

Cadsand, B, B Jex, and M.P Gillingham. 2010. “Modified Clover Trap for Capturing Mountain Goats in Northwest British Columbia.” *Biennial Symposium Northern Wildlife Sheep and Goat Council* 17: 71–77.

Cagnacci, Francesca, Luigi Boitani, Roger A. Powell, and Mark S. Boyce. 2010. “Animal Ecology Meets GPS-Based Radiotelemetry: A Perfect Storm of Opportunities and Challenges.” *Philosophical Transactions of the Royal Society B: Biological Sciences* 365 (1550): 2157–2162. https://doi.org/10.1098/rstb.2010.0107.

Camp, M. J., L. A. Shipley, T. R. Johnson, P. J. Olsoy, J. S. Forbey, J. L. Rachlow, and D. H. Thornton. 2017. "The Balancing Act of Foraging: Mammalian Herbivores Trade-off Multiple Risks When Selecting Food Patches." *Oecologia* 185 (4): 537–49. https://doi.org/10.1007/s00442-017-3957-6.

Churski, Marcin, Jakub W. Bubnicki, Bogumiła Jędrzejewska, Dries P. J. Kuijper, and Joris P. G. M. Cromsigt. 2017. "Brown World Forests: Increased Ungulate Browsing Keeps Temperate Trees in Recruitment Bottlenecks in Resource Hotspots." *New Phytologist* 214 (1): 158–68. https://doi.org/10.1111/nph.14345.

Conradt, Larissa. 1998. "Measuring the Degree of Sexual Segregation in Group-Living Animals." *Journal of Animal Ecology* 67 (2): 217–26. https://doi.org/10.1046/j.1365-2656.1998.00183.x.

Côté, Steeve D., Sandra Hamel, Antoine St-Louis, and Julien Mainguy. 2013. "Do Mountain Goats Habituate to Helicopter Disturbance?" *The Journal of Wildlife Management* 77 (6): 1244–1244. https://doi.org/10.1002/jwmg.565.

Craine, Joseph M., Fiona Ballantyne, Michael Peel, Nick Zambatis, Carl Morrow, and William D. Stock. 2009. "Grazing and Landscape Controls on Nitrogen Availability across 330 South African Savanna Sites." *Austral Ecology* 34 (7): 731–40. https://doi.org/10.1111/j.1442-9993.2009.01978.x.

Davies, Andrew B., Shaun R. Levick, Mark P. Robertson, Berndt J. van Rensburg, Gregory P. Asner, and Catherine L. Parr. 2016. "Termite Mounds Differ in Their Importance for Herbivores across Savanna Types, Seasons and Spatial Scales." *Oikos* 125 (5): 726–734. https://doi.org/10.1111/oik.02742.

Davies, Andrew B., Mark P. Robertson, Shaun R. Levick, Gregory P. Asner, Berndt J. van Rensburg, and Catherine L. Parr. 2014. "Variable Effects of Termite Mounds on African Savanna Grass Communities across a Rainfall Gradient." Edited by Frank Gilliam. *Journal of Vegetation Science* 25 (6): 1405–16. https://doi.org/10.1111/jvs.12200.

Dean, Ben, Robin Freeman, Holly Kirk, Kerry Leonard, Richard A. Phillips, Chris M. Perrins, and Tim Guilford. 2012. "Behavioural Mapping of a Pelagic Seabird: Combining Multiple Sensors and a Hidden Markov Model Reveals the Distribution of at-Sea Behaviour." *Journal of The Royal Society Interface* 10 (78): 20120570. https://doi.org/10.1098/rsif.2012.0570.

DeVoe, J. D., R. A. Garrott, J. J. Rotella, S. R. Challender, P. J. White, M. O'Reilly, and C. J. Butler. 2015. "Summer Range Occupancy Modeling of Non-Native Mountain Goats in the Greater Yellowstone Area." *Ecosphere* 6 (11): 1–20. https://doi.org/10.1890/ES15-00273.1.

Dingle, Hugh. 2014. *Migration: The Biology of Life on the Move*. Oxford University Press.

Dormaar, J. F., and B. D. Walker. 1996. “Elemental Content of Animal Licks along the Eastern Slopes of the Rocky Mountains in Southern Alberta, Canada.” *Canadian Journal of Soil Science* 76 (4): 509–12. https://doi.org/10.4141/cjss96-063.

Farhadinia, Mohammad S., Théo Michelot, Paul J. Johnson, Luke T. B. Hunter, and David W. Macdonald. 2020. “Understanding Decision Making in a Food-Caching Predator Using Hidden Markov Models.” *Movement Ecology* 8 (1): 9. https://doi.org/10.1186/s40462-020-0195-z.

Festa-Bianchet, M, and S.D. Côté. 2008. *Mountain Goats: Ecology, Behaviour and Conservation of an Alpine Ungulate*. Washington, DC: Island Press.

Fortin, Daniel, and Marie-Eve Fortin. 2009. “Group-Size-Dependent Association between Food Profitability, Predation Risk and Distribution of Free-Ranging Bison.” *Animal Behaviour* 78 (4): 887–92. https://doi.org/10.1016/j.anbehav.2009.06.026.

Franke, Alastair, Terry Caelli, and Robert J Hudson. 2004. “Analysis of Movements and Behavior of Caribou (*Rangifer Tarandus*) Using Hidden Markov Models.” *Ecological Modelling* 173 (2–3): 259–70. https://doi.org/10.1016/j.ecolmodel.2003.06.004.

Franke, Alastair, Terry Caelli, Gerald Kuzyk, and Robert J. Hudson. 2006. “Prediction of Wolf (*Canis Lupus*) Kill-Sites Using Hidden Markov Models.” *Ecological Modelling* 197 (1–2): 237–46. https://doi.org/10.1016/j.ecolmodel.2006.02.043.

Fraser, Kevin C., Kimberley T. A. Davies, Christina M. Davy, Adam T. Ford, D. T. Tyler Flockhart, and Eduardo G. Martins. 2018. “Tracking the Conservation Promise of Movement Ecology.” *Frontiers in Ecology and Evolution* 6 (October): 150. https://doi.org/10.3389/fevo.2018.00150.

Freymann, Bernd P., Sara N. de Visser, and Han Olff. 2010. “Spatial and Temporal Hotspots of Termite-Driven Decomposition in the Serengeti.” *Ecography* 33 (January): 443–50. https://doi.org/10.1111/j.1600-0587.2009.05960.x.

Gaynor, Kaitlyn M., Cheryl E. Hojnowski, Neil H. Carter, and Justin S. Brashares. 2018. “The Influence of Human Disturbance on Wildlife Nocturnality.” *Science* 360 (6394): 1232–35. https://doi.org/10.1126/science.aar7121.

Ghanem, Simon J., Hans Ruppert, Thomas H. Kunz, and Christian C. Voigt. 2013. “Frugivorous Bats Drink Nutrient- and Clay-Enriched Water in the Amazon Rain Forest: Support for a Dual Function of Mineral-Lick Visits.” *Journal of Tropical Ecology* 29 (1): 1–10. https://doi.org/10.1017/S0266467412000740.

Giotto, Nina, Jean-François Gerard, Alon Ziv, Amos Bouskila, and Shirli Bar-David. 2015. “Space-Use Patterns of the Asiatic Wild Ass (*Equus Hemionus*): Complementary Insights from Displacement, Recursion Movement and Habitat Selection Analyses.” *PLOS ONE* 10 (12): 1–21. https://doi.org/10.1371/journal.pone.0143279.

Gonzalez-Voyer, Alejandro, Marco Festa-Bianchet, and Kirby G. Smith. 2001. “Efficiency of Aerial Surveys of Mountain Goats.” *Wildlife Society Bulletin (1973-2006)* 29 (1): 140–44.

Goodall, Victoria L., Sam M. Ferreira, Paul J. Funston, and Nkabeng Maruping-Mzileni. 2019. “Uncovering Hidden States in African Lion Movement Data Using Hidden Markov Models.” *Wildlife Research* 46 (4): 296–303. https://doi.org/10.1071/WR18004.

Grant, C.C., and M.C. Scholes. 2006. “The Importance of Nutrient Hot-Spots in the Conservation and Management of Large Wild Mammalian Herbivores in Semi-Arid Savannas.” *Biological Conservation* 130 (3): 426–437. https://doi.org/10.1016/J.BIOCON.2006.01.004.

Hamel, Sandra, Steeve D. Côté, Kirby G. Smith, and Marco Festa-Bianchet. 2006. “Population Dynamics and Harvest Potential of Mountain Goat Herds in Alberta.” *Journal of Wildlife Management* 70 (4): 1044–53. https://doi.org/10.2193/0022-541X(2006)70[1044:PDAHPO]2.0.CO;2.

Harris, Richard B., Clifford G. Rice, and Adam G. Wells. 2017. “Influence of Geological Substrate on Mountain Goat Forage Plants in the North Cascades, Washington State.” *Northwest Science* 91 (3): 301–13. https://doi.org/10.3955/046.091.0309.

Hebblewhite, Mark, and Evelyn Merrill. 2008. “Modelling Wildlife–Human Relationships for Social Species with Mixed-Effects Resource Selection Models.” *Journal of Applied Ecology* 45 (3): 834–44. https://doi.org/10.1111/j.1365-2664.2008.01466.x.

Hebblewhite, Mark, and Evelyn H. Merrill. 2009. “Trade-Offs between Predation Risk and Forage Differ between Migrant Strategies in a Migratory Ungulate.” *Ecology* 90 (12): 3445–54. https://doi.org/10.1890/08-2090.1.

Hebert, Daryl, and I. McTaggart Cowan. 1971. “Natural Salt Licks as a Part of the Ecology of the Mountain Goat.” *Canadian Journal of Zoology* 49 (5): 605–10. https://doi.org/10.1139/z71-097.

Holyoak, Marcel, Renato Casagrandi, Ran Nathan, Eloy Revilla, and Orr Spiegel. 2008. “Trends and Missing Parts in the Study of Movement Ecology.” *Proceedings of the National Academy of Sciences* 105 (49): 19060–65. https://doi.org/10.1073/pnas.0800483105.

Hooten, Mevin B., Henry R. Scharf, and Juan M. Morales. 2019. “Running on Empty: Recharge Dynamics from Animal Movement Data.” *Ecology Letters* 22 (2): 377–89. https://doi.org/10.1111/ele.13198.

Hunter, Malcolm L. 2017. “Conserving Small Natural Features with Large Ecological Roles: An Introduction and Definition.” *Biological Conservation* 211 (July): 1–2. https://doi.org/10.1016/j.biocon.2016.12.019.

Huruba, Rangarirai, Tafadzwa Mlambo, Peter J. Mundy, Allan Sebata, and Duncan N. MacFadyen. 2018. “Short Duration Overnight Cattle Kraaling in Natural Rangelands: Implications for Grass Composition, Quality, above Ground Biomass, Species Diversity and Basal Cover.” *Agriculture, Ecosystems & Environment* 257 (April): 144–51. https://doi.org/10.1016/j.agee.2018.02.004.

Johnson, Devin S., Joshua M. London, Mary-Anne Lea, and John W. Durban. 2008. “Continuous-Time Correlated Random Walk Model for Animal Telemetry Data.” *Ecology* 89 (5): 1208–15. https://doi.org/10.1890/07-1032.1.

Jokinen, M. E., M Verhage, R Anderson, and D Manzer. 2014. “Observational Description of Alpine Ungulate Use at Mineral Licks in Southwest Alberta, Canada.” *Biennial Symposium of the Northern Wild Sheep and Goat Council* 19: 42–63.

Jones, R, L, and H. C. Hanson. 1985. *Mineral Licks, Geography, and Biochemistry of North American Ungulates.* Ames, IA: Iowa State University.

Karelus, Dana L., J. Walter McCown, Brian K. Scheick, Madelon van de Kerk, Benjamin M. Bolker, and Madan K. Oli. 2019. “Incorporating Movement Patterns to Discern Habitat Selection: Black Bears as a Case Study.” *Wildlife Research* 46 (1): 76. https://doi.org/10.1071/WR17151.

Kreulen, D. A. 1985. “Lick Use by Large Herbivores: A Review of Benefits and Banes of Soil Consumption.” *Mammal Review* 15 (3): 107–23. https://doi.org/10.1111/j.1365-2907.1985.tb00391.x.

Krishnamani, R, and William C Mahaney. 2000. “Geophagy among Primates: Adaptive Significance and Ecological Consequences.” *Animal Behaviour* 59: 899–915. https://doi.org/10.1006/anbe.1999.1376.

Kroesen, Laura, David Hik, and Seth Cherry. 2020. “Patterns of Decadal, Seasonal and Daily Visitation to Mineral Licks, a Critical Resource Hotspot for Mountain Goats (*Oreamnos Americanus*) in the Rocky Mountains.” *Wildlife Biology* 2020 (4): 1–12. https://doi.org/10.2981/wlb.00736.

Lai, Sandra, Joël Bêty, and Dominique Berteaux. 2015. “Spatio–Temporal Hotspots of Satellite–Tracked Arctic Foxes Reveal a Large Detection Range in a Mammalian Predator.” *Movement Ecology* 3 (1): 37. https://doi.org/10.1186/s40462-015-0065-2.

Langrock, Roland, Ruth King, Jason Matthiopoulos, Len Thomas, Daniel Fortin, and Juan M. Morales. 2012. “Flexible and Practical Modeling of Animal Telemetry Data: Hidden Markov Models and Extensions.” *Ecology* 93 (11): 2336–42. https://doi.org/10.1890/11-2241.1.

Lee, Alan T. K., Donald J. Brightsmith, Mario P. Vargas, Karina Q. Leon, Aldo J. Mejia, and Stuart J. Marsden. 2014. “Diet and Geophagy across a Western Amazonian Parrot Assemblage.” *Biotropica* 46 (3): 322–30. https://doi.org/10.1111/btp.12099.

Link, Andres, Nelson Galvis, Erin Fleming, and Anthony Di Fiore. 2011. “Patterns of Mineral Lick Visitation by Spider Monkeys and Howler Monkeys in Amazonia: Are Licks Perceived as Risky Areas?” *American Journal of Primatology* 73 (4): 386–96. https://doi.org/10.1002/ajp.20910.

Lowrey, B., R. A. Garrott, H. M. Miyasaki, G. Fralick, and S. R. Dewey. 2017. “Seasonal Resource Selection by Introduced Mountain Goats in the Southwest Greater Yellowstone Area.” *Ecosphere* 8 (4): 1–20. https://doi.org/10.1002/ecs2.1769.

Matsubayashi, Hisashi, Peter Lagan, Noreen Majalap, Joseph Tangah, Jum Rafiah Abd. Sukor, and Kanehiro Kitayama. 2007. “Importance of Natural Licks for the Mammals in Bornean Inland Tropical Rain Forests.” *Ecological Research* 22 (5): 742–48. https://doi.org/10.1007/s11284-006-0313-4.

Mazur, Rachel, and Victoria Seher. 2008. “Socially Learned Foraging Behaviour in Wild Black Bears, (*Ursus Americanus*).” *Animal Behaviour* 75 (4): 1503–8. https://doi.org/10.1016/j.anbehav.2007.10.027.

McClintock, Brett T., Roland Langrock, Olivier Gimenez, Emmanuelle Cam, David L. Borchers, Richard Glennie, and Toby A. Patterson. 2020. “Uncovering Ecological State Dynamics with Hidden Markov Models.” *Ecology Letters* 23 (12): 1878–1903. https://doi.org/10.1111/ele.13610.

McClintock, Brett T., and Théo Michelot. 2018. “MomentuHMM: R Package for Generalized Hidden Markov Models of Animal Movement.” *Methods in Ecology and Evolution* 9 (6): 1518–30. https://doi.org/10.1111/2041-210X.12995.

McTaggart Cowan, I, and V.C Brink. 1949. “Natural Game Licks in the Rocky Mountain National Parks of Canada.” *Journal of Mammalogy* 30: 379–87.

Michelot, Theo, Roland Langrock, and Toby A Patterson. 2016. “MoveHMM: An R Package for the Statistical Modelling of Animal Movement Data Using Hidden Markov Models.” *Methods in Ecology and Evolution* 7: 1308–15. https://doi.org/10.1111/2041-210X.12578.

Montalvo, Victor H., Carolina Sáenz-Bolaños, Luis D. Alfaro, Juan C. Cruz, Flavio H. Guimarães-Rodrigues, Eduardo Carrillo, Christopher Sutherland, and Todd K. Fuller. 2019. “Seasonal Use of Waterholes and Pathways by Macrofauna in the Dry Forest of Costa Rica.” *Journal of Tropical Ecology* 35 (2): 68–73. https://doi.org/10.1017/S0266467418000457.

Mor, Bhavya, Sunita Garhwal, and Ajay Kumar. 2020. “A Systematic Review of Hidden Markov Models and Their Applications.” *Archives of Computational Methods in Engineering*, May. https://doi.org/10.1007/s11831-020-09422-4.

Morales, Juan Manuel, Daniel T. Haydon, Jacqui Frair, Kent E. Holsinger, and John M. Fryxell. 2004. “Extracting More out of Relocation Data: Building Movement Models as Mixtures of Random Walks.” *Ecology* 85 (9): 2436–45. https://doi.org/10.1890/03-0269.

Morneau, Claude, and Serge Payette. 1998. “A Dendroecological Method to Evaluate Past Caribou (*Rangifer Tarandus* L.) Activity.” *Écoscience* 5 (1): 64–76. https://doi.org/10.1080/11956860.1998.11682446.

Morneau, Claude, and Serge Payette. 2000. “Long-Term Fluctuations of a Caribou Population Revealed by Tree-Ring Data.” *Canadian Journal of Zoology* 78 (10): 1784–1790. https://doi.org/10.1139/z00-122.

Mountain Goat Management Team. 2010. “Management Plan for the Mountain Goat (*Oreamnos Americanus*) in British Columbia.” Prepared for the B.C. Ministry of Environment. Victoria, BC.

Muvengwi, Justice, Monicah Mbiba, and Tatenda Nyenda. 2013. “Termite Mounds May Not Be Foraging Hotspots for Mega-Herbivores in a Nutrient-Rich Matrix.” *Journal of Tropical Ecology* 29 (06): 551–558. https://doi.org/10.1017/S0266467413000564.

Myers, Norman. 1990. “The Biodiversity Challenge: Expanded Hot-Spots Analysis.” *The Environmentalist* 10 (4): 243–56. https://doi.org/10.1007/BF02239720.

Nathan, Ran, Wayne M. Getz, Eloy Revilla, Marcel Holyoak, Ronen Kadmon, David Saltz, and Peter E. Smouse. 2008. “A Movement Ecology Paradigm for Unifying Organismal Movement Research.” *Proceedings of the National Academy of Sciences of the United States of America* 105 (49): 19052–59. https://doi.org/10.1073/pnas.0800375105.

Natusch, Daniel James Deans, Jessica Ann Lyons, Gregory P. Brown, and Richard Shine. 2017. “Biotic Interactions Mediate the Influence of Bird Colonies on Vegetation and Soil Chemistry at Aggregation Sites.” *Ecology* 98 (2): 382–92. https://doi.org/10.1002/ecy.1642.

Owen-Smith, N. 2002. *Adaptive Herbivore Ecology: From Resources to Populations in Variable Environments.* Cambridge, UK: Cambridge University Press.

Owen-Smith, N., J. M. Fryxell, and E. H. Merrill. 2010. “Foraging Theory Upscaled: The Behavioural Ecology of Herbivore Movement.” *Philosophical Transactions of the Royal Society B: Biological Sciences* 365 (1550): 2267–2278. https://doi.org/10.1098/rstb.2010.0095.

Panichev, A. M., K. S. Golokhvast, A. N. Gulkov, and I. Yu Chekryzhov. 2013. “Geophagy in Animals and Geology of Kudurs (Mineral Licks): A Review of Russian Publications.” *Environmental Geochemistry and Health* 35 (1): 133–52. https://doi.org/10.1007/s10653-012-9464-0.

Panichev, Alexander M., Vladimir K. Popov, Igor Yu. Chekryzhov, Ivan V. Seryodkin, Tatiana A. Stolyarova, Sergey V. Zakusin, Alexandr A. Sergievich, and Pavel P. Khoroshikh. 2016. “Rare Earth Elements upon Assessment of Reasons of the Geophagy in Sikhote-Alin Region (Russian Federation), Africa and Other World Regions.” *ENVIRONMENTAL GEOCHEMISTRY AND HEALTH* 38 (6): 1255–70. https://doi.org/10.1007/s10653-015-9788-7.

Parsons, E. C. M. 2016. “Why IUCN Should Replace ‘Data Deficient’ Conservation Status with a Precautionary ‘Assume Threatened’ Status—A Cetacean Case Study.” *Frontiers in Marine Science* 3 (193): 1–3. https://doi.org/10.3389/fmars.2016.00193.

Patterson, Marinelle Basson, Mark V. Bravington, and John S. Gunn. 2009. “Classifying Movement Behaviour in Relation to Environmental Conditions Using Hidden Markov Models.” *Journal of Animal Ecology* 78 (6): 1113–23. https://doi.org/10.1111/j.1365-2656.2009.01583.x.

Patterson, L Thomas, C Wilcox, O Ovaskainen, and J Matthiopoulos. 2008. “State–Space Models of Individual Animal Movement.” *Trends in Ecology & Evolution* 23 (2): 87–94. https://doi.org/10.1016/j.tree.2007.10.009.

Pedevillano, Cathy, and G Wright. 1987. “The Influence of Visitors on Mountain Goat Activities in Glacier National Park, Montana.” *Biological Conservation* 39 (1): 1–11. https://doi.org/10.1016/0006-3207(87)90002-4.

Poole, Kim G., Karl D. Bachmann, and Irene E. Teske. 2010. “Mineral Lick Use by Gps Radio-Collared Mountain Goats in Southeastern British Columbia.” *Western North American Naturalist* 70 (2): 208–17. https://doi.org/10.3398/064.070.0207.

Poole, Kim G., and Douglas C. Heard. 2003. “Seasonal Habitat Use and Movements of Mountain Goats (*Oreamnos Americanus*), in East-Central British Columbia.” *Canadian Field-Naturalist* 117 (4): 565–576.

Poole, Kim G., Kari Stuart-Smith, and Irene E. Teske. 2009. “Wintering Strategies by Mountain Goats in Interior Mountains.” *Canadian Journal of Zoology* 87 (3): 273–83. https://doi.org/10.1139/Z09-009.

Reid, Walter V. 1998. “Biodiversity Hotspots.” *Trends in Ecology & Evolution* 13 (7): 275–80. https://doi.org/10.1016/S0169-5347(98)01363-9.

Rice, Clifford G. 2008. “Seasonal Altitudinal Movements of Mountain Goats.” *The Journal of Wildlife Management* 72 (8): 1706–16. https://doi.org/10.2193/2007-584.

Rice, Clifford G. 2010. “Mineral Lick Visitation by Mountain Goats, (*Oreamnos Americanus*).” *The Canadian Field-Naturalist* 124 (3): 225–37. https://doi.org/10.22621/cfn.v124i3.1078.

Rice, Clifford G., Kurt J. Jenkins, and Wan-Ying Chang. 2009. "A Sightability Model for Mountain Goats." *The Journal of Wildlife Management* 73 (3): 468–78. https://doi.org/10.2193/2008-196.

Richard, Julien H., and Steeve D. Côté. 2016. "Space Use Analyses Suggest Avoidance of a Ski Area by Mountain Goats: Avoidance of a Ski Area by Mountain Goats." *The Journal of Wildlife Management* 80 (3): 387–95. https://doi.org/10.1002/jwmg.1028.

Richard, Julien H., John Wilmshurst, and Steeve D. Côté. 2014. "The Effect of Snow on Space Use of an Alpine Ungulate: Recently Fallen Snow Tells More than Cumulative Snow Depth." *Canadian Journal of Zoology* 92 (12): 1067–1074. https://doi.org/10.1139/cjz-2014-0118.

Romeo, G, and S Lovari. 1996. "Summer Activity Rhythms of the Mountain Goat (*Oreamnos Americanus*) (de Blainville, 1816)." *Mammalia* 60: 496–99.

Rose, Jeff. 2013. "Terrain Classification, Climbing Exposure, and Technical Management." *Journal of Outdoor Recreation, Education, and Leadership* 5 (3): 242–57. https://doi.org/10.7768/1948-5123.1176.

Ruckstuhl, K. E., and P. Neuhaus. 2002. "Sexual Segregation in Ungulates: A Comparative Test of Three Hypotheses." *Biological Reviews* 77 (1): 77–96. https://doi.org/10.1017/S1464793101005814.

Sarmento, Wesley, Mark Biel, and Joel Berger. 2019. "Seeking Snow and Breathing Hard – Behavioral Tactics in High Elevation Mammals to Combat Warming Temperatures." *PLOS ONE* 14 (12): e0225456. https://doi.org/10.1371/journal.pone.0225456.

Schmidt, Niels M., Floris M. van Beest, Jesper B. Mosbacher, Mikkel Stelvig, Lars H. Hansen, Jacob Nabe-Nielsen, and Carsten Grøndahl. 2016. "Ungulate Movement in an Extreme Seasonal Environment: Year-Round Movement Patterns of High-Arctic Muskoxen." *Wildlife Biology* 22 (6): 253–67. https://doi.org/10.2981/wlb.00219.

Scoones, Ian. 1995. "Exploiting Heterogeneity: Habitat Use by Cattle in Dryland Zimbabwe." *Journal of Arid Environments* 29 (2): 221–37. https://doi.org/10.1016/S0140-1963(05)80092-8.

Seidel, Dana Paige, Eric Dougherty, Colin Carlson, and Wayne M. Getz. 2018. "Ecological Metrics and Methods for GPS Movement Data." *International Journal of Geographical Information Science : IJGIS* 32 (11): 2272–93. https://doi.org/10.1080/13658816.2018.1498097.

Sen Tran, T, and R.R. Simard. 1993. "Soil Sampling and Methods of Analysis." In , 43–45. Boca Raton, Florida: Lewis Publishers.

Singer, Francis J. 1978. “Behavior of Mountain Goats in Relation to U.S. Highway 2, Glacier National Park, Montana.” *The Journal of Wildlife Management* 42 (3): 591–97. https://doi.org/10.2307/3800822.

Slabach, B L, T B Corey, J R Aprille, P T Starks, and B Dane. 2015. “Geophagic Behavior in the Mountain Goat (*Oreamnos Americanus*): Support for Meeting Metabolic Demands.” *Canadian Journal of Zoology* 93: 599–604. https://doi.org/10.1139/cjz-2015-0067.

Smith, Bruce L. 1988. “Criteria for Determining Age and Sex of American Mountain Goats in the Field.” *Journal of Mammalogy* 69 (2): 395–402. https://doi.org/10.2307/1381400.

Sokal, Robert, and James Rohlf. 2012. *Biometry: The Principles and Practice of Statistics in Biological Research*. New York : W.H. Freeman.

Speer, James H. 2012. *Fundamentals of Tree-Ring Research*. University of Arizona Press.

St-Louis, Antoine, Sandra Hamel, Julien Mainguy, and Steeve D. Côté. 2013. “Factors Influencing the Reaction of Mountain Goats towards All-Terrain Vehicles.” *The Journal of Wildlife Management* 77 (3): 599–605. https://doi.org/10.1002/jwmg.488.

Stokes, K. L., A. C. Broderick, A. F. Canbolat, Y. Levy, A. F. Rees, W. J. Fuller, O. Candan, et al. 2015. “Migratory Corridors and Foraging Hotspots: Critical Habitats Identified for Mediterranean Green Turtles.” *Diversity and Distributions* 21 (6): 665–674. https://doi.org/10.1111/ddi.12317.

Thaker, Maria, Pratik R. Gupte, Herbert H. T. Prins, Rob Slotow, and Abi T. Vanak. 2019. “Fine-Scale Tracking of Ambient Temperature and Movement Reveals Shuttling Behavior of Elephants to Water.” *Frontiers in Ecology and Evolution* 7 (4): 1–12. https://doi.org/10.3389/fevo.2019.00004.

Thurfjell, Henrik, Simone Ciuti, and Mark S. Boyce. 2014. “Applications of Step-Selection Functions in Ecology and Conservation.” *Movement Ecology* 2 (1): 1–12. https://doi.org/10.1186/2051-3933-2-4.

Urmy, Samuel S., and Joseph D. Warren. 2018. “Foraging Hotspots of Common and Roseate Terns: The Influence of Tidal Currents, Bathymetry, and Prey Density.” *Marine Ecology Progress Series* 590: 227–245. https://doi.org/10.3354/meps12451.

Veldhuis, Michiel P., Moniek I. Gommers, Han Olff, and Matty P. Berg. 2018. “Spatial Redistribution of Nutrients by Large Herbivores and Dung Beetles in a Savanna Ecosystem.” Edited by Lorena Gomez-Aparicio. *Journal of Ecology* 106 (1): 422–433. https://doi.org/10.1111/1365-2745.12874.

Viterbi, A. 1967. “Error Bounds for Convolutional Codes and an Asymptotically Optimum Decoding Algorithm.” *IEEE Transactions on Information Theory* 13 (2): 260–69. https://doi.org/10.1109/TIT.1967.1054010.

Vogel, Susanne Marieke, Ben Lambert, Anna Catherine Songhurst, Graham Paul McCulloch, Amanda Lee Stronza, and Tim Coulson. 2020. “Exploring Movement Decisions: Can Bayesian Movement-State Models Explain Crop Consumption Behaviour in Elephants (*Loxodonta Africana*)?” *Journal of Animal Ecology* 89 (89): 1055–68. https://doi.org/10.1111/1365-2656.13177.

Webb, Stephen L., Kenneth L. Gee, Bronson K. Strickland, Stephen Demarais, and Randy W. DeYoung. 2010. “Measuring Fine-Scale White-Tailed Deer Movements and Environmental Influences Using GPS Collars.” Research Article. International Journal of Ecology. Hindawi. March 28, 2010. https://doi.org/10.1155/2010/459610.

White. 1983. “Foraging Patterns and Their Multiplier Effects on Productivity of Northern Ungulates.” *Oikos* 40 (3): 377–84. https://doi.org/10.2307/3544310.

White, Kevin S., Grey W. Pendleton, David Crowley, Herman J. Griese, Kris J. Hundertmark, Thomas Mcdonough, Lyman Nichols, Matt Robus, Christian A. Smith, and John W. Schoen. 2011. “Mountain Goat Survival in Coastal Alaska: Effects of Age, Sex, and Climate.” *The Journal of Wildlife Management* 75 (8): 1731–44. https://doi.org/10.1002/jwmg.238.

Wilson, Ryan R., Lynne Gilbert-Norton, and Eric M. Gese. 2012. “Beyond Use versus Availability: Behaviour-Explicit Resource Selection.” *Wildlife Biology* 18 (4): 424–30. https://doi.org/10.2981/12-044.

Winnie, John A., Paul Cross, and Wayne Getz. 2008. “Habitat Quality and Heterogeneity Influence Distribution and Behavior in African Buffalo (*Syncerus Caffer*).” *Ecology* 89 (5): 1457–1468. https://doi.org/10.1890/07-0772.1.

Wolf, Mosheh, Jacqui Frair, Evelyn Merrill, and Peter Turchin. 2009. “The Attraction of the Known: The Importance of Spatial Familiarity in Habitat Selection in Wapiti (*Cervus Elaphus*).” *Ecography* 32 (3): 401–10. https://doi.org/10.1111/j.1600-0587.2008.05626.x.

Xue, Yadong, Jia Li, Guli Sagen, Yu Zhang, Yunchuan Dai, and Diqiang Li. 2018. “Activity Patterns and Resource Partitioning: Seven Species at Watering Sites in the Altun Mountains, China.” *Journal of Arid Land* 10 (6): 959–67. https://doi.org/10.1007/s40333-018-0028-8.

Yoganand, K., and Norman Owen-Smith. 2014. “Restricted Habitat Use by an African Savanna Herbivore through the Seasonal Cycle: Key Resources Concept Expanded.” *Ecography* 37 (10): 969–982. https://doi.org/10.1111/ecog.00534.

Zalatan, R., A. Gunn, and G. H. R. Henry. 2006. “Long-Term Abundance Patterns of Barren-Ground Caribou Using Trampling Scars on Roots of (*Picea Mariana*) in the Northwest Territories, Canada.” *Arctic, Antarctic, and Alpine Research* 38 (4): 624–630. https://doi.org/10.1657/1523-0430(2006)38[624:lapobc]2.0.co;2.

Zucchini, Walter, Lain MacDonald, and Roland Langrock. 2016. *Hidden Markov Models for Time Series. an Introduction Using R*. Second Edition. Boca Raton, FL, USA: CRC Press.

Appendix A.

Supplemental Figures for Chapter 2

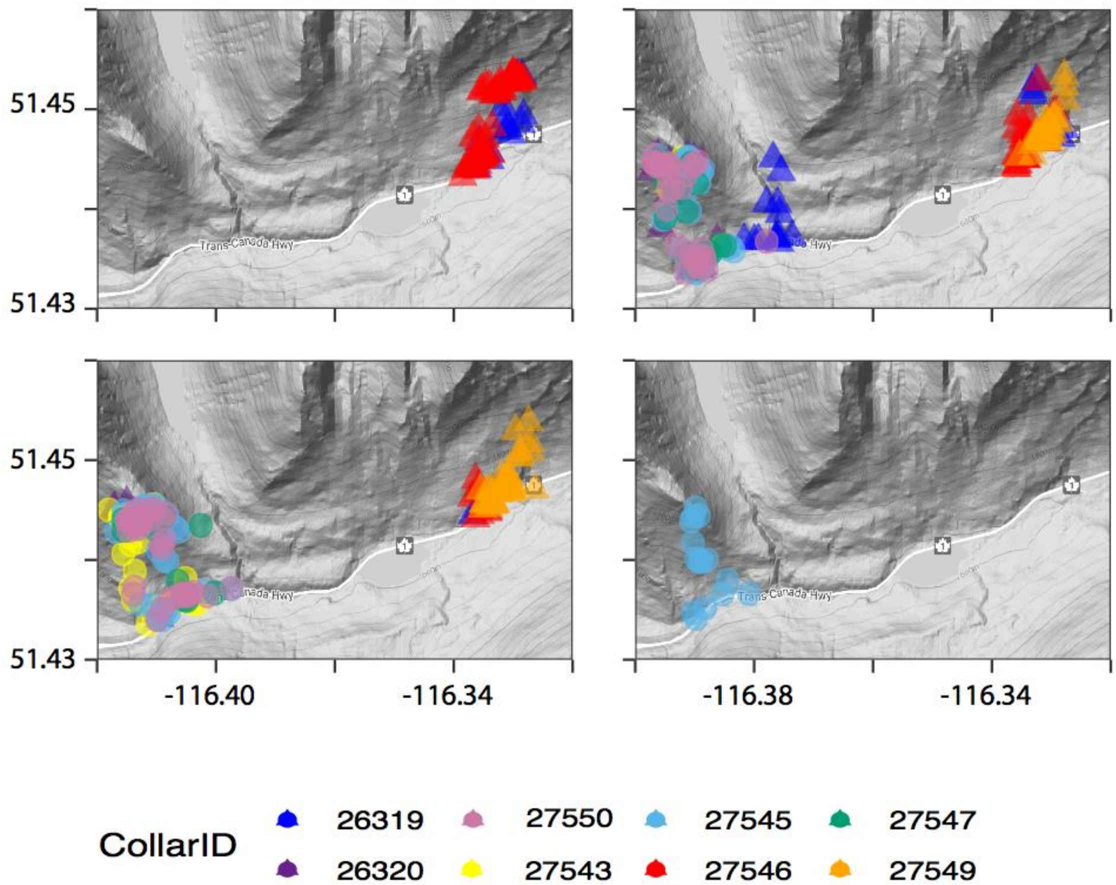


Figure A1 **Individual use of mineral licks in 2018 by GPS collared mountain goats between May and August. Triangles are males, circles are females, each symbol is one hour of time spent at a mineral lick. Each colour represents a different individual (CollarID).**

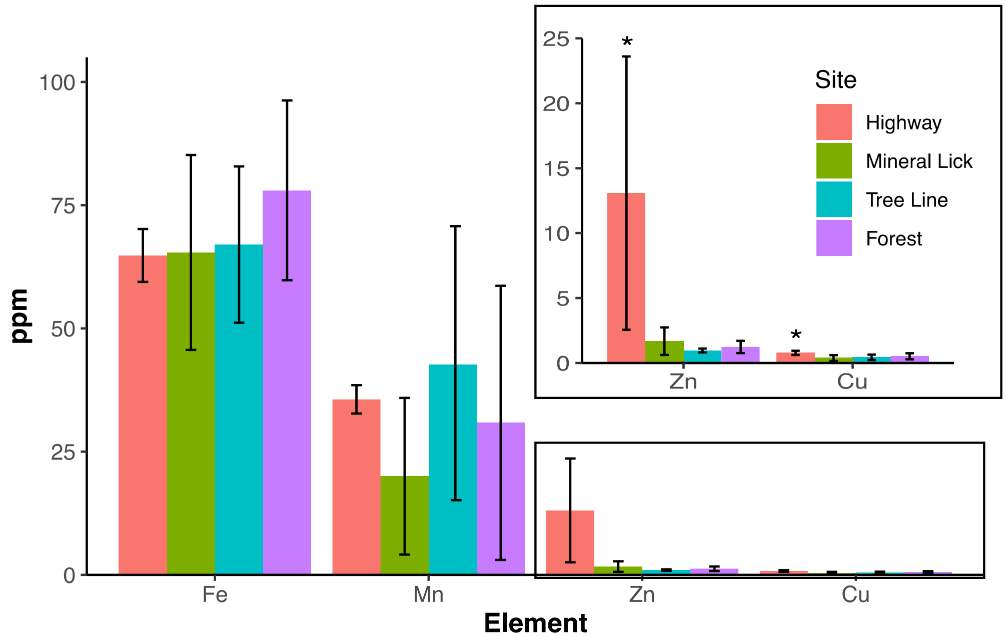


Figure A2 **Concentrations (mean +/- SE) of trace elements (ppm) of soil samples collected from the forest, highway, mineral lick and tree line. Significant differences (* $p < 0.05$) between sites were tested using a one-way ANOVA.**

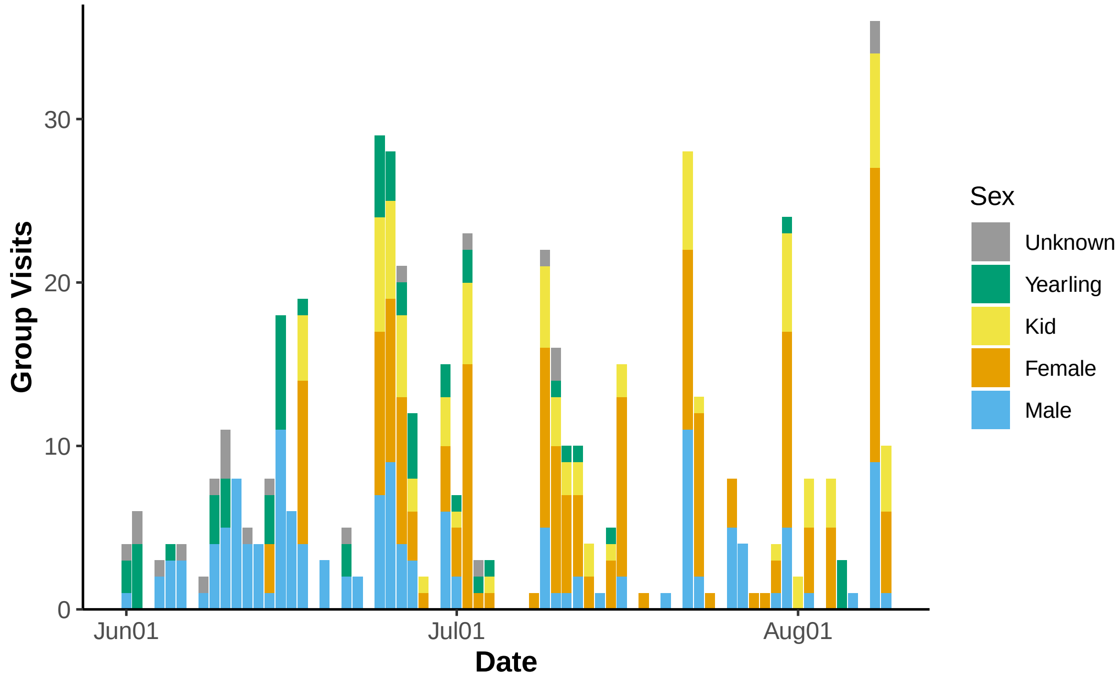


Figure A3 **Daily group size and composition of mountain goats visiting mineral licks in summer 2019. Each stacked bar represents the total number of goats observed in camera traps on each day. Group sizes of each sex and age class are shown for each day**

Appendix B.

Supplemental Table for Chapter 3

Table B1 **State transition probability matrix for three behavioural states in the Sherbrook (upper) and Slate (lower) study groups. Given that a particular state is at time *t*, the matrix displays probabilities of switching to a different state or remaining in the same state at time *t + 1.***

Sh		State at time *t* + 1		
		forage	travel	bed
State at time *t*	forage	0.736	0.121	0.143
	travel	0.212	0.639	0.149
	bed	0.347	0.070	0.583

Sl		State at time *t* + 1		
		forage	travel	bed
State at time *t*	forage	0.762	0.061	0.177
	travel	0.132	0.767	0.101
	bed	0.307	0.070	0.623