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

Authors: Kroesen, Laura P., Hik, David S., and Cherry, Seth G.

Source: Wildlife Biology, 2020(4)

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.00736

Wildlife Biology 2020: wlb.00736
doi: 10.2981/wlb.00736
© 2020 Nordic Society Oikos. This is an Open Access article
Subject Editor: Luca Corlatti. Editor-in-Chief: Ilse Storch. Accepted 5 October 2020

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

Laura P. Kroesen, David S. Hik and Seth G. Cherry

L. P. Kroesen (https://orcid.org/0000-0002-5524-0664) ✉ (lkroesen@sfu.ca) and D. S. Hik (https://orcid.org/0000-0002-8994-9305), Biological Sciences, Simon Fraser Univ., Vancouver, BC, Canada. – S. G. Cherry (https://orcid.org/0000-0003-4242-3629), Parks Canada Agency, Radium Hot Springs, BC, Canada.

Concentrated resources or hotspots, within an individual's usual home range may be strong determinates of movement behavior. 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 behavioral 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 behavior 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: hotspot, mineral lick, mountain goats, *Oreamnos americanus*, sex-specific patterns, temporal patterns

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 behavior 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 et al. 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 et al. 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 behavior (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, 2016, Hunter 2017). Geophagia, the intentional consumption of soil, is a behavior that is frequently observed in many animals within tropical and temperate regions, including bats, parrots, primates and ungulates (Krishnamani and Mahaney 2000, Ayotte et al. 2008, 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, 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 (Jones and Hanson 1985, Atwood and Weeks 2002). 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* preferring 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 et al. 2010), spatial fidelity (Jokinen et al. 2014), licking intensity (Ayotte et al. 2008) and tradeoffs 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 behavior 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, 2008, Slabach et al. 2015).

Our study population of mountain goats access 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 1950s. 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, 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 behavioral 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 behavior 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.

Methods

Study area

We conducted our study in Yoho National Park in the Rocky Mountains, British Columbia, Canada (Fig. 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 unpubl.; Fig. 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

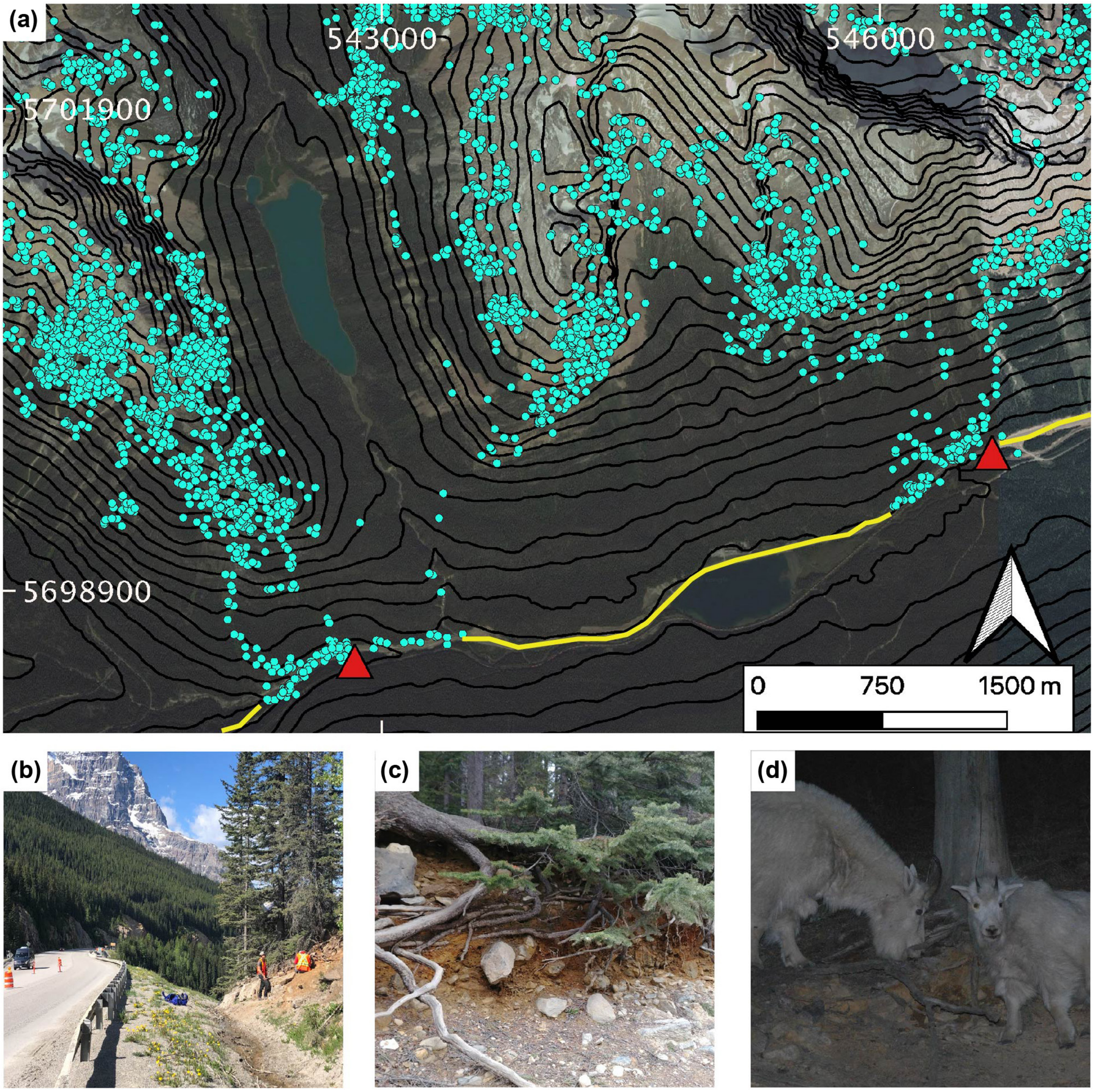

Figure 1. (a) Map of the Sherbrooke mountain goat range in Yoho National Park, British Columbia. The core area includes Sherbrooke Lake in the valley bottom and two mineral lick sites (red triangles) along the Trans-Canada Highway (yellow line). The blue points are individual mountain goat GPS collar 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.

created during highway construction and are situated less than 10 m to the roadside at their closest points (Fig. 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 (Fig. 1c), primarily Douglas-fir, very similar to typical mineral licks in the Rocky and Purcell Mountains (Poole et al. 2010). Mountain goats have been observed consuming soil both underneath the tree caverns (Fig. 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).

We collected soil samples (~ 350 g) around the primary mineral lick site from four different areas: highway ditches, mineral licks excavated under tree roots, treeline and 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 six 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 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 (<www.r-project.org>).

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 et al. 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 (Supplementary material Appendix 1 Fig. A1). 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.

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. 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 et al. 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 no. 30681, Research Permit no. 30681 and no. YNP-2019-32338 and Simon Fraser Animal Care Committee no. 1302B-19). During the two-year analysis period from 1 November 2017 to 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. We used both Ogden and Bosworth mineral lick sites to determine the frequency, duration and timing of mineral lick visits (Supplementary material Appendix 1 Fig. A2). 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 in order 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 to 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. Distinct groups were those that were separated by more than two minutes.

All images were classified using Timelapse ver. 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 from Kroesen et al. (2020).

Results

Soil characteristics

The PCA of element concentrations showed an overall association between the mineral lick, treeline and forest areas, but these areas were different from the highway samples (Fig. 2). The first four principal components explained 90% of the variance using the Kaiser criterion with eigenvalues > 1.

The mineral lick and highway samples had significantly higher concentrations of Na than the forest and treeline samples (Fig. 3). 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 (Supplementary material Appendix 1 Fig. A3). 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.

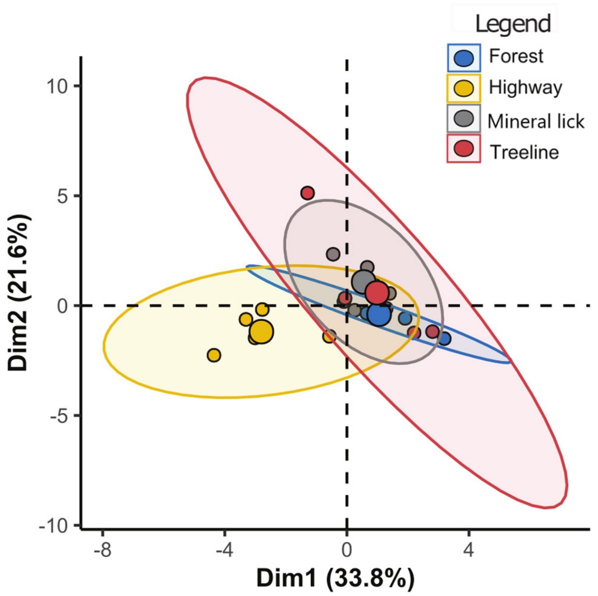

Figure 2. Principal component analysis of macro and trace elements in soil samples from the forest, highway ditches, mineral lick and treeline sites in Yoho National Park.

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 (Fig. 4). The oldest recorded scar was dated from the early 1950s with the highest frequency of scars observed between 2010 and 2018.

Seasonal use of mineral licks

The phenology of seasonal visits to the mineral licks were consistent over both years with the majority of mountain goats accessing mineral licks between May and the end of July (Fig. 5a). 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 male and females overlapped for the months of June and July and females continued to visit the mineral licks in August (Supplementary material Appendix 1 Fig. A2). 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 ($t = -3.49$, $df = 110.55$, $p\text{-value} < 0.001$). 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; Fig. 5b). 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 versus 7.4 ± 0.48 SE: $t = -3.13$, $df = 9.96$, $p\text{-value} < 0.01$; Fig. 5c). However, there was some

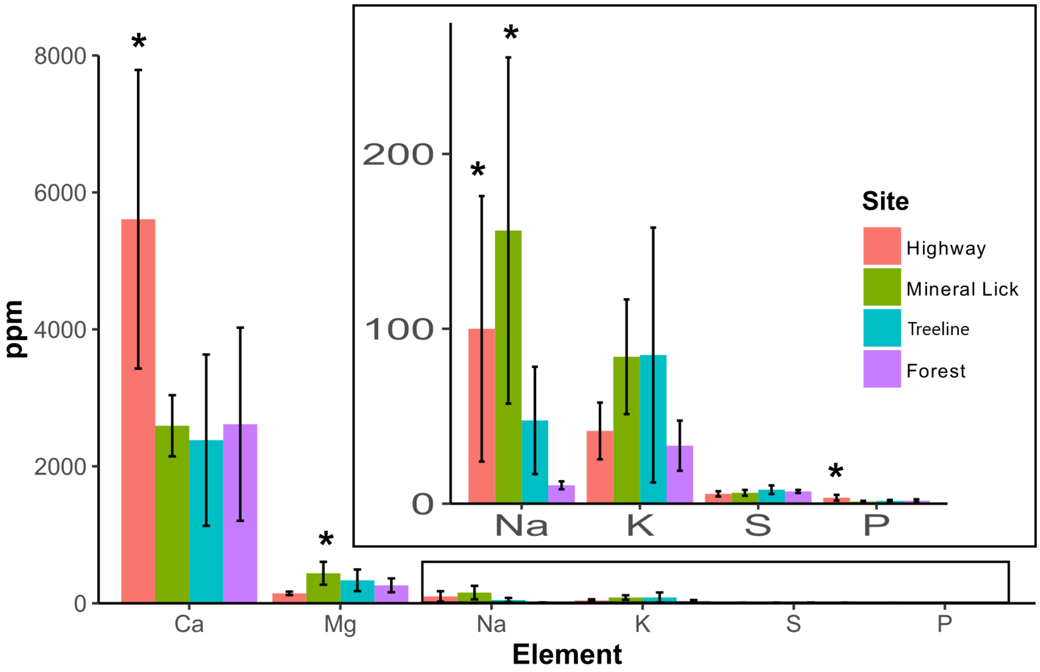

Figure 3. Concentrations (mean ± SE) of macro elements (ppm) of soil samples collected from the forest, highway ditches, mineral lick, treeline and forest. Significant differences (* $p < 0.05$) between sites were tested using a one-way ANOVA.

variation, with a single female visiting a mineral lick 17 times in 2018 but only 6 times during 2019.

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 (Supplementary material Appendix 1 Fig. A4). 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 (Fig. 6). 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*.

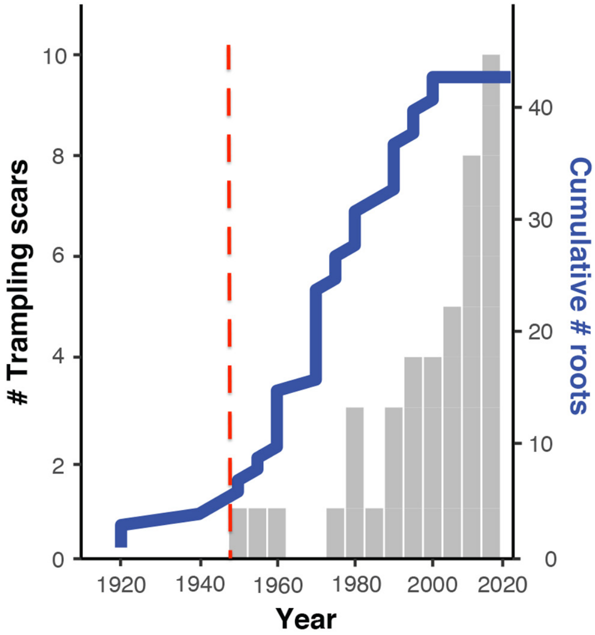

Figure 4. Age of trampling scars on conifer roots (grey bars) pooled into 5-year classes and cumulative number of roots included in the sample for each year class (blue line). Roots were collected along trails leading to mineral licks frequently used by mountain goats following construction of the Trans-Canada Highway (red dotted line).

Discussion

Our findings provide a detailed description of the deliberate and regular behavior of seasonal visits to a resource hotspot and suggest that this behavior 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

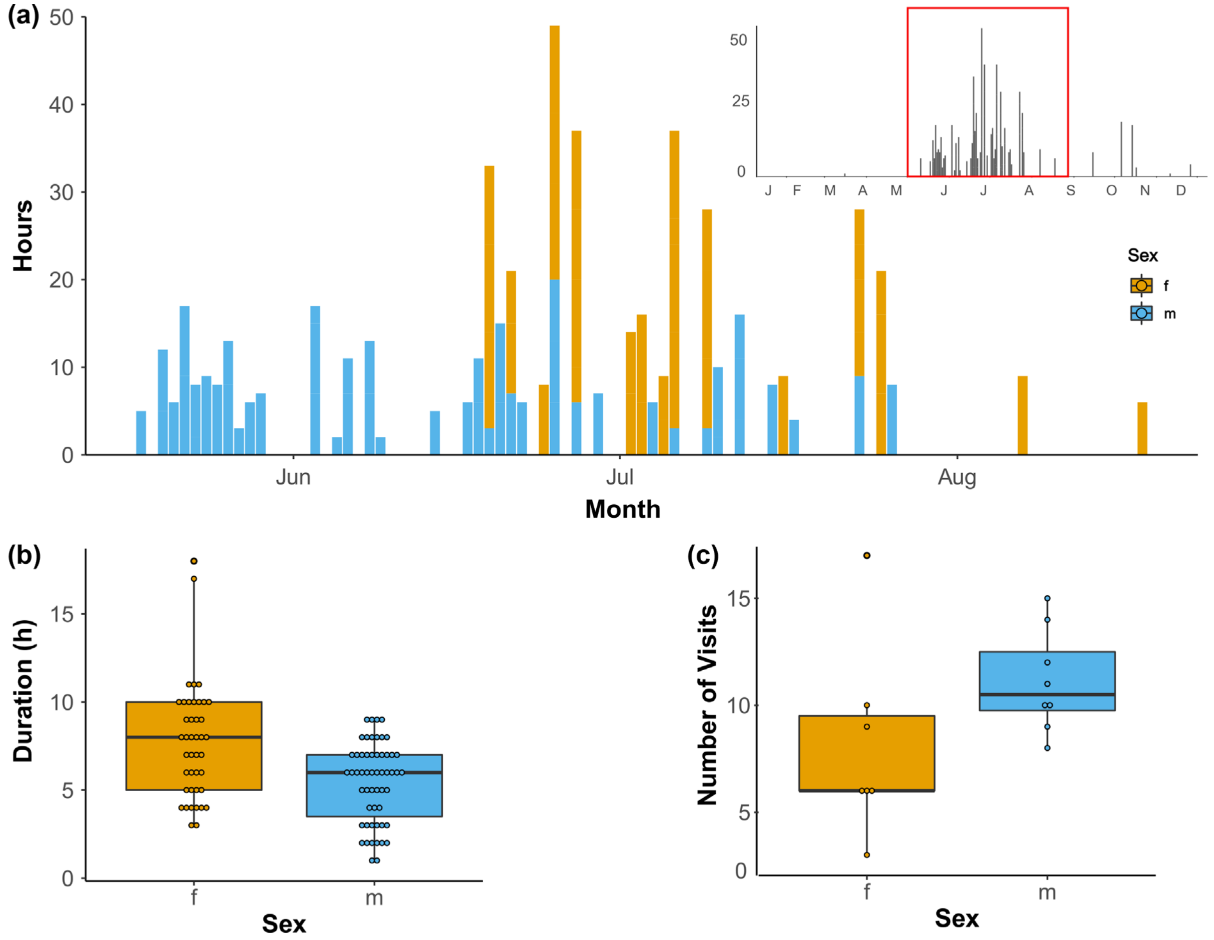

Figure 5. (a) Time spent by GPS collared mountain goats at mineral licks adjacent to the Trans-Canada Highway during May to August 2018 (5 male, 4 female). Top right inset shows mineral lick use during the entire year (2018). (b) The duration and (c) number of female and male mountain goat visits for 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 h (not shown).

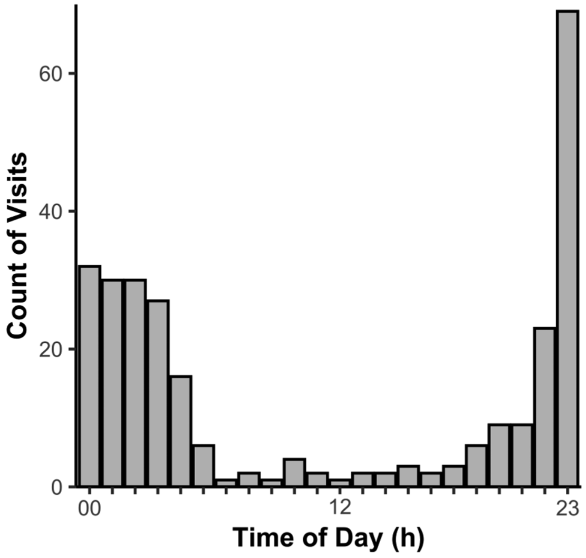

Figure 6. Time of day that mountain goat groups triggered camera traps as they moved down the trails to mineral licks along the TCH during summer 2019.

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 behavioral 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 behavioral 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 et al. 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 (Fig. 2). 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 (Fig. 3).

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 behavior of excavating under trees as documented by other research studies in the Kootenay and Rocky Mountain regions (Hebert and Cowan 1971, Poole et al. 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. 2013) 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 (Fig. 5a). 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 et al. 2008, Poole et al. 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 close 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 tradeoff 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* (Fortin and Fortin 2009, Hebblewhite and Merrill 2009, Camp et al. 2017).

Males arrived earlier in the spring, spent less time at mineral licks than females and visited more frequently (Fig. 5b–c). The later timing of female visits may coincide with the kidding 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 about 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-h period, displayed a nocturnal pattern to access mineral licks and spent the duration of the night at these sites (Fig. 6). 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 (Kroesen et al. unpubl.). 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 (Singer 1978, Pedevillano and Wright 1987). 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-h 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 unpubl.) and mountain goats may have adapted their behavior 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 behavior

Our study provides long-term insights spanning many decades combined with high-resolution contemporary data to analyze how behavioral strategies evolved in animals to access resource hotspots outside of their usual home range. We attempted to assess the tradeoffs 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 behavioral strategies to access mineral licks that are then passed between generations.

Our finding that mountain goats alter their behavior 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 behavior to access these critical resources can provide insight to the behavioral rhythms associated with accessing scarce resources (Freymann et al. 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 behavioral 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 behavior 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.

Data availability statement

Data are available from the Data Dryad Digital Repository: <https://doi.org/10.5061/dryad.44j0zpcb4> (Kroesen et al. 2020).

Acknowledgements – We thank Simon Campbell for assistance collecting data in the field. We thank Dr. Bryan Macbeth, Dr. Todd Shury and Dr. Nigel Caulkett for assisting with mountain goat ground trapping at the licks and Bighorn Helicopters for conducting aerial mountain goat captures. This manuscript benefitted from the insightful comments provided by Kim Poole and conversations with Dr. David J. Green and many other colleagues at Simon Fraser University. We also thank the many Parks Canada staff that helped untangle the history of the Trans-Canada Highway, provided information on the Sherbrooke goat study population, and others for logistical, field and technical support.

Funding – This study was supported by Parks Canada Agency (Lake Louise, Yoho and Kootenay Field Unit), grants from NSERC (RGPIN-06691), and Simon Fraser University (PRSG-8-21).

Author contributions – LK designed this study with input from DH and SC. Field data was collected by LK. LK completed all analysis and wrote the manuscript with input from DH and SC. All authors discussed the results and contributed to the final manuscript.

Conflicts of interest – The authors declare that they have no conflict of interest.

Permits – All procedures followed the Canadian Council of Animal Care guidelines for the safe handling of wildlife (Parks Canada Agency Animal Care Task Force no. 30681, Research Permit no. 30681 and no. YNP-2019-32338 and Simon Fraser Animal Care Committee no. 1302B-19).

References

Anderson, T. M. et al. 2010. Landscape-scale analyses suggest both nutrient and antipredator advantages to Serengeti herbivore hotspots. – Ecology 91: 1519–1529.

Atwood, T. C. and Weeks, H. P. 2002. Sex- and age-specific patterns of mineral lick use by white-tailed deer (*Odocoileus virginianus*). – Am. Midl. Nat. 148: 289–296.

Ayotte, J. B. et al. 2006. Chemical composition of lick soils: functions of soil ingestion by four ungulate species. – J. Mammal. 87: 878–888.

Ayotte, J. B. et al. 2008. Use of natural licks by four species of ungulates in northern British Columbia. – J. Mammal. 89: 1041–1050.

Barrett, M. W. et al. 1982. Evaluation of a hand-held net-gun to capture large mammals. – Wildl. Soc. Bull. 10: 108–114.

Blake, J. G. et al. 2010. Use of natural licks by white-bellied spider monkeys (*Ateles belzebuth*) and red howler monkeys (*Alouatta seniculus*) in eastern Ecuador. – Int. J. Primatol. 31: 471–483.

Cadsand, B. et al. 2010. Modified clover trap for capturing mountain goats in northwest British Columbia. – Bienn. Symp. North. Wildl. Sheep Goat Counc. 17: 71–77.

Camp, M. J. et al. 2017. The balancing act of foraging: mammalian herbivores tradeoff multiple risks when selecting food patches. – Oecologia 185: 537–549.

Conradt, L. 1998. Measuring the degree of sexual segregation in group-living animals. – J. Anim. Ecol. 67: 217–226.

Côté, S. D. et al. 2013. Do mountain goats habituate to helicopter disturbance? – J. Wildl. Manage. 77: 1244–1244.

Davies, A. B. et al. 2016. Termite mounds differ in their importance for herbivores across savanna types, seasons and spatial scales. – Oikos 125: 726–734.

DeVoe, J. D. et al. 2015. Summer range occupancy modeling of non-native mountain goats in the greater Yellowstone area. – Ecosphere 6: 1–20.

Dormaar, J. F. and Walker, B. D. 1996. Elemental content of animal licks along the eastern slopes of the Rocky Mountains in southern Alberta, Canada. – Can. J. Soil Sci. 76: 509–512.

Festa-Bianchet, M. and Côté, S. D. 2008. Mountain goats: ecology, behaviour and conservation of an alpine ungulate. – Island Press.

Fortin, D. and Fortin, M.-E. 2009. Group-size-dependent association between food profitability, predation risk and distribution of free-ranging bison. – Anim. Behav. 78: 887–892.

Freymann, B. P. et al. 2010. Spatial and temporal hotspots of termite-driven decomposition in the Serengeti. – Ecography 33: 443–450.

Gaynor, K. M. et al. 2018. The influence of human disturbance on wildlife nocturnality. – Science 360: 1232–1235.

Ghanem, S. J. et al. 2013. Frugivorous bats drink nutrient and clay-enriched water in the Amazon rain forest: support for a dual function of mineral-lick visits. – J. Trop. Ecol. 29: 1–10.

Giotto, N. et al. 2015. Space-use patterns of the asiatic wild ass (*Equus hemionus*): complementary insights from displacement, recursion movement and habitat selection analyses. – PLoS One 10: e0143279.

Hebblewhite, M. and Merrill, E. H. 2009. Tradeoffs between predation risk and forage differ between migrant strategies in a migratory ungulate. – Ecology 90: 3445–3454.

Hebert, D. and Cowan, I. M. 1971. Natural salt licks as a part of the ecology of the mountain goat. – Can. J. Zool. 49: 605–610.

Hunter, M. L. 2017. Conserving small natural features with large ecological roles: an introduction and definition. – Biol. Conserv. 211: 1–2.

Jokinen, M. E. et al. 2014. Observational description of alpine ungulate use at mineral licks in southwest Alberta, Canada. – Bienn. Symp. North. Wild Sheep Goat Counc. 19: 42–63.

Jones, R. L. and Hanson, H. C. 1985. Mineral licks, geography and biochemistry of North American ungulates. – Iowa State Univ.

Kreulen, D. A. 1985. Lick use by large herbivores: a review of benefits and banes of soil consumption. – Mammal Rev. 15: 107–123.

Krishnamani, R. and Mahaney, W. C. 2000. Geophagy among primates: adaptive significance and ecological consequences. – Anim. Behav. 59: 899–915.

Kroesen, L. et al. 2020. Data from: Patterns of decadal, seasonal and daily visitation to mineral licks, a critical resource hotspot for mountain goats (*Oreamnos americanus*) in the Rocky Mountains. – Dryad Dataset, <https://doi.org/10.5061/dryad.44j0zpcb4>.

Lee, A. T. K. et al. 2014. Diet and geophagy across a western amazonian parrot assemblage. – Biotropica 46: 322–330.

Link, A. et al. 2011. Patterns of mineral lick visitation by spider monkeys and howler monkeys in Amazonia: are licks perceived as risky areas? – Am. J. Primatol. 73: 386–396.

Matsubayashi, H. et al. 2007. Importance of natural licks for the mammals in Bornean inland tropical rain forests. – Ecol. Res. 22: 742–748.

Mazur, R. and Seher, V. 2008. Socially learned foraging behaviour in wild black bears, (*Ursus americanus*). – Anim. Behav. 75: 1503–1508.

McTaggart Cowan, I. and Brink, V. C. 1949. Natural game licks in the Rocky Mountain National Parks of Canada. – J. Mammal. 30: 379–387.

Montalvo, V. H. et al. 2019. Seasonal use of waterholes and pathways by macrofauna in the dry forest of Costa Rica. – J. Trop. Ecol. 35: 68–73.

Morneau, C. and Payette, S. 1998. A dendroecological method to evaluate past caribou (*Rangifer tarandus* L.) activity. – Écoscience 5: 64–76.

Morneau, C. and Payette, S. 2000. Long-term fluctuations of a caribou population revealed by tree-ring data. – Can. J. Zool. 78: 1784–1790.

Muvengwi, J. et al. 2013. Termite mounds may not be foraging hotspots for mega-herbivores in a nutrient-rich matrix. – J. Trop. Ecol. 29: 551–558.

Myers, N. 1990. The biodiversity challenge: expanded hot-spots analysis. – Environmentalist 10: 243–56.

Panichev, A. M. et al. 2013. Geophagy in animals and geology of kudurs (mineral licks): a review of Russian publications. – Environ. Geochem. Health 35: 133–152.

Panichev, A. M. et al. 2016. Rare earth elements upon assessment of reasons of the geophagy in Sikhote-Alin region (Russian Federation), Africa and other world regions. – Environ. Geochem. Health 38: 1255–1270.

Pedevillano, C. and Wright, G. 1987. The influence of visitors on mountain goat activities in Glacier National Park, Montana. – Biol. Conserv. 39: 1–11.

Poole, K. G. and Heard, D. C. 2003. Seasonal habitat use and movements of mountain goats (*Oreamnos americanus*), in east-central British Columbia. – Can. Field-Nat. 117: 565–576.

Poole, K. G. et al. 2010. Mineral lick use by gps radio-collared mountain goats in southeastern British Columbia. – W. N. Am. Nat. 70: 208–217.

Reid, W. V. 1998. Biodiversity hotspots. – Trends Ecol. Evol. 13: 275–280.

Rice, C. G. 2008. Seasonal altitudinal movements of mountain goats. – J. Wildl. Manage. 72: 1706–1716.

Rice, C. G. 2010. Mineral lick visitation by mountain goats, (*Oreamnos americanus*). – Can. Field-Nat. 124: 225–237.

Richard, J. H. and Côté, S. D. 2016. Space use analyses suggest avoidance of a ski area by mountain goats: avoidance of a ski area by mountain goats. – J. Wildl. Manage. 80: 387–395.

Romeo, G. and Lovari, S. 1996. Summer activity rhythms of the mountain goat (*Oreamnos americanus*) (de Blainville, 1816). – Mammalia 60: 496–499.

Ruckstuhl, K. E. and Neuhaus, P. 2002. Sexual segregation in ungulates: a comparative test of three hypotheses. – Biol. Rev. 77: 77–96.

Scoones, I. 1995. Exploiting heterogeneity: habitat use by cattle in dryland Zimbabwe. – J. Arid Environ. 29: 221–237.

Sen Tran, T. and Simard, R. R. 1993. Soil sampling and methods of analysis. – Lewis Publishers, pp. 43–45.

Singer, F. J. 1978. Behavior of mountain goats in relation to U.S. Highway 2, Glacier National Park, Montana. – J. Wildl. Manage. 42: 591–597.

Slabach, B. L. et al. 2015. Geophagic behavior in the mountain goat (*Oreamnos americanus*): support for meeting metabolic demands. – Can. J. Zool. 93: 599–604.

Smith, B. L. 1988. Criteria for determining age and sex of American mountain goats in the field. – J. Mammal. 69: 395–402.

Sokal, R. and Rohlf, J. 2012. Biometry: the principles and practice of statistics in biological research. – W.H. Freeman.

Speer, J. H. 2012. Fundamentals of tree-ring research. – Univ. of Arizona Press.

St-Louis, A. et al. 2013. Factors influencing the reaction of mountain goats towards all-terrain vehicles. – J. Wildl. Manage. 77: 599–605.

Stokes, K. L. et al. 2015. Migratory corridors and foraging hotspots: critical habitats identified for Mediterranean green turtles. – Divers. Distrib. 21: 665–674.

Thaker, M. et al. 2019. Fine-scale tracking of ambient temperature and movement reveals shuttling behavior of elephants to water. – Front. Ecol. Evol. 7: 1–12.

Urmy, S. S. and Warren, J. D. 2018. Foraging hotspots of common and roseate terns: the influence of tidal currents, bathymetry and prey density. – Mar. Ecol. Prog. Ser. 590: 227–245.

White, R. G. 1983. Foraging patterns and their multiplier effects on productivity of northern ungulates. – Oikos 40: 377–384.

Winnie, J. A. et al. 2008. Habitat quality and heterogeneity influence distribution and behavior in African buffalo (*Syncerus caffer*). – Ecology 89: 1457–1468.

Wolf, M. et al. 2009. The attraction of the known: the importance of spatial familiarity in habitat selection in wapiti (*Cervus elaphus*). – Ecography 32: 401–410.

Xue, Y. et al. 2018. Activity patterns and resource partitioning: seven species at watering sites in the Altun Mountains, China. – J. Arid Land 10: 959–967.

Yoganand, K. and Owen-Smith, N. 2014. Restricted habitat use by an African savanna herbivore through the seasonal cycle: key resources concept expanded. – Ecography 37: 969–982.

Zalatan, R. et al. 2006. Long-term abundance patterns of barren-ground caribou using trampling scars on roots of (*Picea mariana*) in the Northwest Territories, Canada. – Arct. Antarct. Alp. Res. 38: 624–630.

Supplementary material (available online as Appendix wlb-00736 at <www.wildlifebiology.org/appendix/wlb-00736>). Appendix 1.