

ECOLOGICAL IMPORTANCE OF LICKS TO FOUR UNGULATE SPECIES IN
NORTH-CENTRAL BRITISH COLUMBIA

by

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ABSTRACT

Elemental deficiencies and digestive disorders of wild ungulates may be improved by soil ingestion at lick areas. I related seasonal patterns of lick use with the composition of lick soils and forage to assess the importance of licks to four ungulate species. Behavioural observations of elk (*Cervus elaphus*), moose (*Alces alces*), Stone's sheep (*Ovis dalli stonei*), and mountain goats (*Oreamnos americanus*) were conducted at two wet licks and three dry licks in the Tuchodi watershed, north-central British Columbia. Three indices of lick use (attendance numbers, length of visit, and time spent licking per visit) from 558 h of observations and remote trail camera data (May – August 2002) were used to estimate species- and sex-specific peak periods of licking activity. Soils sampled from 10 high-use, 10 low-use, and 10 control sites at each lick were analyzed for buffering capacity and extracted with solutions at low pH, characteristic of the ungulate digestive tract, to quantify potentially available elements. The elemental composition of forage samples collected across elevations and time also was determined. Elk spent a higher proportion of time licking during visits to wet licks than moose, and at dry licks, mountain goats spent more time licking than Stone's sheep. Peaks in lick use by elk, Stone's sheep and mountain goats followed transitions to spring green-up and coincided with increased demands associated with lactation. Moose, in contrast, showed higher use in late summer. Concentrations of carbonates and sodium at all licks were higher than control sites. These results suggest that pH adjustments of the rumen and sodium supplementation above levels obtained in the diet are important functions of both wet and dry licks. Seasonal lick use within and among species, however, was variable and concentrations of other elements including iron and magnesium were also high in some lick

soils, implying that explanations of lick function may not be consistent across all species and licks.

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CHAPTER 1: INTRODUCTION

Background

Licks are used by all North American ungulate species (Jones and Hanson 1985). The terms ‘mineral lick’ or ‘salt lick’ are potentially misleading because they imply that the explanation for soil ingestion is to ingest elements. In this thesis, I will follow Klaus and Schmid’s (1998) suggestion to use the neutral terms ‘lick’ or ‘natural lick’. Licks may occur in areas where concentrations of solutes tend to collect: near groundwater springs, around roots of trees, or on bluffs bordering streams (Jones and Hanson 1985). In the Tuchodi Lakes study area in north-central British Columbia (BC), there are two visually distinct types of licks: wet and dry. Wet licks are usually associated with groundwater springs and develop into muddy clearings used mainly by cervids (Williams 1962, Knight and Mudge 1967, Chamberlain et al. 1977, Fraser and Hristienko 1981). Dry licks can be found above valley bottoms on steep rocky banks alongside riverbeds, and are used mainly by bovids (Hebert and Cowan 1971, Heimer 1973, Singer 1978, Watts and Schemnitz 1985). Licks are thought to have a profound impact on the distributions and movements of individuals within populations (Heimer 1973, Watts and Schemnitz 1985). In order to incorporate these small habitat features into landscape-level management plans, attempts should be made to estimate when and why ungulate species use them.

This study focuses on the use of licks by four ungulate species (elk, *Cervus elaphus*; moose, *Alces alces*; Stone’s sheep, *Ovis dalli stonei*; and mountain goats, *Oreamnos americanus*). These species, with a ruminant digestive system, are able to survive on low-quality, high-fiber plants associated with long north-temperate winters. The transition from a reduced metabolic state on a diet of low quality winter forage, to increased physiological

demands of lactation, growth, and/or weight regain in spring/early summer, must be efficient to take advantage of the short period of lush spring growth. Potential physiological constraints during this transition period involve the chemical properties of spring forage that reduce the digestive efficiency of the rumen and impair the absorption and retention of elements. Therefore, ruminants may use licks not only as sources of inorganic supplements deficient in the diet, but also to mitigate against digestive disorders and elemental imbalances associated with the change from high-fiber winter forage to lush spring growth.

Several lick studies have concluded that the use of licks indicates a dietary deficiency of a particular element that exists in unusually high concentrations in lick material (Chamberlain et al. 1977, Klaus and Schmid 1998). There has been a long-held view that sodium is the element in lick material that both attracts and benefits ungulates (Stockstad 1950, Williams 1962, Knight and Mudge 1967). This point of view is based on the critical role of sodium in body fluid volume and osmolarity regulation (Hellgren and Pitts 1997), known seasonal sodium deficiencies in many forage plants (Staaland et al. 1980, Reisenhoover and Peterson 1986, Ohlson and Staaland 2001), and the strong attraction to sodium shown by several ungulate species in cafeteria-style selection experiments (Stockstad 1950, Williams 1962, Fraser and Hristienko 1981).

There are, however, equally viable physiological rationales for the importance of other elements such as magnesium (Heimer 1988) that broaden perspectives on the use of licks by ungulates. The supposition that the use of licks is attributable solely to sodium is refuted by results from numerous analyses of lick soils that have shown compositions of a variety of elements with no single element in high concentrations among licks even within the same area (Stockstad 1950, Williams 1962, Chamberlain et al. 1977, Dormaar and

Walker 1996). Controlled manipulations of elemental intake by captive ungulates using appropriate response variables (e.g., weight gain, milk production) may determine the likelihood of these potential deficiencies, and subsequently, further define the physiological role of lick use.

Two sources of physiological stress associated with adapting to lush spring forage are: (1) extremely high potassium levels that may impair the retention of other elements, and (2) decreased fiber and increased readily fermentable carbohydrates and proteins causing intestinal acidosis that may reduce appetite and efficient rumen function (Kreulen 1985, Klaus and Schmid 1998). Early season vegetation contains high concentrations of potassium that elevate the osmotic pressure of the digestive tract, interfere with fecal water absorption, and lead to potentially harmful electrolyte losses (Weeks and Kirkpatrick 1976). Wet, unformed feces from ungulates in spring often result from a diet of succulent new growth, and may be responsible for loss of physiologically important elements such as sodium and magnesium (Hebert and Cowan 1971, Heimer 1988). To capitalize on the increase in readily fermentable carbohydrates and soluble proteins in spring forage, ruminants must adapt to this reduction in dietary fiber. A decrease in dietary fiber reduces the secretion of saliva that helps to buffer the rumen environment against pH fluctuations with sodium bicarbonate (Church 1975). Without the buffering role of saliva, the increase in acids from rapid fermentation of high protein and sugar levels in spring forage can cause various intestinal ailments such as acidosis, which reduces appetite and weight gain (Kreulen 1985, Klaus and Schmid 1998). Clays and carbonates ingested from lick soils may facilitate this transition to spring forage (Kreulen 1985, Klaus and Schmid 1998).

Therefore, licks may function as sources of: (1) nutritionally important elements deficient in forage plants, (2) nutritional elements that become deficient during the transition to spring forage change, (3) clays and carbonates to buffer against intestinal disorders associated with spring forage change, and/or (4) combinations of the above.

Objectives

1) To document the patterns of lick use by four ungulate species.

Peaks in seasonal timing of lick use by specific ungulate species and sexes (e.g., Fraser and Hristienko 1981, Heimer 1973, Williams 1962) may indicate periods of greatest physiological demand for lick soil. In my study, behavioural observations of four ungulate species were conducted from May – August 2002 at two wet licks and three dry licks.

2) To describe the chemical composition of wet and dry licks in the Tuchodi Lakes watershed, north-central British Columbia.

The diversity of results from various chemical descriptions of lick soils has discredited the theory of a universal function of licks and supported the notion of licks serving multiple roles across times, locations, and species (Kruegen 1985). In my study, available macro- and trace elements, and buffering compounds in soil samples from sites at licks where animals were known to have ingested soil, were compared to control sites outside the lick area.

3) To estimate dietary concentrations of elements in the primary forage species across elevation and time (May – August 2002).

Regional variation in the elemental content of plants has been associated with seasonal migration of some ungulates to coastal foraging sites where sodium concentration in forage is higher (e.g., reindeer (*Rangifer tarandus*), Stalaand and White 2001). Elements that are elevated in lick soil may be deficient in forage, suggesting that travel to licks to ingest soil may be a strategy to increase intake of these elements. Primary forages used by the four ungulate species in my study area were sampled and analyzed for differences in concentration of macro- and trace elements over elevation and time.

4) To estimate the potential contribution of clay ingested from lick soils to buffering capacity.

Recent studies on licks have suggested that clay minerals from lick soils may benefit ruminants as a form of self-medication (Kreulen 1985, Klaus and Schmid 1998). Ingested clay may buffer against seasonal fluctuations in pH, maintaining a rumen environment that supports efficient microbial activity. In my study, the extracted elements and buffering capacities of fecal material containing clay from lick areas were compared to fecal material collected at distances away from licks. Differences in the concentrations of elements in fecal material may reflect different retention and conservation of specific elements, suggestive of deficiencies. High buffering capacity in clay-filled fecal material may indicate that ingested clay from licks contributes to maintenance of neutral rumen pH.

The overall framework of this research, therefore, was to integrate the results of objectives 1-4 with previously documented foraging strategies, digestive processes, and elemental requirements of ungulates. I expected that peaks in intensity of lick use would

coincide with periods of known high physiological demands if these demands could not be met by available forage, and if licks helped meet those requirements. Licks may help meet requirements if they contain higher concentrations of nutritional elements than control sites and/or if digestive processes can be ameliorated by buffering or binding compounds concentrated in lick soil.

Organization of thesis

The behavioural component of my research, as outlined in the first objective, is presented in Chapter 2 (*Use of natural licks by four ungulate species in north-central British Columbia*). The methods, results, and discussions involved in meeting the chemical-based objectives 2, 3 and 4 are given in Chapter 3 (*Chemical characterization of lick soils: potential benefits for ungulates*). Chapter 4 (*Implications for Northern Rockies Provincial Park*) summarizes conclusions from Chapters 2 and 3 and incorporates observations of riverboat use to provide suggestions for consideration in access management in the Tuchodi watershed of Northern Rockies Provincial Park. Throughout this thesis, I used the first person plural in recognition of the contributions from field assistants and members of the supervisory committee. Chapters 2 and 3 will acknowledge specific contributions through co-authorship in peer-reviewed publications.

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CHAPTER 2: USE OF NATURAL LICKS BY FOUR UNGULATE SPECIES IN NORTH-CENTRAL BRITISH COLUMBIA.¹

Abstract

Three indices of lick use (attendance numbers, length of visit, and time spent licking per visit) by four ungulate species at wet and dry licks were combined to estimate species- and sex-specific intensity of licking, and to propose physiological influences on the timing of lick use. At wet licks, elk (*Cervus elaphus*) spent a significantly higher proportion of time licking per visit than moose (*Alces alces*), and similarly at dry licks, mountain goats (*Oreamnos americanus*) licked for a greater proportion of time per visit than Stone's sheep (*Ovis dalli stonei*). High-use of wet licks by both female and male elk in late May followed the timing of green-up at low elevations. Average attendance by female elk was also high in late June, coinciding with high lactation demands. Lick activity by moose was similar between sexes, but peaked later in mid-July, potentially influenced by other aspects of forage phenology such as plant defensive compounds. The timing of use at the dry licks by Stone's sheep and mountain goats was highly variable across the spring and summer with two periods of high use common to both species in early July, possibly related to forage change, and in early August, potentially related to lactation demands. Photographs from remote trail cameras on trails to two of the dry licks underestimated attendance, but were an index of frequency of use by recognizable Stone's sheep and mountain goats. Wet and dry lick soils

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may contain inorganic elements that allow ungulates to improve rumen function and nutrient absorption during the transition to spring forage and to supplement intake by females during the nutritional stress associated with lactation.

Introduction

Soil ingestion from lick areas is a widespread behaviour among large herbivores at specific times of the year (Kreulen 1985, Klaus and Schmid 1998). Licks can be either wet or dry; both are created by natural deposition and concentration of dissolved elements and/or clays. In north-central British Columbia (BC), wet licks are associated with groundwater springs, often becoming treeless areas of deep mud after years of use by moose (*Alces alces*) and elk (*Cervus elaphus*). Dry licks usually occur along streams or riverbeds, where unweathered deposits of soluble elements have concentrated above less-impervious layers, and become exposed by erosion. Stone's sheep (*Ovis dalli stonei*) and mountain goats (*Oreamnos americanus*) ingest soil from these steep features, which are often separated from alpine habitats by several kilometers.

The effect of lick use on ungulate physiology is believed to have a profound impact on distributions and movements of populations (Heimer 1973, Watts and Schemnitz 1985). Studies on the use of licks in temperate ecosystems suggest that peaks in attendance typically occur during the spring and summer months with females often using licks earlier than males (moose, Tankersley and Gasaway 1983; elk, Williams 1962; Dall's sheep (*Ovis dalli dalli*), Heimer 1973, Tankersley 1984; mountain goats, Singer 1978). During the spring and summer, ungulates must acquire inorganic elements not only to meet the physiological demands associated with reproduction and improving over-winter body condition, but also to

maintain the proper rumen environment for digestion and absorption of plant tissue. An abrupt change to spring forage is known to change the chemical properties of the rumen environment (Kreulen 1985). Chronic elemental deficiencies in forage and imbalances related to forage change, may not have overt physical symptoms that permit diagnosis (Robbins 1993). Although potentially overlooked, these stresses may increase susceptibility to opportunistic factors (e.g., bacteria, viruses, and predation) causing mortality (O'Hara et al. 2001).

Klaus and Schmid (1998) reported that licks may serve a social role as well as a physiological function. Observational data collected on the intensity of soil ingestion and attendance are needed to separate physiological influences on the timing of the use of licks from social influences. Commonly, studies on the use of licks present only attendance data (Dalke et al. 1965, Singer 1978, Tankersley 1984, Watts and Schemnitz 1985, Reisenhoover and Peterson 1986, Heimer 1988) showing peaks in timing of the use of licks, but no information on numbers of individuals that might ingest little or no lick material. Consequently, it is difficult to separate apparent nutritional requirements from social dynamics. Carbyn (1975) reported that postpartum elk nursery bands visiting licks increased the numbers of recorded daily visits by female elk, although few individuals ingested soil from the lick, which suggests that patterns of lick use based only on attendance numbers may be misleading. Most reviews of studies on licks have emphasized the importance of using appropriate methods to collect and analyze samples of lick soil (Fraser et al. 1980, Kreulen 1985, Klaus and Schmid 1998), but in contrast, they have not included observational data in their recommendations for a more rigorous approach. Few observational studies have examined lick use by more than one species, and different methods of sampling and indices

of use have made interspecific comparisons difficult if not impossible. Comparisons of lick use among species with different physiological demands and forage intake may help to identify elemental deficiencies and imbalances and estimate the relative importance of licks to each species.

This research documented lick use by elk, moose, Stone's sheep and mountain goats at two wet and three dry licks, and compared licking intensity and peak periods of use among species and between sexes. We focused observations on collecting attendance data and recording length of lick visits and time spent licking by species/sex groups. The research is part of a larger study that also documents chemical composition of the licks and available forage (see Chapter 3).

Study area

The five licks chosen for behavioural observations are located near the Tuchodi Lakes (800 m elevation, 58°10'N 124°30'W), within the Muskwa-Kechika Management Area, 120 km southwest of Fort Nelson, BC (Fig. 2.1). The study area extends approximately 55 km along the Tuchodi River system, from the most western point at the upper Tuchodi River lick east to the Childers Creek lick in the Rocky Mountain foothills. Vegetation in the watershed is dominated by white (*Picea glauca*) and black spruce (*P. mariana*) at low elevations, by black spruce, willow (*Salix* spp.), and birch (*Betula glandulosa*) in the sub-alpine, and alpine tundra. The area is known for its high density and diversity of large mammal species, populations of which are supported by extensive areas of high-capability ungulate winter habitat on many south- and west-facing slopes exposed to periodic chinook winds (Peck 1987). Access to this remote study area is by air, riverboat, or horseback. The five licks were

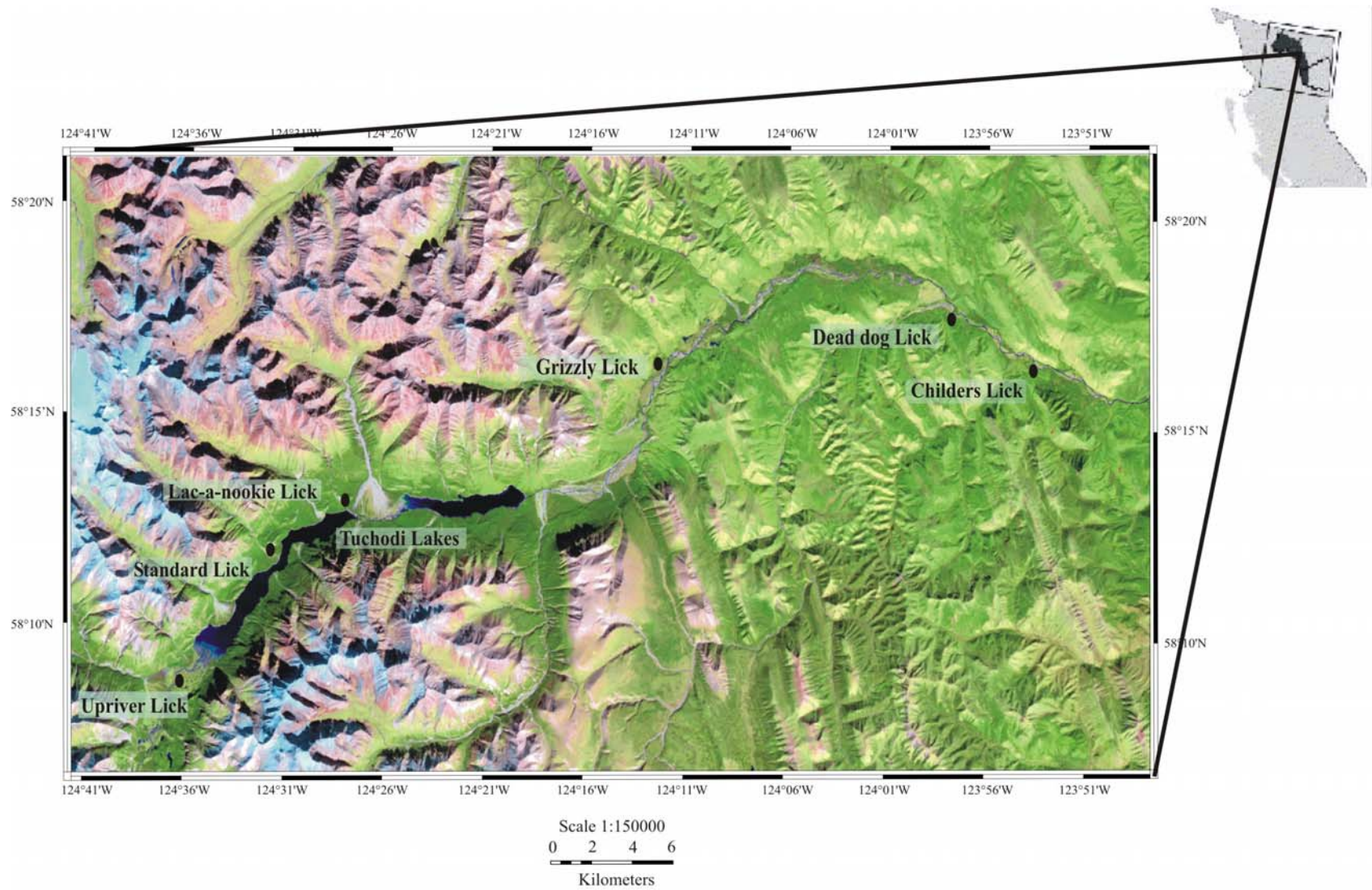


Figure 2.1. The six natural licks studied in the Tuchodi River watershed, Muskwa-Kechika Management Area, BC. No observations of animal use were collected at Grizzly Lick.

chosen based on historic ungulate use, adequate observation points, and access by researchers.

The three dry licks chosen for study were the upper Tuchodi River (Upriver) lick, Standard lick, and Lac-a-nookie lick (Fig. 2.1). Steep mountainous peaks and ridges typical of Stone's sheep and mountain goat habitat surround these dry licks. The Upriver lick is along a reach of the Tuchodi River above the upper Tuchodi Lake, and is visually distinct from the other two dry licks. The Upriver lick area is on the inside of a curve in the Tuchodi River extending ~250 m along the shore and ~60 m upslope into the forest. Our observation point at the Upriver lick was directly across the river and afforded observers the closest view point of all the dry licks. Lac-a-nookie and Standard licks are similar in appearance and ~5 km apart on the north side of the upper Tuchodi Lake. These two licks are composed of steep gravel/cobble spires extending along an old riverbed for ~350 m and rising ~60 m above the lakeshore. All three licks have well-used trails connecting them to alpine habitats.

The two wet licks (Childers and Dead dog licks; Fig. 2.1) are situated within 25 km of each other in the eastern foothills of the Northern Rocky mountains. Both wet licks are near creek confluences with the Tuchodi River, downstream from the Tuchodi Lakes. Dead dog lick (50 m x 30 m) is much smaller than Childers lick (200 m x 50 m), but both licks have a history of heavy use as indicated by the surrounding network of deeply eroded trails.

Methods

Visual observations

Visual observations were made with 8 x 30 binoculars and 20-45 variable spotting scopes from locations established during a reconnaissance trip the summer before fieldwork. At each of the two wet licks, we built temporary tree blinds to enable observers to reduce the

effects of their presence while remaining within 10 m of the licks to document individual animal behaviours. The blinds were 1.5-m x 2-m log platforms with tarp roofs and mesh mosquito netting. Spruce boughs were used to further improve the concealment of the blinds from animals at the lick below. The Childers lick blind was built 5 m off the ground between two trees within a few meters of the edge of the lick, facilitating a clear view of the lick area from a position generally downwind of the main trails entering the lick. The Dead dog lick blind was a freestanding platform 4 m off the ground set back from the edge of this lick in a stand of young spruce trees. This blind was well camouflaged typically downwind from lick activities with a clear view of the entire lick area. Following completion of fieldwork in late July, both blinds were dismantled.

Because of the shape and deeply eroded topography of two of the dry licks, there were no locations along their edges that enabled views of the entire lick area. Observations were instead made from distant viewpoints (600 m from Lac-a-nookie lick, and 800 m from Standard lick) across the lake. At the third dry lick (Upriver lick), we built a low blind 75 m directly across the river from the lick area using natural deadfall and brush. A tarp and mosquito net were erected at the beginning of each observation period.

Two, two-person field crews conducted visual observations between 24 May and 11 August (one crew observed wet licks and the other dry licks). Observations were usually made on three consecutive days at each lick, alternating between the two wet licks, or rotating among the three dry licks. The data were collected over 6-h shifts, with start times beginning at 0500, 1100, or 1700 h to capture daily variations of lick use. The beginning and end of the summer field season were constrained by spring snow and access to the study area, and the effects of hunting pressures in the fall.

During each shift, one person conducted scan sampling every 15 min to document all individuals present by species and sex and their locations at the lick area. These data were plotted on hand-drawn maps of the licks before being transferred to digital maps for which the boundaries were recorded with a GPS unit. The data were used to quantify high- and low-use areas of each lick for subsequent soil sampling (see Chapter 3). Another observer collected focal animal data during each shift by continuously monitoring behaviours of one individual for the duration of time it was at the lick. Behaviours included licking, standing (including walking), lying and out of sight. The time when an animal stopped one behaviour and started another was recorded for all behaviours >3 sec in duration. If an animal was out of sight for >30 min, focal sampling efforts were switched to another individual. This rule needed to be employed only at the dry licks. After a focal sample was collected from one species/sex group, an individual from another group was chosen as the next focal animal if other groups were present at the lick. If an animal was already present at the lick before focal data collection began or if an observation shift ended while a focal animal remained at the lick, it was noted as an incomplete observation of a visit, hereafter referred to as ‘incomplete visit’. Notes were collected on weather (rain, temperature, wind, cloud cover) and any noticeable observer effects on behaviours of animals. We also kept a record of recognizable individuals with unique scars, coats, or antlers to help in estimating numbers of different animals using each lick.

Remote trail cameras

To supplement visual observations at Lac-a-nookie and Standard licks, we placed a remote trail camera (Trailmaster, TM 1500, active infra-red system, Lenexa, Kansas USA) on the main access trail within 200 m of each of the licks. These two dry licks were the most

accessible to researchers. The multiple trails radiating from the wet licks did not permit similar use of trail cameras. Close-range photographs and a time/date event log of trail use provided data on seasonal trail use, as well as duration of time at the lick and frequency of lick visits for those individuals recognizable in multiple photographs.

Photographs were taken when the infrared beam projected across the trail was broken. To avoid exhausting rolls of film on animals that may stay stationary or cross back and forth through the beam, we set the camera activation to a 1-min delay, while still collecting the time and date of all beam-breaking events on the data logger. The transceiver and receiver/event logger were mounted to trees to project an infrared beam ~60 cm off the ground so that young animals would also break the beam and trigger the camera shutter. Each camera shutter was set to activate if a minimum of five infrared pulses were not received from the transceiver, reducing the number of unwanted photographs of small objects (e.g., birds, falling leaves). A 6-m cable from the infrared receiver allowed placement of the 35-mm camera to capture a wide field of view centered on the infrared beam across the trail. The fields of view for both remote trail cameras favoured the uphill direction (away from the licks).

Data analyses

Scan data

We chose to use the highest number of individuals counted at one scan during each 6-h shift as an index of the timing of lick use during the summer season. This index describes attendance by the maximum number of individuals observed at one time, but is likely an underestimate of the daily number of animal visits. We also calculated the cumulative number of visits to licks (the sum of all animals observed every scan during each shift),

which reflects intensity of animal use at the lick without regard to the number of different individuals in attendance. We used Pearson correlations (Zar 1999) to compare the two indices of use for each species/sex group.

Differences in hourly patterns in the use of licks were analyzed with analysis of variance (Zar 1999). Patterns in the use of licks across the spring and summer were graphically presented after grouping observation shifts that were conducted on consecutive days. The mid-date of three-shift observation periods and the first date of two-shift periods were used in all graphical analyses. Because of distances to the dry licks from viewpoints, accurate sex identification was not always possible for Stone's sheep and mountain goats, and therefore the seasonal patterns in use of dry licks were not analyzed by sex.

Focal animal data

Focal animal data from wet and dry licks were not included in analyses if observer effects had been noted (e.g., if movement/noise in the blind caused animals to leave the lick). Focal data from wet licks were not used if visits were incomplete or if sex was unknown. Both complete and incomplete visits were used from dry licks because of low sample sizes. Also at the dry licks, focal animals were often out of sight from observers, and therefore, we chose to present the length of lick visit as the length of time that the animal was in sight of observers (subtracting the time out of sight from the total length of the observed visit). Relationships between time spent licking and the duration of lick visit (linear regressions) were compared between species at each type of lick using Student's *t*-test for difference in slopes (Zar 1999). Between sexes of each species, differences in length of lick visit and time spent licking were tested with a non-parametric test (Mann-Whitney U test; Zar 1999)

because data were not normally distributed. The same periods of grouped observation shifts were used when graphing seasonal patterns of both focal and scan data. All means are presented as $\bar{X} \pm 1 \text{ SE}$. Statistica 6.1 (Statsoft Inc. 2002) software was used for all tests; significant differences were assumed at an α of 0.05.

Results

We observed use of wet licks (Childers, Dead dog) by elk and moose from 24 May to 19 July, during 41 observation shifts (246 h) and documented specific behaviours of 300 focal animals (Table 2.1). We conducted observations of Stone's sheep and mountain goats at the dry licks (Lac-a-nookie, Standard, Upriver) from 29 May to 12 August, for 312 h over 52 observation shifts and monitored 58 focal animals. We distributed observation periods relatively evenly across daylight hours (Table 2.1).

We removed data from analyses on 33 focal animals at wet licks for which we had noted observer effects (27), incomplete visits (5), and/or unknown sex (1). Because of the topography (hoodoo formations) and distant viewpoints at the dry licks, few complete visits (5 of 58 focal animals) were documented when focal animals were observed from arrival until departure. Therefore, incomplete visits were not removed from dry lick data. We removed data on 10 focal animals of unknown sex from sex-specific analyses of dry lick data.

The relationships between the highest number of individuals observed at one scan per shift and the cumulative number of animals observed during one entire shift generally varied together from May – August, 2002 ($r = 0.55$ to 0.94 , all $P \leq 0.01$; Appendix A, Figs. A.1-A.10). When averaged over consecutive shifts, the cumulative number of animals observed

Table 2.1. Number of observation shifts, scans, and focal animals, at five licks in the Tuchodi watershed, May – August 2002.

Lick	Shift (h)			Scans (n)	Focal Animals (n)
	0500-1100	1100-1700	1700-2300		
Childers	7	6	7	500	148
Dead dog	7	6	8	525	152
Lac-a-nookie	6	9	5	500	22
Standard	6	7	5	450	16
Upriver	6	4	4	350	20
Total	32	32	29	2325	358

per shift was more variable than the highest number of animals observed at one scan per shift.

Rainfall patterns may have reduced attendance numbers at wet licks. No animals were observed during 2 of 11 observation shifts conducted at wet licks in the rain. Only 1 of 30 shifts conducted without rain documented no animal use. At dry licks, no animals were observed during 6 of 15 shifts conducted in the rain, in comparison to 5 of 37 shifts conducted without rain. Species-specific attendance in relation to rain days is given in Appendix B.

Elk were present at wet licks in greater numbers during morning (0500-1100 h) compared to day or evening shifts, although this trend was significant only for female elk at Childers lick (Table 2.2). Peak use at Childers lick by female elk appeared to be at ~1000 h (Fig. 2.2). In contrast, the number of moose observed at wet licks was highest between 1700-2300 h, although this was significant only for male moose at Childers lick and differences

Table 2.2. Averages of the highest number of animals ($\bar{X} \pm \text{SE}$) observed at one scan by species/sex groups during observation shifts at five licks in the Tuchodi watershed. Data were combined across May – August 2002.

Lick	Species/sex	Shifts (h)			P-value
		0500-1100	1100-1700	1700-2300	
Childers	Elk female	12.7 ± 2.6	6.7 ± 2.3	3.6 ± 1.3	0.02
	Elk male	4.0 ± 0.9	2.3 ± 0.7	1.6 ± 0.6	0.07
	Moose female	0.7 ± 0.3	1.2 ± 0.3	1.9 ± 0.5	0.10
	Moose male	1.0 ± 0.3	0.3 ± 0.2	1.3 ± 0.2	0.04
Dead dog	Elk female	5.7 ± 1.8	3.2 ± 1.4	3.5 ± 1.2	0.44
	Elk male	1.7 ± 0.6	0.5 ± 0.3	1.4 ± 0.4	0.24
	Moose female	0.7 ± 0.3	0.5 ± 0.2	0.8 ± 0.3	0.82
	Moose male	0.0 ± 0.0	0.2 ± 0.2	0.3 ± 0.2	0.42
Lac-a-nookie	Stone's sheep	3.4 ± 2.0	2.0 ± 0.9	3.8 ± 1.4	0.67
Standard	Stone's sheep	0.7 ± 0.7	1.7 ± 0.9	0.4 ± 0.4	0.44
	Mountain goats	2.0 ± 0.9	1.3 ± 0.7	0.6 ± 0.4	0.43
Upriver	Stone's sheep	3.0 ± 2.3	6.0 ± 3.7	2.3 ± 1.4	0.73
	Mountain goats	4.3 ± 3.1	5.3 ± 4.0	4.3 ± 1.9	0.80

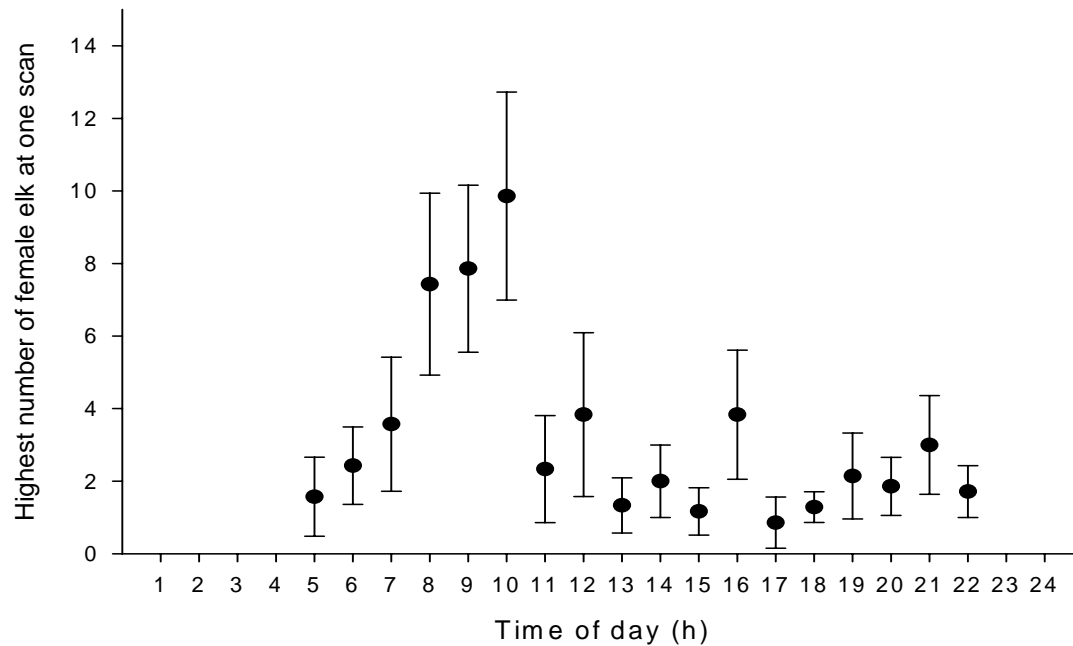


Figure 2.2. Hourly variation in attendance by female elk during observation shifts at Childers lick ($\bar{X} \pm \text{SE}$) in the Tuchodi watershed, May – July 2002.

were small (Table 2.2). There were no trends in the hourly use of dry licks by Stone's sheep or mountain goats.

The time spent licking per lick visit increased linearly with the length of visit, using data combined across the spring and summer for each species (Fig. 2.3). At the wet licks, the relationship between the length of lick visits and the time spent licking per visit was stronger for elk ($r^2 = 0.95$, Fig. 2.3) than moose ($r^2 = 0.57$, Fig. 2.3). Elk showed a wider range in the lengths of lick visits (0.1 - 194 min) and the time spent licking per visit (0 - 164 min) than moose (length of visit: 1 - 93 min; time licking: 0 - 38 min). Elk showed a stronger licking intensity (slope of the relationship = 0.79) than did moose (slope = 0.29; $P < 0.001$; Fig. 2.3). At the dry licks, the length of lick visit explained more variation in the time spent licking by

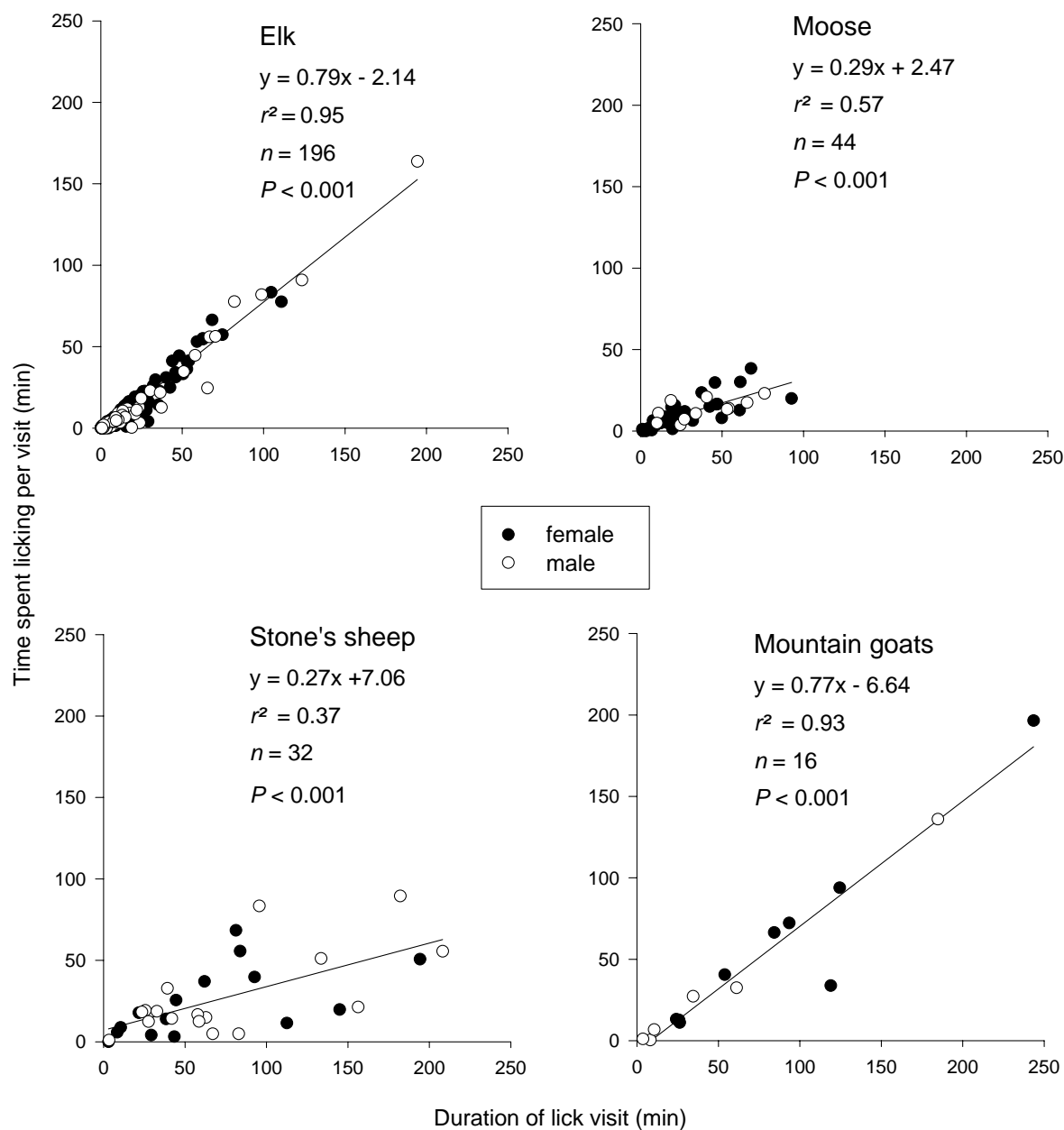


Figure 2.3. Relationships between the time spent licking by ungulates per visit and the length of lick visits at wet licks (elk and moose) and dry licks (Stone's sheep and mountain goats) in the Tuchodi watershed (May – August 2002). The slope of each relationship was assumed to be a measure of licking intensity.

mountain goats ($r^2 = 0.93$) than Stone's sheep ($r^2 = 0.40$). The ranges in duration of time spent at dry licks and time spent licking per visit were more similar between Stone's sheep and mountain goats, although goats spent a significantly greater proportion of time licking (slope = 0.77) than sheep (slope = 0.40; $P = 0.015$; Fig. 2.3).

Within each species, sexual differences were not consistent. Females had a higher licking intensity (proportion of time spent licking per visit) than males, but this was significant ($P = 0.047$) only for female elk (Table 2.3). Females of all species except mountain goats spent shorter lengths of time at licks per visit, although this was significant only for moose ($P = 0.048$).

Timing of spring and summer use of licks

Elk

We observed more female elk using wet licks than males. The disproportionately high presence of female elk at the wet licks resulted in more focal sampling of individual female elk than any other group at the wet licks (147 of 240 focal animals, Table 2.3). The highest number of elk recorded at one time (42) was at the largest lick (Childers) on 1 June, but this observation was made between the scans recorded each 15 min, and average attendances from scan data during this period were much lower (females: 10.3 ± 7.4 , males: 4.3 ± 2.4). Average attendance by female elk was highest in late June at both licks (Childers: 21 June; Dead dog: 27 June) (Fig. 2.4). There appeared to be another peak in attendance common to both males and females at Childers lick and females at Dead dog lick in late May.

The length of visit and the time spent licking varied with attendance patterns at Childers, but not at Dead dog lick. At both licks, however, the longest lick visits (Childers: 43.2 ± 11.3 min by females, 74.9 ± 45.8 min by males; Dead dog: 37.5 ± 12.4 min by

Table 2.3. Length of lick visits, time licking, and proportion of time licking per visit ($\bar{X} \pm SE$) by species/sex groups at licks in the Tuchodi watershed. Data were combined across May – August 2002, with observer-affected and incomplete visits (elk and moose only) removed.

Species/sex	Focal animals (n)	Time observed (h)	Length of visit (min)	Time licking (min)	Proportion licking
Elk female	147	40.47	16.8 ± 1.5	11.5 ± 1.2	0.58 ± 0.02
Elk male	49	19.28	21.8 ± 4.4	14.6 ± 3.6	0.49 ± 0.04
Moose female	33	15.19	26.1 ± 3.5	10.4 ± 1.5	0.41 ± 0.04
Moose male	11	7.11	37.7 ± 5.7	6.5 ± 1.8	0.40 ± 0.08
Stone's sheep female	15	24.09	110.4 ± 26.2	24.1 ± 5.5	0.44 ± 0.08
Stone's sheep male	17	27.30	119.1 ± 20.8	27.7 ± 6.4	0.41 ± 0.06
Mountain goat female	10	18.44	110.7 ± 30.3	54.0 ± 18.6	0.56 ± 0.08
Mountain goat male	6	6.41	64.2 ± 30.6	34.0 ± 21.1	0.50 ± 0.12

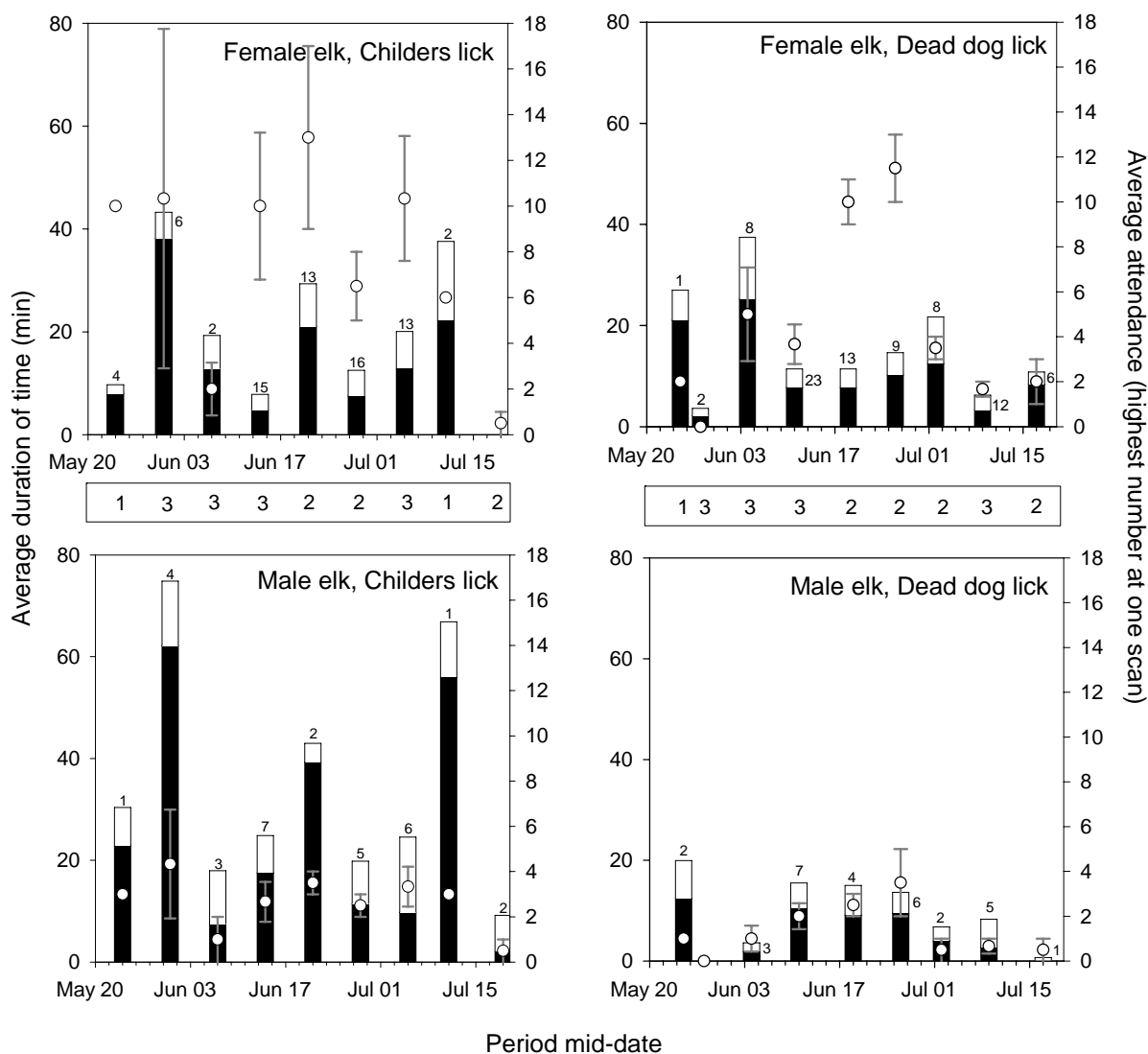


Figure 2.4. Female and male elk attendance, as indexed by the highest number of individuals observed at one scan (plot of means with SE error bars), at two wet licks in the Tuchodi watershed. The numbers of observation shifts grouped from consecutive days are presented in the horizontal bar between the graphs. The average lengths of time spent licking ■ and not licking □ per period by focal animals are presented with the number of focal animals (above each histogram bar) sampled in that period.

females, 19.9 ± 4.9 min by males) and the greatest time spent licking per visit (Childers: 38.2 ± 9.97 min by females, 62.2 ± 38.8 min by males; Dead dog: 25.2 ± 9.8 min by females, 12.4 ± 5.8 min by males) occurred in late May or early June. The average length of lick visit and the proportion of time spent licking by elk were both higher at the larger Childers lick than at Dead dog lick. The first young of the year were observed on 19 June at Dead dog lick and a week later on 28 June at Childers lick. The highest number of elk calves observed at one scan was three on 18 July at Dead dog lick.

Moose

As with elk, more female moose visited wet licks than male moose. Both sexes showed similar patterns of attendance and licking activity at Childers lick, but there were no similarities between sexes at Dead dog lick (Fig. 2.5). The highest number of moose observed at one scan was six (four females, one calf, and one male) on 4 July at Childers lick. Highest average attendance was recorded across July (Childers: 5 July for females, 11 July for males; Dead dog: 17 July for females, samples too low to estimate for males). There were often only one to two focal animals per observation period which resulted in considerable variation across the spring and summer in data on length of visits and time spent licking. Peaks in length of visit and time spent licking per visit coincided with peaks in attendance for both sexes at Dead dog lick, but not at Childers lick (Fig. 2.5). The average length of visit and the proportion of time spent licking by moose were not consistently different between the two wet licks of different size. The first moose young of the year was observed on 13 June at Childers lick and on 8 July at Dead dog lick. We did not observe more than two young of the year at one time at either lick.

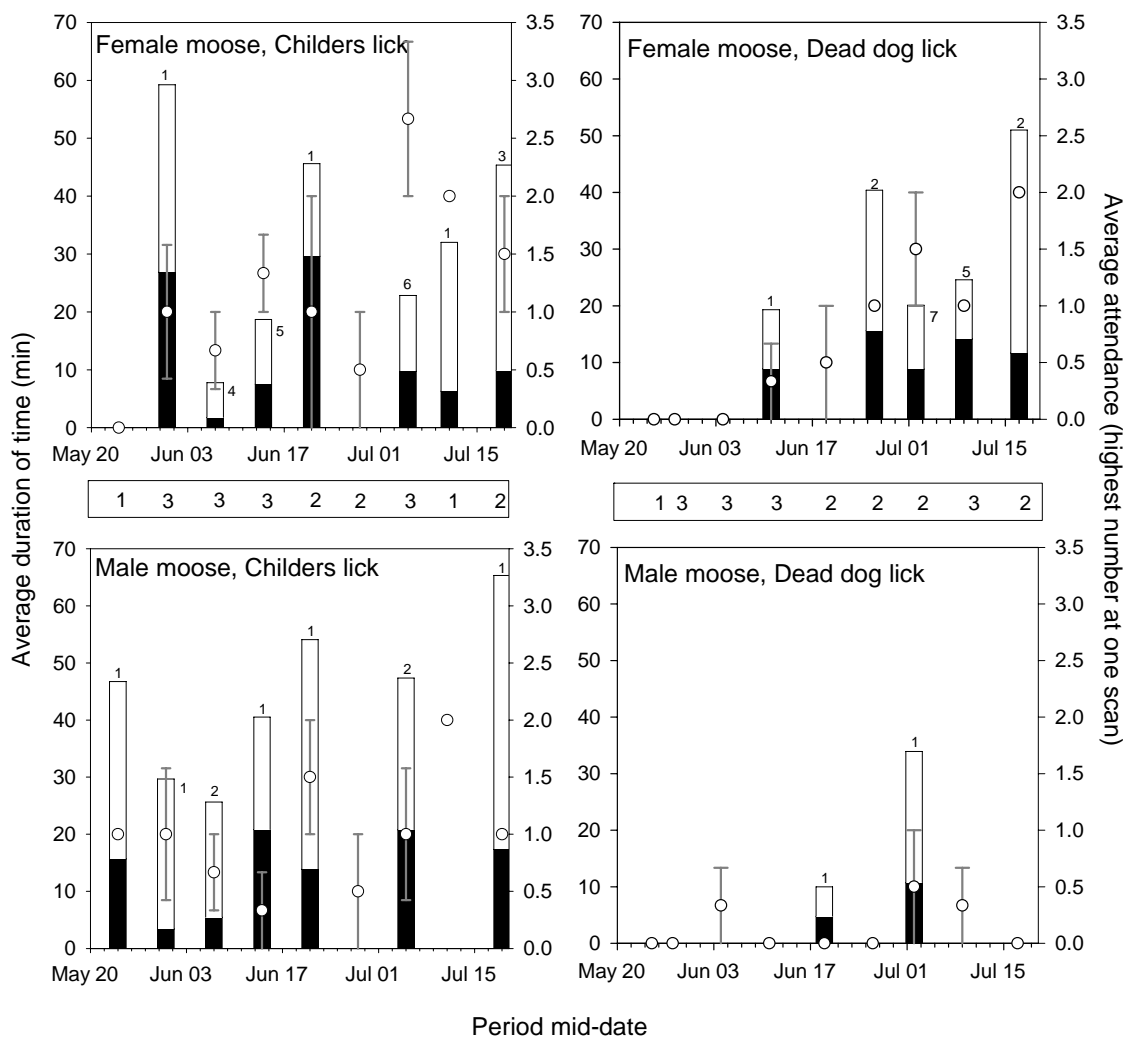


Figure 2.5. Female and male moose attendance, as indexed by the highest number of individuals observed at one scan (plot of means with SE error bars), at two wet licks in the Tuchodi watershed. The numbers of observation shifts grouped from consecutive days are presented in the horizontal bar between the graphs. The average lengths of time spent licking and not licking per period by focal animals are presented with the number of focal animals (above each histogram bar) sampled in that period.

Stone's sheep

Data were combined for both sexes at all three dry licks to improve continuity of data and examine seasonal trends. Attendance by Stone's sheep was highly variable across the season and many shifts were conducted when no Stone's sheep were observed at the licks (24 of 52 shifts). We observed some of the largest groups of Stone's sheep at the Upriver lick in early July (groups of 9-15 individuals), although data collection there did not begin until 25 June (compared with 29 May at Lac-a-nookie lick) because of high water and access problems. The highest average attendance by Stone's sheep occurred during early August (Fig. 2.6). The length of visits and time spent licking were highly variable across the season and did not show any relationship with attendance, although the longest time spent licking (46.7 ± 9.5 min) was also in early August (7 August). Stone's sheep young of the year were first seen at Upriver lick on 25 June, at Standard lick on 28 June and at Lac-a-nookie lick on 29 June. Sightings of lambs were sporadic over the summer, with the largest number observed in one shift ($n = 4$) at the Upriver lick on 7 August (in a group of ewes and yearlings).

Remote trail cameras complemented observational data of both Stone's sheep and mountain goats at two dry licks (Lac-a-nookie and Standard licks). On days when observational shifts were conducted at the lick, the trail cameras generally photographed half of the animals that were visually documented. The remote trail cameras also photographed other species using the dry lick trails that were not documented by observers: moose ($n = 2$), elk ($n = 11$), mule deer (*Odocoileus hemionus*, $n = 11$), black bear (*Ursus americanus*, $n = 3$),

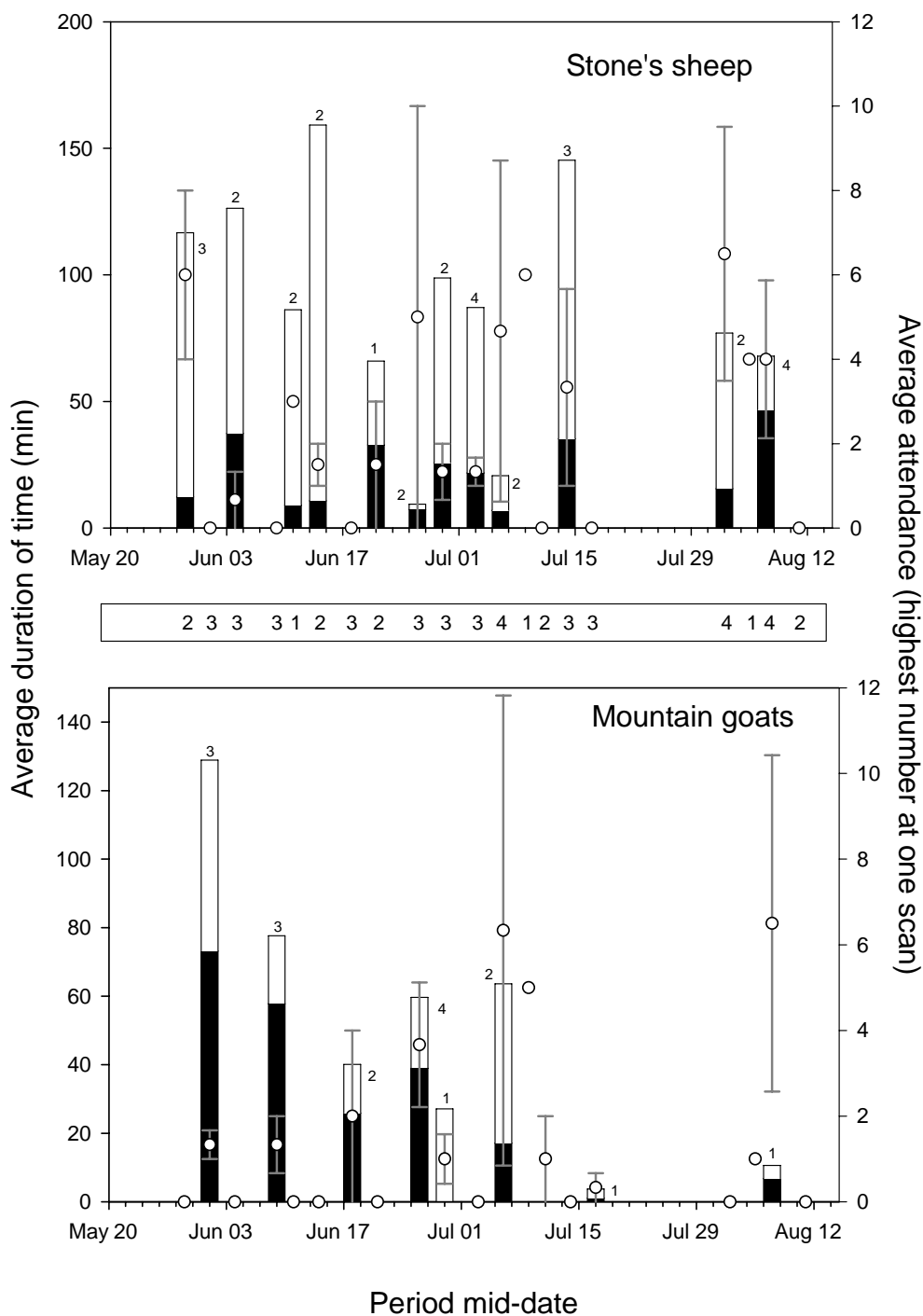


Figure 2.6. Stone's sheep and mountain goat attendance, as indexed by the highest number of individuals observed at one scan (plot of means with SE error bars), at three dry licks in the Tuchodi watershed. The numbers of observation shifts grouped from consecutive days are presented in the horizontal bar between the graphs. The average time spent licking and not licking per period by focal animals are presented with the number of focal animals (above each histogram bar) sampled in that period.

and wolf (*Canis lupus*, $n = 1$).

Stone's sheep generally used the licks between 0400 and 2300 h, with little or no travel after dark (two individuals between 2300 and 0400 hrs; Appendix C: Fig. C.1). Stone's sheep appeared to use main trails at both licks more often when traveling away from the licks than when traveling towards them (towards: 59 individuals photographed, away: 113). To estimate seasonal patterns of lick use from trail camera photographs, we chose to use only those photographs of sheep moving away from the licks because of the larger data set. The peak in trail camera photographs of Stone's sheep on 11 July (10 sheep photographed, Fig. 2.7) was not synchronous with the highest attendance from our observation data (2 August).

Several individual Stone's sheep were recognizable in multiple photographs, which provided another source of data on length of time spent at licks as well as our only estimate of frequency of lick use by individual sheep in a season. The times between arrival and departure photographs (length of lick visit) of two different Stone's sheep were 4.3 h and 8 h. One female Stone's sheep with a young of the year made a repeat visit to the lick 39 h after the first visit.

Mountain goats

Attendance by mountain goats at the three dry licks was also highly variable across the spring and summer and many shifts were conducted when no goats were observed at the licks (31 of 52 shifts). In our observation data, there appeared to be a general trend of increasing attendance through June to 6 July and an isolated spike in attendance on 7 August (Fig. 2.6). The largest number of goats observed at one time was 19 at the Upriver lick on 6 July. The seasonal trend in the mean length of visit showed an inverse relationship with

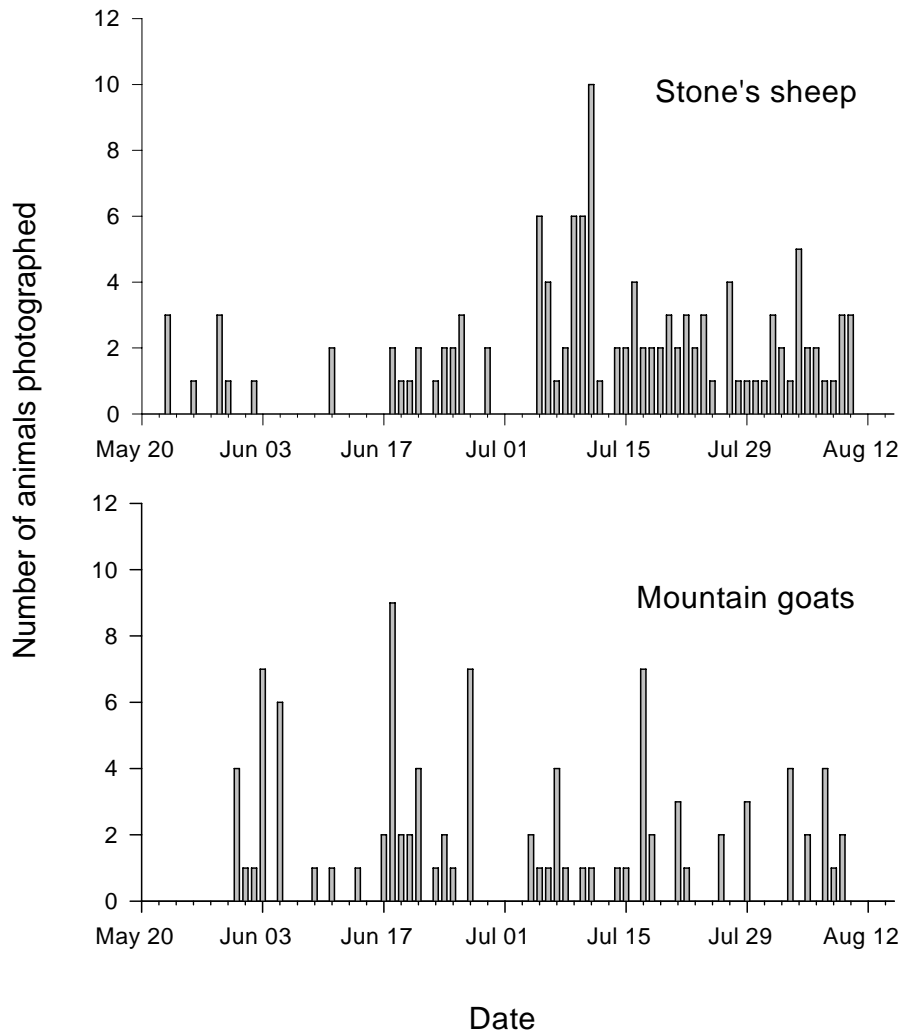


Figure 2.7. Spring and summer attendance at two dry licks by Stone's sheep and mountain goats as indexed by number of daily photographs from remote trail cameras, Tuchodi watershed (May – August 2002).

attendance where the longest visits (142.1 ± 50.7 min) and the most time spent licking per visit (93.6 ± 54.3 min) occurred on 1 June when attendance was low. The first mountain goat young of the year was observed at Standard lick on 19 June and on 25 June at Upriver lick. The most young of the year ($n = 5$) observed at one time was at the Upriver lick on 6 August.

Although there were no observations of mountain goats at Lac-a-nookie lick during observation shifts, a remote trail camera recorded mountain goats approaching and leaving this lick on eight different days. On each of these dates, observation shifts did not cover the time the photos were taken. Photographs from trail cameras at both Lac-a-nookie and Standard licks showed that mountain goats generally used the licks at all times of the day (0100 to 2300 h) including after dark (13 individuals between 2300 and 0400 h) (Appendix C: Fig. C.2). Mountain goats appeared to use the main trails more often while traveling to the licks than when traveling away (towards: 110 individuals photographed, away: 75 individuals), which contrasts with the use of these trails by Stone's sheep. To examine seasonal use of trails by mountain goats, we plotted the largest data set (photographs of goats traveling to the licks). This photographic index of lick use by mountain goats showed more variable attendance across the season than Stone's sheep (Fig. 2.7). The highest number of mountain goats photographed was on 18 June when nine goats passed by the cameras in one 24-h period, which is more than two weeks earlier than our highest attendance recorded during observation shifts.

There were 11 recognizable mountain goats in trail camera photographs. Duration of time spent at the licks for nine individuals photographed arriving and departing varied between 2.75 h and 30.22 h (two individuals apparently remained at the lick overnight). Our only data on frequency of lick use came from photographs of two female goats with young.

One group visited the lick twice in two days (25/27 July) and another visited the lick three times in six days (7-13 August).

Discussion

The universal function of licks to ungulates has been proposed to be the maintenance of mineral homeostasis (Jones and Hanson 1985). Physiologically, licks may serve to supplement dietary deficiencies or imbalances of specific elements, or to mitigate against intestinal ailments associated with forage phenology (Kreulen 1985, Klaus and Schmid 1998). Each of these nutritional limitations is recognized as an important determinant of animal condition. Accordingly, attempts should be made to further define the physiological function of licks in order to quantify their relative importance to each species and predict otherwise overlooked periods of nutritional stress. Limiting this objective is the lack of detailed information necessary to understand inorganic elemental metabolism and requirements of wildlife in relation to maintenance and production and the potentially misleading assumption that domestic animal requirements apply directly to wildlife (Robbins 1993). The information is fundamental to estimating the links between peaks in lick use and physiological demand for lick soil. We, therefore, discuss our findings in terms of relative differences between species and sexes and propose possible causal mechanisms for these differences that suggest directions for future studies on elemental requirements and metabolism.

Elk and moose

Elk are much more abundant than other ungulates in the Tuchodi watershed (Peck 1987), and therefore comparing the importance of licks between species based solely on

attendance numbers would have been misleading. Accordingly, comparisons of focal data between elk and moose based on records of individual licking activity (Fig. 2.3, Table 2.3), indicated that elk used wet licks more intensively than moose. This suggests that some aspect of elk physiology or forage composition may result in elk having a stronger appetite for wet lick soil than moose. Elk have been classified as intermediate mixed-feeders compared to the more concentrate-browser classification of moose (Bubenik 1982). The digestive adaptability of elk that allows them to capitalize on young plant growth and extensive changes in forage species over the summer (Nelson and Leege 1982), may require inorganic supplements from wet licks to maintain the proper digestive environment for rumen microbes to function efficiently.

At the end of May we noticed that many primary grass and browse species used by elk and moose were greening-up. The high lick use by both sexes of elk at the end of May (in contrast to moose) may imply that elk are more susceptible to digestive ailments associated with spring forage change than moose. Livestock studies have shown that the largest and most consistent benefits of clay and salt rations (improved intake, food conversion, and productivity) occur during a 2-4 week adaptation period following abrupt dietary change to more digestible feeds (Kruelen 1985). Elk in Idaho also utilized salt blocks extensively after they had been feeding on succulent forage for 2-3 weeks (Dalke et al. 1965).

There also was high use of wet licks by female elk from 21-27 June. Robbins et al. (1981) found that milk intake by captive elk calves increased in the first 3 weeks to a peak 21 days after parturition. Peak calving for elk in the Tuchodi watershed is likely near the end of May (peak calving for elk in Banff and Jasper National Parks in Alberta is 24 May and 1

June respectively; Taber et al. 1982), suggesting that the late June period of high lick use by female elk coincides with demands associated with milk production.

There were no increases in the use of wet licks by female or male moose that seemed to be related to spring forage change. Several other lick studies, however, have suggested that maximal use of wet licks by moose is influenced by spring forage change or leaf flush dates, even though the physiological explanation for the long time lag between leaf flush and peak use was not discussed. Maximal use of several licks by moose during a 3-year study in Quebec occurred in late July (Couturier and Barrette 1988), which is similar to our observed peaks in mid-July. In contrast, in Alaska, Fraser and Hristienko (1981) observed peak attendance by moose at licks in late May/early June over 4 consecutive years, and Tankersley and Gasaway (1983) recorded peak use in mid/late June over 2 consecutive years. All three of these studies linked peak use of licks to spring forage change or leaf flush dates that cause a deficiency in sodium; the timing of peak lick use following leaf flush dates varied from 3 weeks (Tankersley and Gasaway 1983) to 5 weeks (Fraser and Hristienko 1981) to 7 weeks (Couturier and Barrette 1988). More detailed information from captive wildlife studies on the physiological effects and associated response times of spring forage ingestion on rumen processes would strengthen discussions relating the timing of lick use to this seasonal change of diet.

Both female and male moose attendance at licks appeared to increase later in the summer (5-17 July) than elk and may be due to differences in the concentrations of plant defense compounds in forage between spring and summer. Tannins and other plant secondary compounds are typically high in the browse consumed by moose with concentrations in individual plants increasing throughout the summer (Bryant and Kuropat

1980). In southern Norway, for example, zoopathological studies on moose have documented the occurrence of toxic nephrosis (kidney damage) that may be due to excessive intakes of toxic plant secondary compounds in moose forage (Ohlson and Staaland 2001). The large salivary glands in moose produce tannin-binding proteins (Renecker and Schwartz 1997), implying that moose are chronically exposed to high tannin levels in forage. Clay ingestion has been suggested to improve palatability and digestibility for other herbivorous animals foraging on seeds and unripe fruits by absorbing tannins and other potential toxins (Johns and Duquette 1991, Diamond 1999). Clay also has been used as an additive in domestic ruminant rations as a binding agent to reduce the effects of toxic plant chemicals (Smith 1992) and, therefore, may be an important component of lick soil for moose consuming forages in summer when tannin content is elevated (see Chapter 3).

Stone's sheep and mountain goats

Our estimates of the duration of time spent at dry licks by Stone's sheep and mountain goats are likely underestimated because few animals were observed from arrival to departure. In comparison to elk and moose using wet licks, however, the durations of lick visits by Stone's sheep and mountain goats were long (Table 2.3). The difference may be more related to the long distance that sheep and goats traveled to the dry licks from their typical alpine foraging sites than a demand for lick soil. The strategy of Stone's sheep and mountain goats may be to make longer, less frequent trips compared to elk and moose. Behaviours not common at the wet licks, such as bedding and foraging, were often observed at dry licks.

Mountain goats showed a higher intensity of licking and appeared to have a stronger appetite for lick soil than Stone's sheep (Fig. 2.3, Table 2.3). Stone's sheep were often

observed bedded on the edge of a lick for up to an hour, apparently waiting to return to the alpine in a group. This suggests that the length of visits to dry licks by Stone's sheep is influenced by their gregarious behaviour. This behavioural tendency may have contributed to the higher variability in the relationships between time licking and length of lick visit, and consequently, the lower proportion of time spent licking by Stone's sheep than mountain goats. The conclusion that mountain goats have a stronger appetite for lick soil is also supported by anecdotal observations of mountain goats displacing sheep from high-use sites at lick areas. The stronger appetite for dry lick soil suggests that some aspect of mountain goat physiology or forage composition increases the appetite for dry lick soil over that of Stone's sheep. Mountain goats forage on a wider variety of plants than Stone's sheep that are less dependent on browse (Shackleton 1999). Throughout the spring and summer, we observed several mountain goats with signs of scouring (diarrhea) on their back legs. Hebert and Cowan (1971) also observed that mountain goats coming to a dry lick in southeastern BC were scouring. These observations imply that mountain goats may be particularly sensitive to the osmotic imbalance in the digestive tract that is thought to be associated with spring forage change (Kreulen 1985, Klaus and Schmid 1998). Mountain goats may require inorganic supplements from licks to buffer against such ailments (see Chapter 3) and maintain their adaptability to a wide range of spring forages.

The highly variable attendance and licking activity over time observed by Stone's sheep and mountain goats is difficult to interpret in terms of suggesting important periods of lick use. Combining the data from both remote trail cameras and observations of attendance, there appear to be similar bimodal peaks of dry lick use (early July, early August) common to both Stone's sheep and mountain goats. The first peak period (6 July) may partially reflect

physiological stress brought on by the late greening of alpine forage in comparison to vegetation at lower elevations. In mid-June, we observed the initial growth of several typical forage plants in alpine areas, which was 3 weeks before the observed increase in attendance by both Stone's sheep and mountain goats at dry licks. Maximum use by Dall's sheep in Alaska during 3 consecutive years at a well-used dry lick occurred 6 June, 19 June, and 27 June, with different maximums and periods apparently dependent on spring warming and snow melt (Heimer 1973). Collared Stone's sheep in BC, north of our study area, traveled down to forage in sub-alpine clearings in late April (Seip 1983). These reports imply that even with the late green-up in the spring of our study, the August peak in lick use that we observed was too late to be related to forage change.

Part of the variability in our results is likely due to the combining of both female and male animals for analysis. High use of licks by goats in Montana occurred during two separate peaks in late June for males and early July for females with yearlings and kids (Singer 1978). Dall sheep rams in Alaska used licks earlier (mid-May) than ewes (late June) (Heimer 1973, Tankersley 1984) and early spring rains forced Desert Bighorn (*Ovis canadensis mexicana*) ewes with lambs to travel to licks too early, significantly increasing predator-related lamb mortality (Watts and Schemnitz 1985). In our study area, both Stone's sheep and mountain goats traveled a minimum of 3 km over 700 m elevation change from their alpine foraging habitats to the dry licks on valley bottoms. The trails between the dry licks and the alpine consistently followed patches of rocky bluffs and cliff bands. Stone's sheep and mountain goats generally lamb during May or June (Shackleton 1999). The second peak in attendance (2-7 August) at licks may be due to females that have avoided traveling to the dry licks to reduce the threat of predation on their young and that may be

suffering from deficiencies in nutritional elements associated with lactation. This is supported by our observations of the largest groups of females with young of the year on 6-7 August. Although predators were never visually observed at any of the dry licks, remote trail cameras photographed three black bears (one in May and two in June) and a wolf (in June) on the trails to the dry licks, and what appeared to be an abandoned wolf den was found within 50 m of the top of one of the licks.

Recommendations for future research

Our observations on the use of licks by multiple ungulate species were collected during a single field season using several sampling techniques. Although additional field seasons might be useful for confirmation of our results, other multi-year studies have found that the variations in the timing of peaks in lick use among years were fairly consistent and did not change the proposed causal mechanisms that influenced the use of licks (Dalke et al. 1965, Fraser and Hristienko 1981, Tankersley and Gasaway 1983, Watts and Schemnitz 1985, Reisenhoover and Peterson 1986, Couturier and Barrette 1988).

We used data from both visual observations and remote trail cameras at two of the dry licks to document attendance by ungulates. Cameras tended to record less than half of the number of animals that observers documented. This discrepancy was likely due to the use of alternate trails as animals approached and left the lick. Moving the cameras further away from the licks, although reducing accessibility for researchers and increasing possible disturbance to animals on the trail, would likely improve the correlation of these two indices of lick use. Photographs from trail cameras did provide a more continuous hourly record, a more complete seasonal record during times when observers were absent, and an ability to recognize individuals and estimate frequency of lick visits. Additional research though is

needed using telemetered animals and/or numerous cameras to conclusively define frequencies of visits to licks by species and sex.

Our comparisons of the use of licks among the four ungulate species through the combination of scan and focal data suggested periods when elemental deficiencies and imbalances may influence lick use and indicated the relative intensity of the demand for lick soil among ungulate species. The field of nutritional physiology is limited in its understanding of the effects of chronic or marginal elemental deficiencies, requirements for various metabolic processes, and feeding strategies that improve intake (Robbins 1993). The use of licks by ungulates may be viewed as a strategy to improve the intake of elements, and alleviate the digestive ailments associated with the transition to spring forage change. This may be particularly important to animals in poor condition with increased susceptibility to acidosis (Kreulen 1985).

Species-specific intensities of licking behaviour may imply different demands for licks soils within foraging strategies. Our results suggest that supplemental elements and buffers are required by wild ungulates, especially elk and mountain goats, specifically during periods of forage change and lactation demands. We are currently directing research efforts towards characterizing soil samples from inside and outside lick areas as well as representative forage species (see Chapter 3). Additional experimental investigations are needed to more precisely quantify elemental requirements and metabolism of ungulates, and the nutritional value and health benefits of lick soils. The use of licks, however, is likely a complex function of physiology, diet, and tradeoffs with predation risk and other life history requisites.

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CHAPTER 3: CHEMICAL COMPOSITION OF LICK SOILS: POTENTIAL BENEFITS FOR UNGULATES²

Abstract

Perspectives on the importance of licks to ungulates have been broadened beyond the universal role of sodium previously attributed to ‘salt’ licks. Not all lick soils contain high sodium concentrations and other elements such as magnesium, buffering compounds such as carbonates, and binding agents such as clays, are concentrated in some lick soils suggesting that licks may serve multiple functions. This study examined the chemical compositions of three wet and three dry licks in the Tuchodi watershed of north-central British Columbia, and the potential benefits of licks to elk (*Cervus elaphus*), moose (*Alces alces*), Stone’s sheep (*Ovis dalli stonei*), and mountain goats (*Oreamnos americanus*). Soils sampled from 10 high-use, 10 low-use, and 10 control sites at each lick were analyzed for buffering compounds and extracted with solutions at a low, digestive tract pH to estimate available elements. The elemental composition of forage samples collected over an elevation range at three collection periods was analyzed to estimate dietary intake of elements. Soils at both wet and dry licks contained significantly higher carbonate levels relative to controls, suggesting that a common role of licks is to improve buffering capacity by adjusting pH of the rumen to minimize digestive disorders associated with spring forage change. Sodium was higher than controls only in dry lick soils, although water samples collected at inflows to wet licks also contained higher sodium concentrations than controls. Iron was consistently higher than controls in soil at wet licks, but not at dry licks. Magnesium was high in inflow water at both wet licks

² A version of this chapter will be submitted for publication with the following authorship: J.B. Ayotte, K.L. Parker, and J.M. Arocena.

sampled and in soil at two dry licks. Estimates of dietary sodium levels from forage analyses were below requirements of domestic and captive wild ungulates, suggesting that intake of sodium at both wet and dry licks helps meet demands. Magnesium and iron in lick soils may also supplement diets when elemental content of forage appears to just meet requirements. To assess the role of clay in lick soil, the buffering capacity of clay-filled fecal material collected at licks was compared with fecal material collected away from licks. Clay did not appear to be a major buffering component for ungulates using lick soils, but additional analyses are recommended.

Introduction

Areas where ungulates actively ingest soil have commonly been referred to as salt licks. This name implies that licks serve a universal role of supplementing diets with sodium. Sodium is the dominant cation in the body fluids of terrestrial animals and the potential exists, especially for herbivores, to become sodium-deficient (Robbins 1993). Wild ungulates have a strong attraction to sodium salts (Stockstad 1950, Dalke et al. 1965, Fraser and Reardon 1980) and many studies have reported elevated concentrations of sodium in lick material (Knight and Mudge 1967, Hebert and Cowan 1971, Weeks and Kirkpatrick 1976, Fraser et al. 1980, Fraser and Reardon 1980, Tankersley and Gasaway 1983, Tankersley 1984, Reisenhofer and Peterson 1986, Tracy and McNaughton 1995, Kennedy et al. 1995). The supposition that the use of licks is attributable to a universal function, however, is potentially refuted by the results from other analyses of lick soils showing low sodium contents and the presence of other elements (Chamberlain et al. 1977, Coates et al. 1990, Heard and Williams 1990, Dormaar and Walker 1996). Variation in chemical composition of

lick material suggests that licks may serve multiple functions for different species at different times of the year (Kreulen 1985). While considering mammalian adaptations to regulate sodium balance (Hoar 1983), and the potential stress associated with forage transition for ungulates in the spring, the relative importance of other elements such as magnesium (Heimer 1988), buffering compounds such as carbonates (Kreulen 1985), and binding agents such as clays (Klaus and Schmid 1998), has broadened our perspectives on possible reasons for the use of licks by ungulates.

Deficiencies in macro- and trace elements may not necessarily be a result of limited dietary intake, but rather a symptom of digestive disorders associated with spring forage change. The attendance at licks by many ungulate species appears to peak in the spring (moose (*Alces alces*), Tankersley and Gasaway 1983; elk (*Cervus elaphus*), Williams 1962, see Chapter 2; Dall's sheep (*Ovis dalli dalli*), Heimer 1973, Tankersley 1984; mountain goats (*Oreamnos americanus*) Singer 1978). This period coincides with the increased physiological demands of lactation, growth, and/or weight regain, which may be aggravated by electrolyte loss related to the stress of abrupt changes in forage chemistry. Two sources of physiological stress associated with adapting from highly fibrous winter diets to lush spring plant growth are: (1) a decrease in fiber and an increase in readily fermentable carbohydrates and proteins, which may alter rumen pH and impair proper microbial function, and (2) extremely high potassium levels, which may reduce the absorption and retention of other elements (Kreulen 1985, Klaus and Schmid 1998).

Ruminants exposed to sudden drops in dietary fiber produce less saliva, which is high in bicarbonates (Kreulen 1985). With less saliva, the buffering capacity of the rumen is reduced (Church 1975) and may lead to a drop in pH below optimal conditions for rumen

microbes, creating various intestinal ailments that reduce appetite and weight gain (Kreulen 1985, Klaus and Schmid 1998). Early season vegetation also contains concentrations of potassium that elevate the osmotic pressure of the digestive tract, interfere with fecal water absorption, and lead to potentially harmful electrolyte losses (Weeks and Kirkpatrick 1976, Kreulen 1985, Klaus and Schmid 1998). Wet, unformed feces from ungulates in spring often result from a diet of succulent new growth, and may be responsible for loss of physiologically important elements (Hebert and Cowan 1971, Jones and Hanson 1985, Heimer 1988).

Supplemental sources of carbonates during the transition to spring forage may help improve the buffering capacity of the rumen when saliva secretion is compromised (Kreulen 1985). Clay minerals, which also enhance buffering capacity, are composed of sheets of aluminium-silicate crystals, often with high cation exchange capacities (CEC) (Cairns-Smith and Hartman 1986). Within the inorganic fraction of soil, CEC is essentially due to the contribution by clay minerals, because there are very few cation exchange sites in the sand and silt fractions (Brady and Weil 1999). The benefits of specific clay minerals during spring forage change may be associated with the adsorption of potassium and short chain fatty acids to cation exchange sites, helping to adjust and maintain proper osmotic balance and pH of the rumen (Kreulen 1985, Klaus and Schmid 1998). Certain types of absorptive clays are also able to bind secondary plant compounds such as tannins (Johns and Duquette 1991) and improve digestibility and feed conversion in domestic animals (Smith 1992).

Studies on licks tend to focus on a single ungulate species using one type of lick (i.e., wet licks or dry licks). Attempts to compare the chemical composition of lick material across different types of licks in the context of the role of licks to different ungulate species are

made difficult because of different methods employed in soil sampling and analytical procedures (Klaus and Schmid 1998). In addition, sampling at both lick and control sites in many studies has been highly subjective. Lack of controls and overall low sample sizes prevented 8 of the 33 studies reviewed by Klaus and Schmid (1998) from using statistical tests to examine differences in the composition of lick soils. To represent available versus selected resources, control sites should remain in the same geological formation, but avoid seepage influences from the lick site (Kennedy et al. 1995). Subjectivity in the sampling of lick sites may be reduced by documenting the spatial use of licks by ungulates prior to soil sampling (see Chapter 2).

Another difficulty with comparing results from past lick research is the variability in the methods used for chemical analyses. Some studies failed to mention the extraction method applied (e.g., Hebert and Cowan 1971, Tracy and McNaughton 1995). Klaus and Schmid (1998) summarized the common extraction methods as (1) extracting the water soluble fraction, (2) extracting the water soluble fraction and the cations adsorbed to colloids with ammonium acetate (Stockstad et al. 1953, Fraser et al. 1980, Klein and Thing 1989, Kennedy et al. 1995, Bechtold 1996, Klaus et al. 1998), and (3) measuring the total elemental content of the soil with X-ray fluorescent analysis. Each method extracts a specific part of the sample, such that results from two different extraction methods on the same sample are not comparable. Many pre-treatments of soil material also may affect results by destroying and preventing detection of potentially important clay minerals (Kabata-Pendias and Pendias 1992). Very few studies have selected a pH for extraction solutions that is similar to the pH of absorption sites in the digestive tract (e.g., Mahaney et al. 1997).

The objective of this study was to determine the differences in chemical composition of lick soils within and among licks. Following behavioural observations of lick use by elk, moose, Stone's sheep (*Ovis dalli stonoi*), and mountain goats (see Chapter 2), we used consistent soil sampling and methods of analysis across multiple wet and dry licks in one watershed. The compositions of lick soil, primary forages, and fecal samples (comparing the loss of electrolytes between animals that had recently ingested lick material and those that had not) were incorporated with a review of elemental requirements, to examine the plausibility of several theories on the functions of licks. We assumed that (1) if periods of peak use at licks coincided with known periods of elevated physiological demands, (2) if forage content of specific elements was less than requirements, (3) if those elements were in greater concentration in lick soils than control sites, and/or (4) if lick soils contained buffering/binding compounds that might help accommodate spring green-up and plant defensive compounds, functions of licks would be clarified.

Methods

Samples of lick soil, forage species, and ungulate feces were collected in the Tuchodi watershed of Northern Rocky Mountains Provincial Park in north-central British Columbia (BC), Canada. A detailed description of the study area is found in Chapter 2.

Soil collection and analyses

Locations for soil sampling were determined following behavioural observations of elk and moose at two wet licks (Childers and Dead dog) and Stone's sheep and mountain goats at three dry licks (Lac-a-nookie, Standard, and Upriver), from 17 May - 11 August 2002 (see Chapter 2; Fig. 2.1). During 41, six-h observation shifts at two wet licks, and 58 shifts at three dry licks, scan samples of the lick area every 15 min were used to record

locations of all animals. All animal locations were plotted on a 4 x 4-m grid map of the lick area. The 4 x 4-m dimensions reflect the accuracy of an observer in nearby blinds recording animal locations. The boundaries of the licks were determined by the edge of exposed soil. Soil samples were collected between the end of July and early August to allow sufficient observations to establish the locations of high-use sites within the lick areas and to avoid disturbing the licks during peak use. Ten high-use, 10 low-use, and 10 control sites (Klaus and Schmid 1998) were sampled at each lick (see Appendix D); all sampling sites were 4 x 4 m. If there were more than 10 high- or 10 low-use sites at each lick, random selections were made. Control sites were exposed soil with no signs of use, sampled 10 m beyond the edge of the lick area, with sites spread evenly around the perimeter of the lick unless possible seepage influences were suspected. Soil was collected from a third wet lick (Grizzly) without prior observations of animal use and analyzed relative to lick and control sites.

Within each high-use, low-use, and control site, composite samples of 12 sub-samples were collected, and pooled to ensure a consistent sampling intensity among sites. Several high-use sites at dry licks, however, were sampled from isolated excavations smaller than 4 x 4 m. All composite samples from all sites weighed approximately 300 g. To describe a relative distribution of elements at licks, additional transect samples were collected at one wet lick (Childers) and one dry lick (Lac-a-nookie). At the wet lick, three parallel 192-m transects, spaced 8 m apart were established along the length of the lick. Five soil samples were collected at 48-m intervals along each transect. At the dry lick, 5 samples were collected at 8-m intervals along a single vertical 40-m transect at the center of the lick. A total of 200 soil samples were collected and analyzed.

Soil samples were air-dried in paper bags (Stockstad et al. 1953, Chamberlain et al. 1977, Klaus et al. 1998), ground lightly (Kennedy et al. 1995, Bechtold 1996, Dormaar and Walker 1996) with a glass rolling pin, and passed through a 2-mm sieve (Stockstad et al. 1953, Kennedy et al. 1995, Dormaar and Walker 1996, Klaus et al. 1998) to homogenize the sample prior to chemical analyses. Sub-samples of the fine soil fractions were used to determine: (1) pH, (2) carbonate equivalent, (3) cation exchange capacity (CEC), (4) available macro-elements (Na, Ca, Mg, K, P, and S) and trace elements (Fe, Mn, Cu, and Zn) at both pH 7 and pH 2.5, (5) total carbon and nitrogen, and (6) clay fraction and clay mineral type. Replicate sub-samples were analyzed from a random selection of the sample set to determine analytical error.

Soil analyses were conducted at the University of Northern British Columbia (UNBC) and the British Columbia Ministry of Forests Analytical Research Lab (ARL) in Victoria, BC. Soil pH, cations extracted at pH 7, clay fraction and clay mineral type were determined at UNBC. Cations and sulfur extracted at pH 2.5, total carbon and nitrogen, and the calcium carbonate equivalent of each sample were determined at the ARL. Determination of the CEC involved analyses at both UNBC and the ARL.

Soil pH was determined in 0.01 M CaCl₂ suspensions equilibrated overnight (Peech 1965). In the determination of pH, the soil-to-solution ratios varied from 1:2 to 1:4 (e.g., 5 g soil : 10-20 ml CaCl₂) due to the range in organic content of the soil samples (high- and low-use, controls).

The calcium carbonate equivalent was determined by acid neutralization procedure (USDA 1954) as an estimate of total carbonates. Soil CEC was determined by extracting samples with 1N ammonium-acetate adjusted to pH 7 (Kalra and Maynard 1991) to reflect

the pH of the rumen (5.5-7, Church 1975). Ammonium ions that had exchanged with the soil cations and saturated exchange sites in the soil were removed with acidified sodium chloride. This sodium chloride extract was used to determine the amount of ammonium ions with an autoanalyzer. The concentration of ammonium ions (meq/L) was used as an index to calculate the CEC (cmol(+)/kg). Soil cations (Na, Mg, Ca, K, Mn, Zn, Cu, Fe, Co) displaced by ammonium ions at pH 7 were analyzed by inductively coupled plasma-atomic emission spectroscopy (ICP-AES) (as done in most studies on lick soils; e.g., Stockstad et al. 1953, Kennedy et al. 1995, Bechtold 1996, Klaus et al. 1998).

The pH 2.5 soil extraction estimated the cations that may become available as the soil passes through the abomasum (pH ~2.5) just prior to the major sites of elemental absorption in the small intestine (Church 1975). We specifically used a pH 2.5 extraction solution to best represent the concentrations of elements that likely become available to the animal. All soil samples were analyzed for cations (Na, Mg, Ca, K, P, Mn, Zn, Cu, Fe, Co, B) using the Mehlich III procedure (Sen Tran and Simard 1993), because the pH of the extractant is very close to 2.5. Sulfur in the form of sulfate (SO_4) was the only anion extracted using a 500 ppm phosphorus method (Kowalenko 1993) with extraction solutions adjusted to pH 2.5. Total C and N were determined with a carbon and nitrogen analyzer.

Clay separations and identification of clay mineral types were conducted on a small sub-sample of soils. Three high-use and three control samples from one wet lick (Childers) and one dry lick (Lac-a-nookie) were separated into sand, silt, and clay fractions after pre-treating samples to remove organic matter and carbonates (Kalra and Maynard 1991). Slides of isolated clays were scanned with an X-ray diffractometer (XRD) using methods adapted from Whittig (1965). Clay slides were scanned to determine the presence or absence of

expandable clays (high CEC) by measuring the expansion of silicate clay layers with chemical and environmental (humidity) treatments. Bulk samples (containing all soil fractions) from one high-use and one control site at the representative wet (Childers) and dry (Lac-a-nookie) licks were scanned with the XRD to determine the mineral composition of the bulk sample.

Water samples from two wet licks (Childers and Dead dog) were collected during a return visit to the study area in July 2003. At each wet lick, three samples were collected from the inflow (apparent groundwater spring), the outflow, and from control sites (the closest body of water outside the lick) for a total of nine samples from each lick. Water samples were collected in 60-ml Nalgene bottles with a few drops of concentrated nitric acid added to preserve trace elements in solution for later analysis. The cations in each water sample (Na, Mg, K, Ca, P, Fe, Mn, Cu, Zn, Co, and Mo) were analyzed with ICP-AES.

Analysis of variance (Zar 1999) ($\alpha = 0.05$) was used to test for significant differences in the concentrations of each element extracted at pH 2.5 among high-use, low-use, and control sites at each lick area and in the concentrations of each element among inflow, outflow, and control water samples. Tukey's test of multiple comparisons (Toothaker 1993) was used as a post-hoc test to determine which sites contained significantly different concentrations of each chemical component. Statistica 6.1 (Statsoft Inc. 2002) was used for all statistical testing. All data are presented as $\bar{X} \pm 1 \text{ SE}$, unless otherwise noted.

Forage collections and analyses

Three collections of forage were made for each ungulate species: moose and elk forage was collected in early June, early July, and late July; Stone's sheep and mountain goat forage was collected in early June, mid-July, and early August. We attempted to collect six

species of preferred forage used by each ungulate species at three different elevation zones during each period. These plant species were identified previously as important in several local and regional studies (Table 3.1). Grasses and herbs were generally collected as whole plants, whereas leaves and twigs were sampled from browse species.

Forage collection areas in each elevation zone were selected using signs of recent ungulate presence (grazing/browsing, pellets, and tracks), mainly on south- and west-facing slopes. The lowest elevation zone (800-959 m) for collection of elk and moose forage was in the valley bottom near the wet licks, in stands of aspen/balsam poplar (*Populus* sp.) within the boreal white spruce (*Picea glauca*), and black spruce (*Picea mariana*) (BWBS) biogeoclimatic zone. The mid-elevation zone (1000-1150 m) was in young shrub/sapling communities in the BWBS, and the high zone (1250-1400 m) was in open poplar stands/upland shrub communities in the spruce, willow (*Salix* spp.), and birch (*Betula* spp.) (SWB) zone (Peck 1987). Collection areas for Stone's sheep and mountain goat forage began near the dry licks close to the valley bottom, in plant communities similar to those for elk and moose forage collections, but at slightly higher elevations and often near rock outcrops, with the highest zone (1400-1650 m) in alpine plant communities. Each forage sample from an elevation zone consisted of ~10 randomly chosen plants. Each sample weighed ~250 g to ensure a dry weight of 25 g for analysis (Ohlson and Staalnd 2001). Plant samples were air-dried in the field, and later oven-dried for 72 h at 40° C before being ground and sieved with a Wiley mill using a 0.25-mm sieve screen (Staalnd and White 2001). Plant samples were prepared for elemental analysis by microwave digestion using nitric acid and hydrogen peroxide (Kalra and Maynard 1991). Plant extracts were analyzed for macro elements (Na, Mg, K, Ca, and P) and trace elements (Fe, Mn, Cu, Zn, Co, and Mo) by ICP-AES.

Table 3.1. Primary forage and estimated percent composition of the diet for four ungulate species, based on local and regional sources. Data were not available to distinguish between spring and summer diets of moose and mountain goats.

Ungulate	Preferred forage	Composition of diet		Source*
		Spring	Summer	
Elk	<i>Populus balsamifera</i>	shrubs: 3%	shrubs: 33%	1
	<i>Rosa acicularis</i>	herbs: 7%	herbs: 50%	
	<i>Elymus</i> sp.	grasses: 90%	grasses: 17%	
	<i>Viburnum edule</i>			
	<i>Vicea americana</i>			
	<i>Bromus</i> sp.			
Moose	<i>Populus balsamifera</i>		<i>Salix/Betula</i> : 75%	2, 3
	<i>Salix</i> spp.		<i>Alnus/Cornus/Populus</i> : 20%	
	<i>Alnus</i> sp.		herbs: 5%	
	<i>Cornus canadensis</i>			
	<i>Betula papyrifera</i>			
	<i>Epilobium</i> sp.			
Stone's sheep	<i>Agropyron</i> sp.	grasses: 80%	grasses: 60%	4, 5
	<i>Zygodenus</i> sp.	herbs: 20%	herbs: 40%	
	<i>Oxytropis</i> sp.			
	<i>Poa</i> sp.			
	<i>Elymus</i> sp.			
	<i>Hordeae</i> sp.			
Mountain goat	<i>Agropyron</i> sp.		grasses: 5%	6
	<i>Artemesia</i> sp.		<i>Carex</i> : 20%	
	<i>Lupinus</i> sp.		herbs: 75%	
	<i>Carex</i> sp.			
	<i>Epilobium</i> sp.			
	<i>Festuca altaica</i>			

*Sources: 1 (Peck 1987), 2 (Singleton 1976), 3 (Cushwa and Coady 1976), 4 (Seip 1983), 5 (Luckhurst 1973), 6 (Hjeljord 1973).

To examine the elemental variability in each ungulate species' diet over time, data from all forage species, weighted by their proportion in the hypothetical diet (Table 3.1), were combined for each elevation zone as one dietary estimate. Analysis of variance ($\alpha = 0.05$) was used to test for significant differences in the concentrations of each dietary element among collection periods, and Tukey's test was used for post-hoc analyses (Zar 1999). During the early June collection period, plants were available (and therefore collected) only from low elevations, resulting in a single estimate of diet compared to three (low, mid-, and high elevations) for other collection periods. Accordingly, for elk and moose diets, *t*-tests (Zar 1999) were used to determine significant differences in elemental concentrations between the second (early July) and third (late July) collection periods. Data were also grouped across collection periods to examine patterns in elemental concentrations over elevation.

Fecal collections and analyses

Fecal samples were collected at lick areas (lick fecal samples) and from distances at least 2 km from licks (non-lick fecal samples). Fecal samples at lick areas were collected if they contained a noticeable amount of inorganic material (typically white or grey-coloured in fresh samples). Only fecal samples that appeared organic were collected away from licks and grouped as non-lick fecal samples. Each fecal sample consisted of material from one pellet group. Elk and moose pellets were distinguishable, but Stone's sheep and mountain goat pellets were grouped together. Most fecal samples from non-lick areas were collected during the summer (July 2003) following sample collections at licks. Differences in the concentrations of cations between lick and non-lick fecal material were tested with *t*-tests.

Because the CEC of digesta in the gastrointestinal tract of ungulates that have ingested soil is made up of both inorganic and organic contributions, analyses were conducted on both inorganic and organic components in the feces. Fecal samples were air-dried in the field, and later oven-dried for 72 h at 40° C before being ground and sieved (Wiley mill with 0.25-mm sieve). Five grams of each sample were left overnight in 1 *N* ammonium acetate at pH 7 solutions to extract cations and determine CEC with the same procedures used on soil samples. The extractions were analyzed for macro-elements (Na, Mg, K, and Ca) and trace elements (Fe, Mn, Cu, Zn, Co, and Mo) by ICP-AES. The concentration of ammonium in each extract was analyzed and used as an index to calculate the CEC.

To quantify the amount of organic matter in each fecal sample, a few mg of the remaining unextracted sample were reground with liquid nitrogen (rather than a mechanical grinder to conserve material because samples were small), and analyzed for total carbon with an elemental analyzer. The percent organic matter was calculated from the amount of total carbon (organic matter = 1.72 x percent carbon; Brady and Weil 1999) and used to estimate its contribution to the total CEC of the sample. The contribution of inorganic clay to an animal's buffering capacity was determined by the difference between total and organic CEC.

Results

The concentrations of all cations in soils are presented based on pH 2.5 extractions, which approximates digestive pH just prior to elemental absorption in the gastrointestinal

tract. Cation concentrations from pH 2.5 extractions were consistently higher than pH 7 extractions (see Appendix E: Figs. E.1, E.2).

Wet licks

There were no consistent patterns in the mean concentrations of soil components among the three wet licks (see Appendix F: Table F.1). For example, Childers lick soils contained twice the concentration of calcium, 10 times the concentration of sulphate, six times the CEC, and one third the copper concentration of Dead dog and Grizzly licks. Iron was the only chemical component significantly more concentrated in lick soil compared to controls at all three wet licks (Fig. 3.1). Significantly high sodium concentrations in lick soils were found at only one wet lick (Dead dog). Although soil at Childers lick was higher in sodium, differences were not significant ($P = 0.07$). Sulfate was significantly higher only in soils at Dead dog lick. At Childers lick, however, sulfate concentration was the only soil component to vary consistently along transects, with levels increasing along all three transects from the high-use (water inflow) end of the lick to the low-use end (water outflow).

Carbonate content was higher in soil from all wet licks, although not significantly at Grizzly lick ($P = 0.07$). The difference in carbonate concentrations among high-use, low-use, and control sites, however, was only large enough to detect in a post-hoc analysis at Childers lick. Compared to controls, total carbon and nitrogen content were significantly lower in soil at Childers and Dead dog lick (both $P < 0.009$), but not at Grizzly lick. The CEC was significantly lower in soils at Dead dog and Grizzly licks compared to controls ($P \leq 0.032$), but not at Childers lick (Fig. 3.1).

From analyses on a small sub-sample of all soil samples from Childers lick, the clay content of high-use soils was not significantly different than controls (high-use: $63.2 \pm$

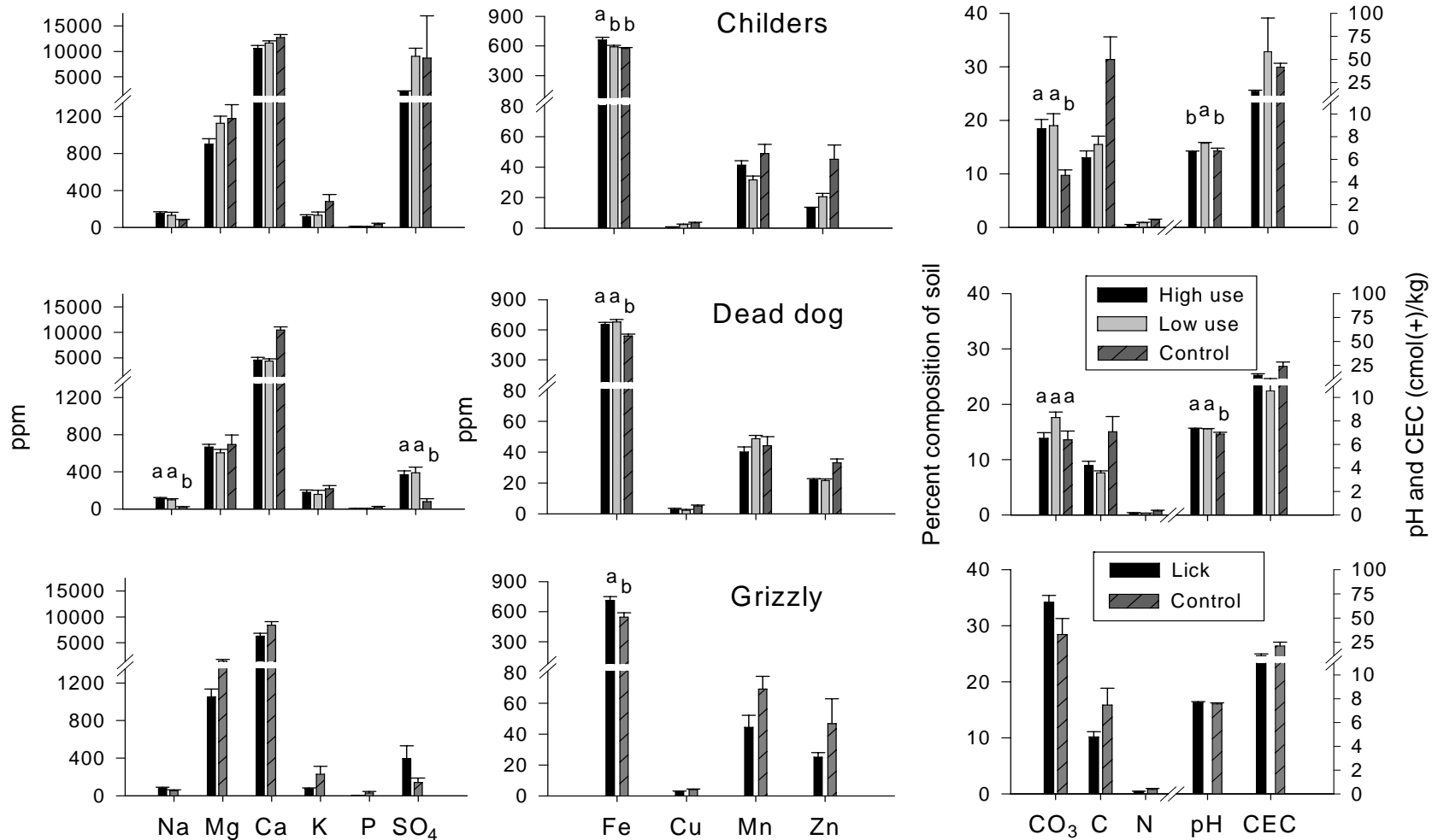


Figure 3.1. Chemical composition of soil samples from high-use, low-use, and control sites at three wet licks in the Tuchodi watershed, 2002. Data are presented as $\bar{X} \pm SE$ ($n = 10$ for each type of site). Cations were extracted at pH 2.5 using Mehlich III procedure. All elemental results are expressed on an oven-dry basis. Soil components with letters above bars were significantly different via ANOVA; within soil components, bars sharing the same letter were not different according to Tukey's multiple range test.

3.02%, $n = 3$; controls: $67.2 \pm 2.54\%$, $n = 3$). X-ray analyses of isolated clay fractions showed no differences in the type of clay mineral: both high-use and control samples contained mica, quartz, and chlorite. No expandable clays (high CEC) were present in any of these isolated clay fractions. XRD scans of bulk samples (not separated into inorganic fractions) showed mineral composition of mainly quartz (see Appendix G: Fig. G.1).

Elemental composition of water samples varied among and within licks (see Appendix H: Table H.1). Higher sodium concentrations were measured in inflows compared to outflows or controls at Dead dog (Fig. 3.2). The sodium concentrations in water entering Dead dog lick were five times higher than those at Childers lick where, in contrast, sodium concentrations were not significantly elevated above outflows or controls (Fig. 3.2). Magnesium, calcium, potassium, and molybdenum were all more concentrated in inflow and outflow water samples than control samples at both Childers and Dead dog licks. Iron, the only element consistently elevated in all wet lick soils, was more concentrated in water samples from outflows, but not inflows, at Dead dog lick, and not at all in lick water compared to control water at Childers (Fig. 3.2).

Dry licks

Concentrations of elements and compounds were relatively similar across all three dry licks (see Appendix F: Table F.2) except for sodium, zinc, carbonates, and CEC (Fig. 3.3). Soils from Lac-a-nookie and Standard licks, which are both steep gravel bluffs at the same elevation (see Study Area, Chapter 2), contained carbonates that were 10% higher, and concentrations of zinc and CEC that were one third lower than at the physically different (river bank) Upriver lick. Sodium concentrations in soils from Lac-a-nookie, however, were more similar to Upriver lick, and were nearly twice the levels at Standard lick.

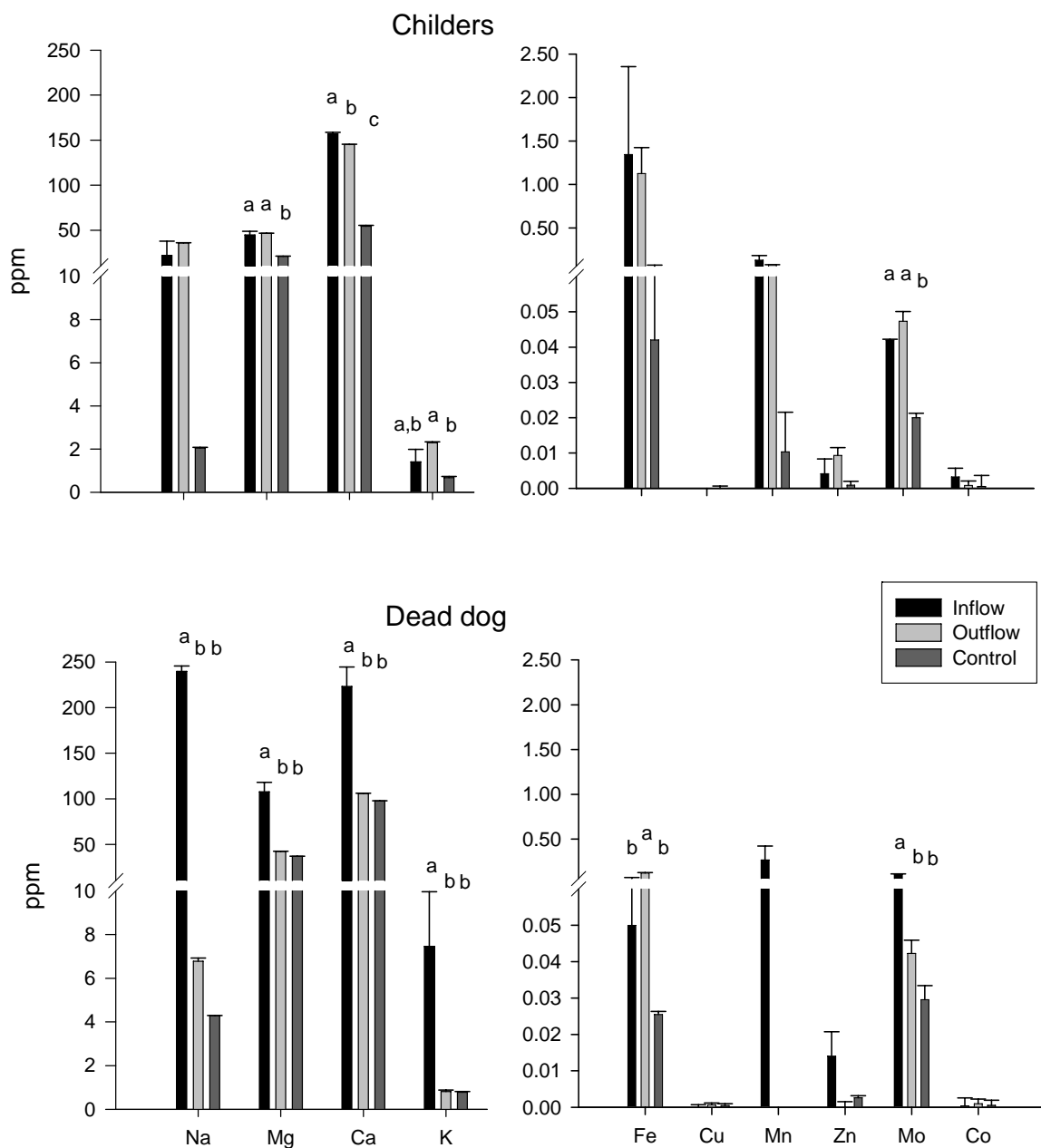


Figure 3.2. Elemental composition ($\bar{X} \pm SE$) of water samples collected at two wet licks ($n = 3$) for each inflow, outflow, and control) in the Tuchodi watershed, 2003. Elements with letters above bars were significantly different via ANOVA; within soil components, bars sharing the same letter were not different according to Tukey's multiple range test.

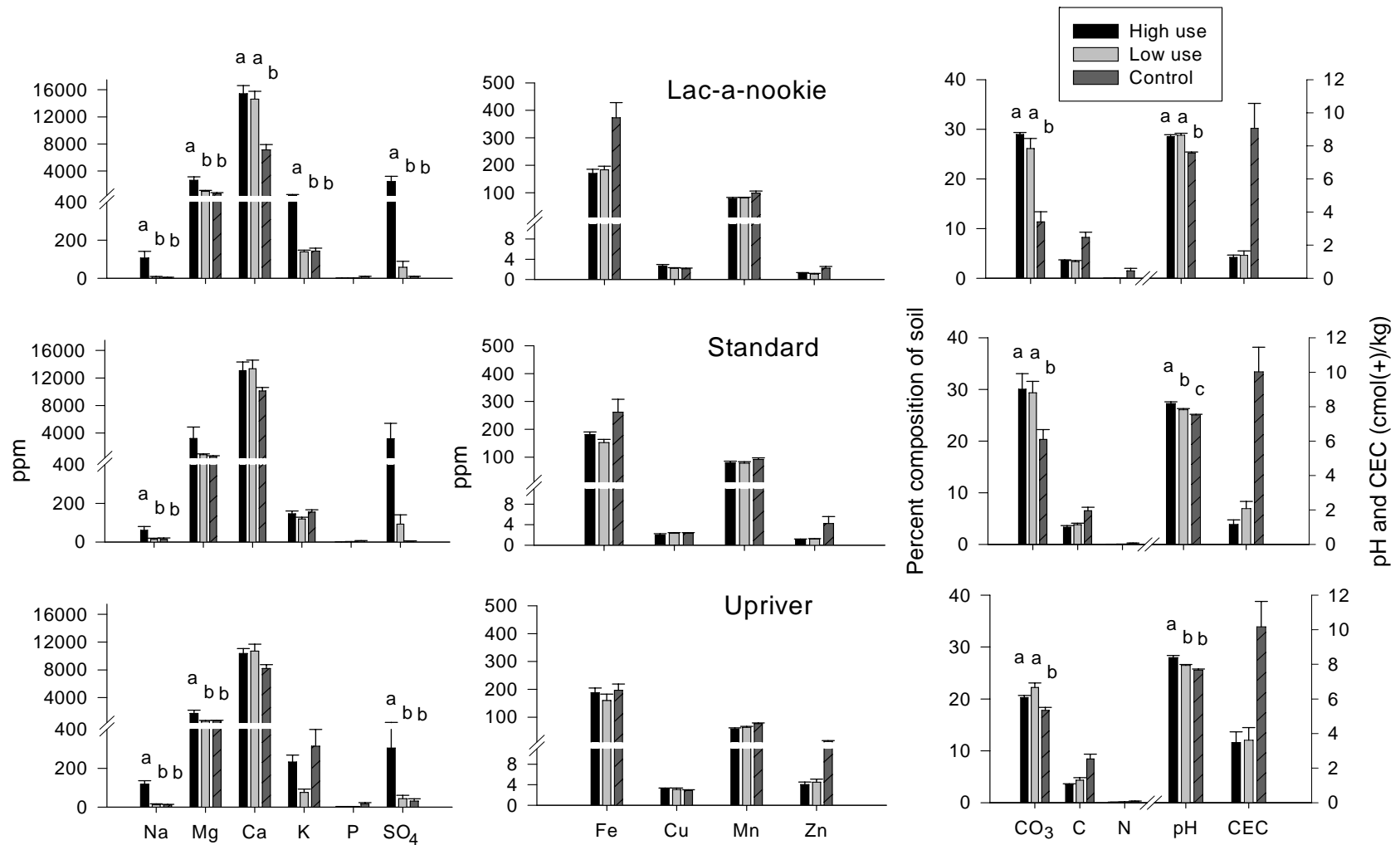


Figure 3.3. Chemical composition of soil samples from high use, low use, and control sites at three dry licks in the Tuchodi watershed, 2002. Data are presented as $\bar{X} \pm SE$ ($n = 10$ for each type of site). Cations were extracted at pH 2.5 using Mehlich III procedure. All elemental results are expressed on an oven-dry basis. Soil components with letters above bars were significantly different via ANOVA; within soil components, bars sharing the same letter were not different according to Tukey's multiple range test.

The chemical composition of soil from dry licks differed from that of wet licks. In contrast to consistently elevated iron levels in soil at wet licks, iron was less concentrated at dry licks than control sites. Concentrations of sodium and carbonates, as well as pH, were significantly greater than controls at all three dry licks (Fig. 3.3). Magnesium and sulfate concentrations were elevated at two of the dry licks (Lac-a-nookie and Upriver); calcium and potassium concentrations were higher than controls at only one lick (Lac-a-nookie). In contrast to the wet licks, the carbon, nitrogen, and CEC of soils from all three dry licks were significantly lower than controls (all $P < 0.004$). Over the single transect sampled at Lac-a-nookie lick, magnesium and iron increased, and the CEC of the soil decreased from the top of the lick to the bottom.

High-use soils analyzed from Lac-a-nookie lick contained more than twice the amount of clay as control samples (high-use: $49.7 \pm 0.67\%$, $n = 3$; control: $20.8 \pm 8.37\%$, $n = 3$; $P = 0.026$). There were no differences in the types of clay minerals present in the isolated clay fractions of high-use samples compared to controls. Quartz, mica, and chlorite were present in all samples, and no expandable clays with high CEC were found in any samples. X-ray scans of a bulk high-use and a bulk control sample (both from Lac-a-nookie lick) indicated that the soluble minerals dolomite ($\text{CaMg}(\text{CO}_3)_2$), calcite (CaCO_3), tamarugite ($\text{NaAl}(\text{SO}_4)_2(\text{H}_2\text{O})_6$), and bloedite ($\text{Na}_2\text{Mg}(\text{S}_4)_2\text{H}_2\text{O}_4$) were present in larger amounts in the high-use sample than the control (see Appendix G: Fig. G.1).

Forage

The differences in elemental concentrations of plants grouped by elevation zone were not significant (all $P \geq 0.08$). Consequently, data across elevations were combined in subsequent analyses (see Appendix I: Tables I.1, I.2). Statistical testing of the seasonal

elemental variation in elk and moose diets was limited by small sample sizes during spring forage collections in early June. The diets of elk, however, were high in potassium and sodium and low in iron during the spring forage collection period (Fig. 3.4). Levels of calcium, phosphorous, and manganese were significantly higher in elk forage in early July compared to late July (Fig. 3.4). No significant differences in elemental concentrations were observed in moose diets across the summer. Sheep diets were elevated in phosphorus and molybdenum in early June compared to mid-July, and in cobalt in mid-July compared to early August (Fig. 3.4). Mountain goat diets increased in calcium from early June to early August, and were higher in cobalt in early June compared to early August (Fig. 3.4).

Fecal samples

Only elk fecal samples were collected at wet licks. Samples from moose were too few to present in a comparison with non-lick samples. The presence of inorganic material in elk fecal samples collected at wet licks was not as obvious as the grey/white fecal samples from Stone's sheep and mountain goats collected at dry licks. Fecal samples that were collected at dry licks contained significantly more inorganic material than fecal samples from distances away from dry licks (at dry licks: $80.1 \pm 2.4\%$, $n = 22$; away from dry licks: $15.5 \pm 1.3\%$, $n = 10$; $P < 0.001$). In contrast, the inorganic content was not significantly different between samples collected at wet licks and those collected at distances away from wet licks (at wet licks: 14.4 ± 2.8 , $n = 6$; away from dry licks: 17.3 ± 4.5 , $n = 14$; $P = 0.68$) (Fig. 3.5).

The CEC of fecal samples decreased with increasing amounts of inorganic material (Fig. 3.5). The expected CEC contribution of organic material (297 cmol(+)/kg is the estimated CEC contribution for an organic soil type, Stevenson 1994) was higher

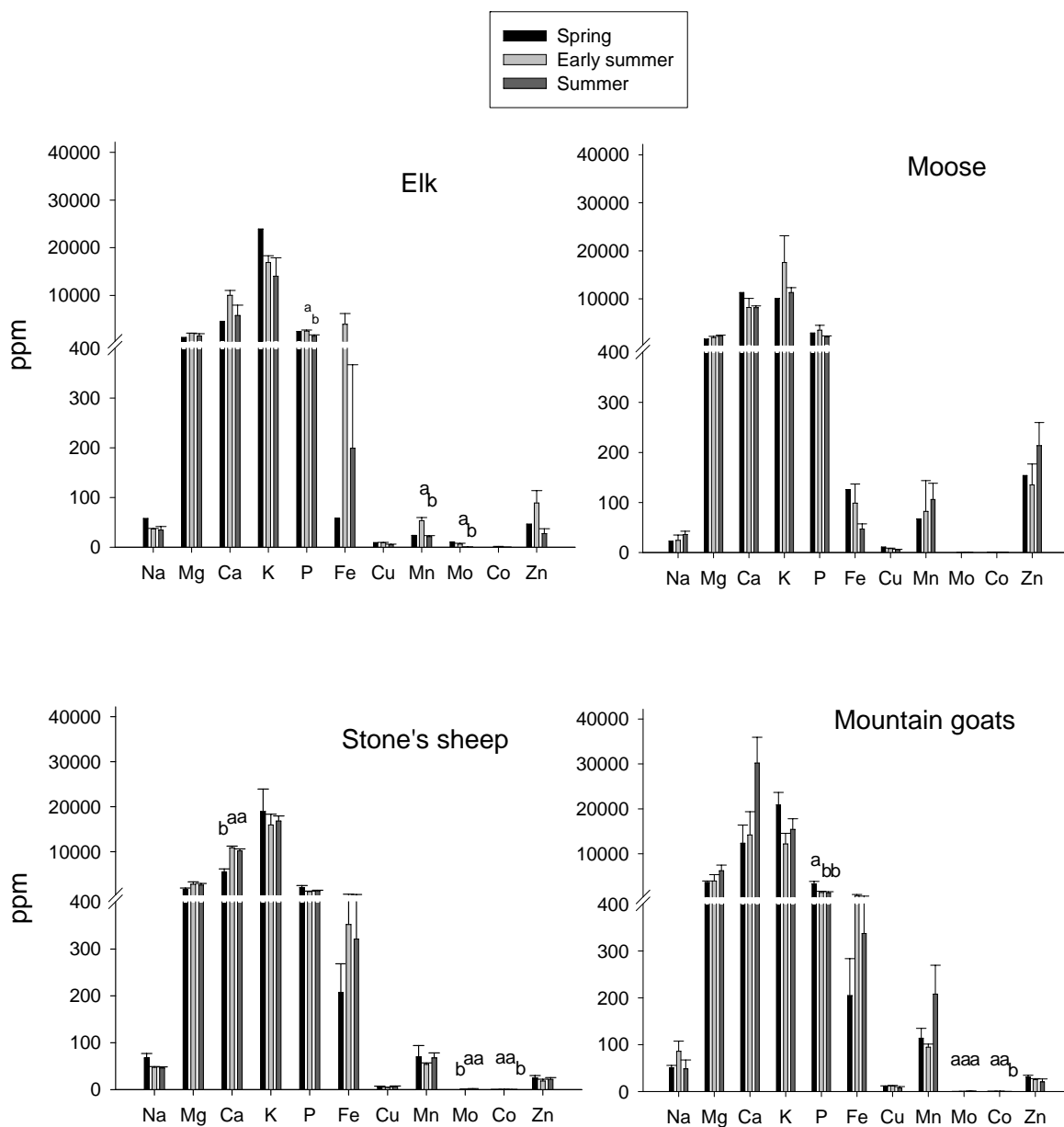


Figure 3.4. Elemental composition of ungulate diets based on preferred forages sampled in the Tuchodi watershed during three collection periods: spring (early June), early summer (early/mid July), and summer (late July/early August), 2002. Data are presented as $\bar{X} \pm SE$. Forage elements with letters above bars were significantly different via ANOVA; within soil components, bars sharing the same letter were not different according to Tukey's multiple range test.

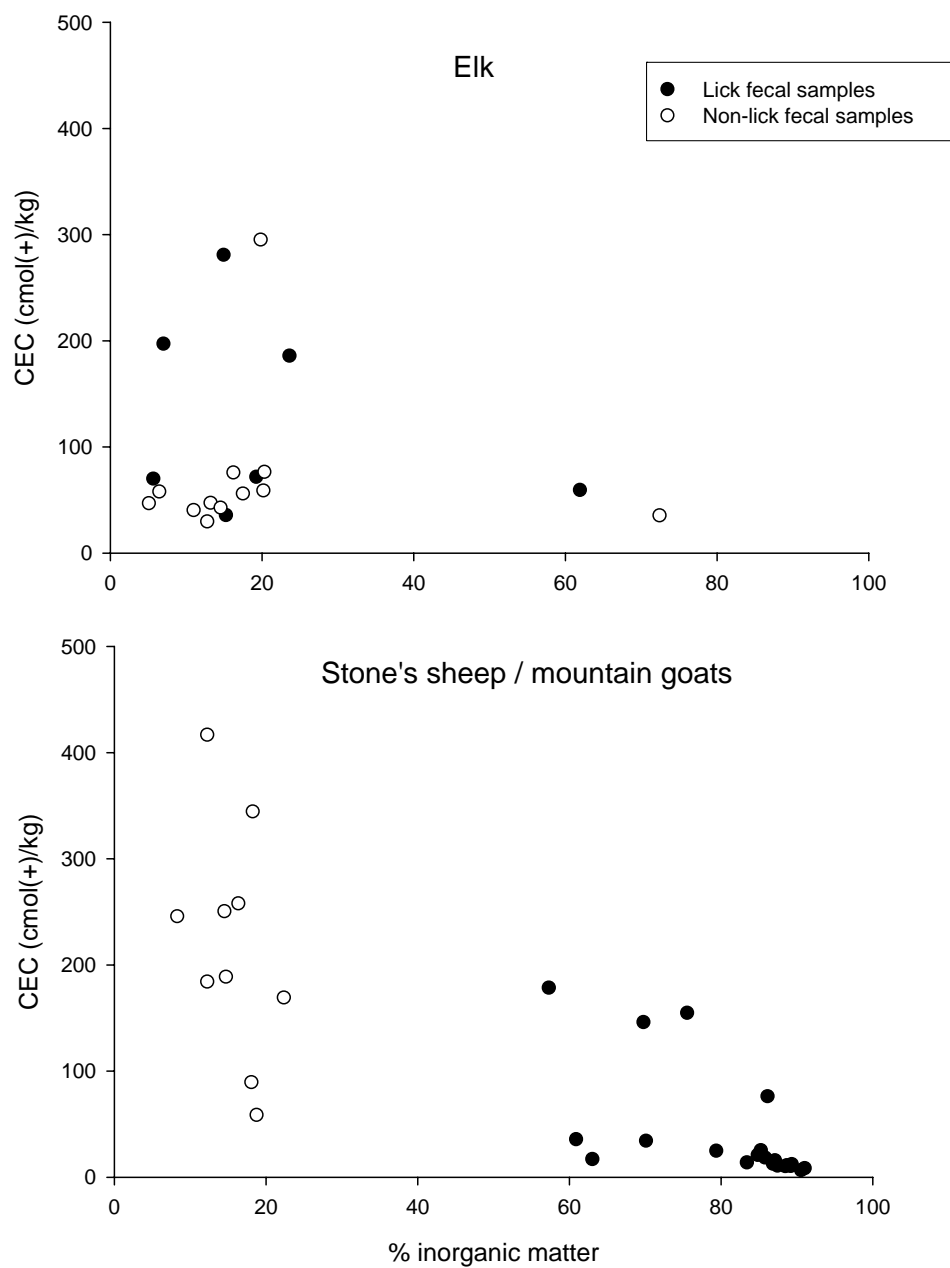


Figure 3.5. Cation exchange capacity (CEC) of ungulate fecal samples in relation to content of inorganic matter. Lick fecal samples were collected at two wet licks (top) and three dry licks (bottom) in the Tuchodi watershed, BC.

than the observed CEC (contributed to by both organic and inorganic fractions of fecal samples) of 17 out of 21 samples.

The concentration of sodium, calcium, and copper in feces collected at wet licks was significantly lower than feces collected away from licks (Fig. 3.6). Stone's sheep and/or mountain goat fecal samples collected at dry licks contained more iron, and less sodium, potassium, copper, zinc, and magnesium, although magnesium was not significantly less ($P = 0.067$) than non-lick fecal material (Fig. 3.6).

Discussion

The variation in composition of lick soils across studies has called into question a universal function of licks and supported the notion of licks serving multiple roles (Kruelen 1985). Our results, however, suggest some similarities in function across all licks in our study area. Carbonate content and pH were higher in soils from all six licks than from control sites (although not significantly at Grizzly lick, $P = 0.070$). The elevated concentration of carbonates in lick soils in the Tuchodi watershed implies that licks play an important buffering role in the rumen of ungulates during the transition each spring from fibrous winter forage to lush spring growth, as documented in other studies (e.g., Knight and Mudge 1967, Fraser et al. 1980, Bechtold 1996). Fluctuation in rumen pH is a critical factor in rumen microbiology, and salivary bicarbonates buffer against the rumen pH becoming too acidic (Church 1975). In both salivary bicarbonate (HCO_3^-) and the inorganic carbonates found in soils (CaCO_3 , $\text{CaMg}(\text{CO}_3)_2$), the hydrolyzing ability of CO_3^- contributes to the buffering capacity by neutralizing the acidity produced in the rumen (Brady and Weil 1999).

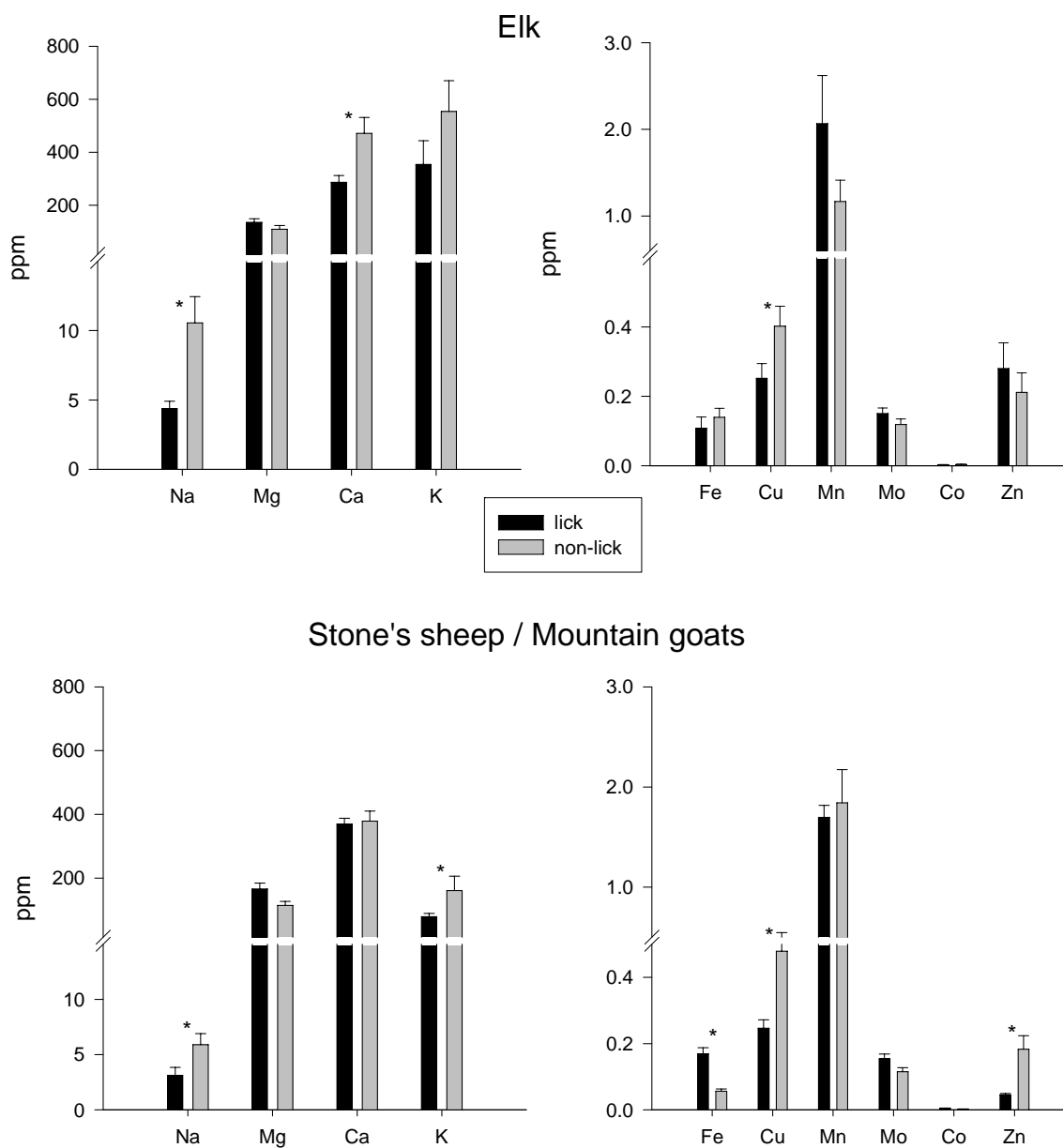


Figure 3.6. Cations extracted with ammonium acetate at pH 7 from fecal material (top: elk; bottom: Stone's sheep and mountain goats) collected at licks and from non-lick areas >2 km away from licks, June – July (2002/2003). Data are presented as $\bar{X} \pm SE$ (Stone's sheep/mountain goats: lick $n = 32$, non-lick $n = 17$; elk: lick $n = 15$, non-lick $n = 17$). Significant differences between lick fecal and non-lick fecal cation concentrations are indicated with * ($P \leq 0.05$).

A drop in rumen pH below optimum levels (e.g., ≤ 4.3 - 5.3 for domestic sheep; Church 1975) may cause a number of ailments such as depressed forage intake, diarrhea, and reduced absorption of macro- and trace elements that are in solution in the digestive tract (Kreulen 1985). The effectiveness of sodium bicarbonate (NaHCO_3) in alleviating acidosis and improving feed conversion and milk production in dairy cows on concentrate feed has been consistently noted in domestic ruminant research (Fisher and Mackay 1983). Susceptibility to the conditions of acidosis is also increased by poor condition (Kreulen 1985). Therefore, licks may be important for ungulates to minimize acidosis following spring forage change, especially for those individuals in poor condition following severe winters.

Clays did not appear to be important buffering components of soil at licks in our study area. Although the clay content in soil from the one dry lick analyzed was higher than control samples, the low cation exchange capacity in all lick soils, and the absence of expandable clays (e.g., smectite) in the XRD scans of clay fractions of soil from both wet and dry licks, suggest that clay minerals present in ingested soil do not contribute much to the buffering capacity in the rumen.

In our analyses of fecal material, only four samples had total CEC higher than the expected CEC contributed to by organic matter (based on the contribution of $297 \text{ cmol}(+)/\text{kg}$ by organic matter (Stevenson 1994)), implying that, in these samples, inorganic matter increased the samples' CEC. Within inorganic fractions, clay particles generally have far greater surface area with negative charge than sand and silt, therefore comprising the entire CEC of the inorganic fraction of a sample (McBride 1994). Clays such as smectites can contribute substantially (CEC of smectite clays: 80 - $150 \text{ cmol}(+)/\text{kg}$, Monger and Kelly 2002; CEC of organic matter: 134 - $297 \text{ cmol}(+)/\text{kg}$, Stevenson 1994) to the overall CEC of a sample

containing both organic and inorganic material. The relative contribution of organic matter, however, may confound our assessment of the contribution of clays. Decomposition of organic matter and its effect on particle size and surface charge, determine the contribution from organic matter to the overall CEC (Deng and Dixon 2002). The level of decomposition of the organic matter in fecal pellets is likely higher than organic matter in the rumen, where the buffering role of clay is considered important (Kreulen 1985, Klaus and Schmid 1998). In consideration of this, clay ingested from lick soil could still potentially contribute to the CEC and buffering capacity of rumen digesta, if the relative contribution of rumen organic material was low. In addition, the CEC and buffering capacity of organic matter declines more rapidly than expandable clays as pH is lowered (Brady and Weil 1999). Consequently, for individuals suffering from acidosis and low rumen pH (< 4.3-5.3, Church 1975), it may be possible to improve buffering capacity and adjust rumen pH by ingesting clay soils from licks.

Another possible role of ingested clay is the potential to bind secondary plant compounds such as tannins that decrease forage digestibility (Johns and Duquette 1991, Smith 1992). This would be most useful to species such as moose and mountain goats consuming significant amounts of browse and herbaceous forages that produce defensive compounds. Highest use of licks in mid-July by moose (see Chapter 2) would correspond with highest forage biomass and intake levels at this time. Similarly, use of licks may ameliorate the digestive ailments (i.e., soft, unformed diarrheic feces) frequently observed in mountain goats in mid-summer.

Concentrations of sodium and copper in fecal material from licks were less than non-lick fecal material. This suggests that individuals using both wet and dry licks excrete less

sodium and copper, and therefore, may be retaining these elements to ameliorate or prevent deficiencies. In contrast, Klein and Thing (1989) reported that several cations were elevated in fecal material collected near licks, which they believed reflected increased consumption of lick materials high in those elements.

Although there were no elements that were consistently elevated across all licks, there were several that were common to each type of lick soil. The significance of these elements may be explained by comparing soil and forage analyses with ungulate requirements. Because there are likely complex mechanisms whereby ungulates are able to balance their requirements of the 24 elements essential for growth and reproduction (Staal and White 2001), we used our forage analyses as estimates of general trends in the availability of elements in the diet.

Iron was significantly elevated in soil at all three wet licks. High iron levels in lick soils were also noted by Klein and Thing (1989), Tracy and McNaughton (1995), and Dormaar and Walker (1996). Elk diets contained the lowest concentration of iron in early June, although this estimate of dietary iron was based on only one sample (one composite sample of five forage species) (Fig. 3.4). This spring period also coincided with observed peaks in the use of wet licks by elk (end of May, late June; see Chapter 2), although the dietary concentration of iron at this time (58.4 ppm, Fig. 3.4) appeared to meet maintenance and lactation requirements (27-45 ppm, Table 3.2). Iron concentrations in moose diets tended to be lowest in late July, which also corresponded to the period of peak lick use (Fig. 3.4; see Chapter 2). Estimates of iron content in moose diets (46.9 ppm) appeared to meet proposed requirements for maintenance reported for other wild ungulates (27-45 ppm), but were slightly below requirements of cattle (50 ppm, Table 3.2).

Table 3.2. Estimated elemental (iron, sodium, magnesium) requirements as a component of dry matter intake (ppm) of captive wild and domestic animals. Requirements for lactation and antler growth include maintenance demands.

Element	Ruminant	Maintenance	Lactation	Antler growth	Source*
Fe	grazers / browsers	27-45			1
	454 kg beef cow	50	50		2
	domestic lambs	25-40			3
Na	grazers / browsers	500-1600			1
	454 kg beef cow	600-800	1000		2
	domestic sheep	2500			4
	<i>Odocoileus virginianus</i>			136	5
Mg	grazers / browsers	900-1800			1
	454 kg beef cow	1200	1700-2000		2

*Sources: 1 (Lintzenich and Ward 1997), 2 (NRC 1996), 3 (Underwood 1977), 4 (Church 1975), 5 (Hellgren and Pitts 1997).

Iron deficiencies are not problematic in domestic ruminants (Church 1975), but soil ingestion provides some wildlife species such as pronghorn (*Antilocapra americana*) and black-tailed jackrabbits (*Lepus californicus*) with ~80 % of their total iron intake (Robbins 1993). Iron content of milk can range up to 15 times more concentrated in the milk of wild ungulates than in domestic cattle (Robbins 1993). Estimated iron requirements of dairy cows during gestation and lactation are 50 ppm (Table 3.2). Deficiencies in pregnant and lactating females do not appear to affect iron status of the suckling young (Underwood 1977), implying that there are metabolic adaptations to low iron intake that ensure adequate supply of iron to the newborn. Soil at wet licks in the Tuchodi watershed may be an important source of iron for elk and moose.

Sodium in soil was significantly elevated above controls at all three dry licks and one wet lick (Dead dog lick). At that wet lick, the highest use areas were also associated

with water inflows having the highest sodium concentrations measured (240 ppm). At the dry licks, where Stone's sheep and mountain goats were observed ingesting soil from isolated pockets, high-use sites contained significantly higher sodium than low-use sites and controls. Chemical differences between high- and low-use sites at wet licks were not detectable due to the effects of soil mixing, movement of water through the lick, and the absence of the isolated pockets. Elevated concentrations of sodium in lick soils have been reported frequently (e.g., Jones and Hanson 1985, Bechtold 1996, Dormaar and Walker 1996).

Estimates of the sodium required by captive ungulates as a component of dry matter intake (136-1600 ppm; Table 3.2) are much greater than the average concentrations of sodium (<86 ppm) measured in the diets of the four ungulate species in our study area. Sodium demands are increased by 40% of predicted maintenance requirements during early lactation (Staaland et al. 1980), corresponding with periods of highest use of wet licks by female elk (late June; see Chapter 2). If sodium levels are low in diets during most of the year, females may visit licks when predator threats to young are minimized, as potentially exemplified by Stone's sheep and mountain goats that tended to use dry licks later in the summer (early July/early August; see Chapter 2). Sodium demands of antlerogenesis are small compared to those of lactation (sodium concentration of antlers is 0.45-0.49%; Hellgren and Pitts 1997), although the increased demand (especially during the latter half of the antlerogenesis period when growth is highest; Bubenik 1982) may precipitate sodium deficiency in some male cervids, stimulating lick use. The strong selective appetite for sodium shown by wild ungulates (Stockstad 1950, Dalke et al. 1965, Fraser and Reardon 1980) implies an adaptive response to sodium stress in which depleted sodium pools may be replaced by short periods of high intake (Staaland et al. 1980). The high sodium

concentrations in dry lick soils (60-120 ppm) and in water entering wet licks (22-240 ppm) suggest that licks provide this important source of sodium.

As well as dietary deficiencies, sodium stress may be influenced by high levels of potassium in forage that inhibit the retention of sodium and other elements in solution in the fecal tract (Kreulen 1985). Staaland et al. (1980) found that lowest plasma sodium levels in reindeer (*Rangifer tarandus*) were associated with summer (late May to mid October) forage high in potassium and low in sodium. Sodium deficiencies may be aggravated if the sodium to potassium ratio in saliva ranges below 1.4:1 to 1.6:1 (Staaland et al. 1980). The ratio of sodium to potassium in the diets of all ungulate species in our study was $< 0.004:1$. Although not directly related to saliva production, this ratio implies a potential osmotic imbalance that supplemental sources of inorganic material from licks could alleviate. Supplementing domestic sheep feed with calcium carbonate (CaCO_3) has been shown to elevate urinary potassium excretion (Yano et al. 1979), reducing the inhibitory effects on sodium. Zeolite and smectite clay minerals (with a strong affinity for potassium; Brady and Weil 1999) have been shown to alleviate potassium imbalances by stimulating potassium excretion (Kreulen 1985). X-ray analyses on a larger number of soil samples from each lick are needed before ruling out the presence of these clay minerals and their potential importance to ungulate species using licks.

Sulfur in the form of sulfate was significantly concentrated in lick soil at one wet lick and two dry licks (Fig. 4). Concentrations of sulfate in lick materials have rarely been reported (Heard and Williams 1990). Sulfur comprises 4-5% of hair and wool and is an important element in rumen microbe metabolism (Church 1975). Sulfur deficiencies are associated with deficiencies in sulfur-containing amino acids (methionine and cysteine;

Robbins 1993) that may cause decreased appetite and milk production, and poor pelage (Church 1975). The concentration of sulfate (an anion) in forage samples was not able to be detected by the ICP-AES analysis for cations. It is possible that sulfate was elevated in lick soil due to the dissolution of sodium sulfate minerals, further confounding which elements are most attractive and beneficial to ungulates using lick soil. In soil from a high-use site at a dry lick, X-ray analyses detected the presence of sodium sulfate minerals such as tamarugite and bloedite not found in the control.

Magnesium was elevated in water flowing into the wet licks (close to the high-use sites) and in soil at two dry licks (Lac-a-nookie and Upriver). Elevated concentrations of magnesium are common in lick soils across North America (e.g., Heimer 1988, Jones and Hanson 1985, Bechtold 1996). The inaccessible form of stored magnesium in the mammalian body (70% in bone, Robbins 1993) and the common occurrence of grass tetany (low serum magnesium) in domestic livestock (Heimer 1988), support the importance of a supplementary source of magnesium. Estimates of dietary magnesium for the ungulate species in our study (1187-6221 ppm, Fig. 3.4) may meet requirements (900-2000 ppm, Table 3.5), but other dietary properties of spring forage, particularly high potassium levels, can affect the absorption of magnesium, causing symptoms of grass tetany (reduced appetite and digestibility, and reluctance to stand; Church 1975) especially in lactating ungulates in the spring (Robbins 1993). Therefore, lick soil and water may be an important source of magnesium during the transition to spring forage.

Ingesting soil from licks may be a fundamental component of the foraging strategies of wild ungulates in north-central BC. Given that the use of licks is high following spring green-up as well as during periods of high lactation demands (see Chapter 2), that sodium in

forage is below dietary requirements, and that sodium and carbonates are in higher concentrations in lick soil/water compared to controls, the role of licks for ungulates may be both as a source of sodium and as a source of carbonates important in the stabilization of rumen pH following forage changes in spring. Wet licks appear to play an important role in supplementing elk and moose diets with iron. High concentrations of magnesium may also be useful to ameliorate high levels of potassium in spring forage. Although the presence of expandable clays was not detected, we suggest that further analyses of clay in lick soils should be pursued, in view of the role of clay in the foraging strategies of other herbivores to improve palatability and digestibility (Diamond 1999, Krishnamanj and Mahaney 2000), and the use of licks by ungulates later in the summer (see Chapter 2) when secondary plant compounds in forage are likely high.

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CHAPTER 4: IMPLICATIONS FOR NORTHERN ROCKIES PROVINCIAL PARK

Since the construction of the Alaska Highway in the 1950's, guide outfitters and their clients have flown into the Tuchodi watershed primarily during the fall hunting season (Peck 1987). Boat access to the Tuchodi Lakes by resident hunters and other recreationists has increased during the past 10 years with improved design and construction of jet-powered riverboats. With increasing human use of the area, and the proximity of licks to the Tuchodi River and Lakes, there is potential for detrimental disturbance.

The following estimated periods of important lick use are based on intensive behavioural observations from 24 May – 12 August 2002 in the Tuchodi watershed, and incorporate both attendance numbers and licking behaviour data (see Chapter 2). Those periods of high-use may change with the timing of spring green-up, and consequently, high use before or after those dates might occur. In general, elk exhibited a stronger demand for wet lick soil than moose. High use for elk occurred at the end of May and again at the end of June. The spring use of licks by elk likely was related to a combination of the need to adjust rumen pH with carbonates during spring forage change, and the increased sodium and iron demands associated with lactation. There was a more pronounced use of wet licks by moose later in the summer, appearing to increase across July. This period was probably too late to be influenced by digestive ailments associated with spring forage change, and could be a response to low dietary levels of sodium and iron, or increased plant secondary compounds (e.g., tannins) typically elevated in moose forage later in the summer.

Data on the use of dry licks by Stone's sheep and mountain goats were highly variable across the months of this study. With the incorporation of photographs from remote trail cameras at the dry licks, early July appeared to be an important period of lick use by

mountain goats and Stone's sheep, possibly influenced by the late green-up of alpine forage. There was a second peak in the use of dry licks by both species in early August. Sodium demands of lactating females of both species may have influenced lick use when travel from the alpine to licks at lower elevations was within an acceptable level of predation risk.

Carbonates were elevated in soil across all licks in the study area (see Chapter 3). The use of carbonates in lick soil to minimize the effects of digestive acidosis, and the suggestion that poor condition increases susceptibility to acidosis (Kreulen 1985), implies that access to licks may allow weak individuals an opportunity to improve their poor condition in a relatively short amount of time. Therefore, licks may provide a means for ameliorating digestive imbalances and elemental deficiencies that may indirectly result in increased mortality through opportunistic factors that may follow poor health (e.g., predation) (O'Hare et al. 2001).

The theory that animals in poor condition often use licks may partially explain the lack of clear peaks in the timing of lick use observed in the Tuchodi watershed. In a study on the elemental composition of moose hair, Franzmann et al. (1975) suggested that although there are periods of peak condition common across populations of moose, consistent peaks in the timing of elemental deficiencies should not be expected because of the presence of many variables influencing the availability and selection of forage during poor foraging seasons. Similarly, symptoms of acidosis could be expected to develop to a threshold that stimulates travel to licks, with some temporal variability if individuals of a population are in significantly different body condition.

From May to August 2002, my field assistants A. Anderson, P. Hirshfield, and M. Shook, and I kept a daily record of riverboats traveling on the Tuchodi watershed between

the Childers creek confluence and the upper Tuchodi Lake. These observations suggest two peaks in riverboat use in this area (Fig. 4.1). During the first peak in use (6-16 June), the river volume was increasing quickly and was likely the first time that spring that riverboat enthusiasts were able to access remote watersheds such as the Tuchodi. Boats were observed sporadically through July with many resident hunters taking advantage of high water to haul heavy camp supplies into hunting camps. Another peak in the number of riverboats was observed on 16 August with the opening of hunting season for cervids. The most likely periods when human and animal presence overlap are at the end of June during high use of wet licks by elk, and in early August during high use of dry licks by Stone's sheep and mountain goats (see Chapter 2).

On one occasion, we were changing film in a remote trail camera at a dry lick above the upper Tuchodi Lake when a riverboat passed below (~300 m away, in clear sight of the lick). Several Stone's sheep at that lick did not change behaviour as the boat passed. In contrast, during one of our observation shifts at a well-used dry lick located along the bank of the Upper Tuchodi River, a riverboat passed within 10 m of the lick. Before the boat came into view of the lick, all animals (Stone's sheep and mountain goats) left the lick and did not return during the remaining 3.5 h of our shift, even though the sound of the boat engine had faded. Therefore, there is some level of anthropogenic disturbance to ungulates using licks close to the river.

Additional research on licks in the Tuchodi watershed may be useful to confirm our results and expand on the findings from this thesis. For instance, the low sample size for moose recorded in our observations between 24 May and 19 July (see Chapter 2) suggests

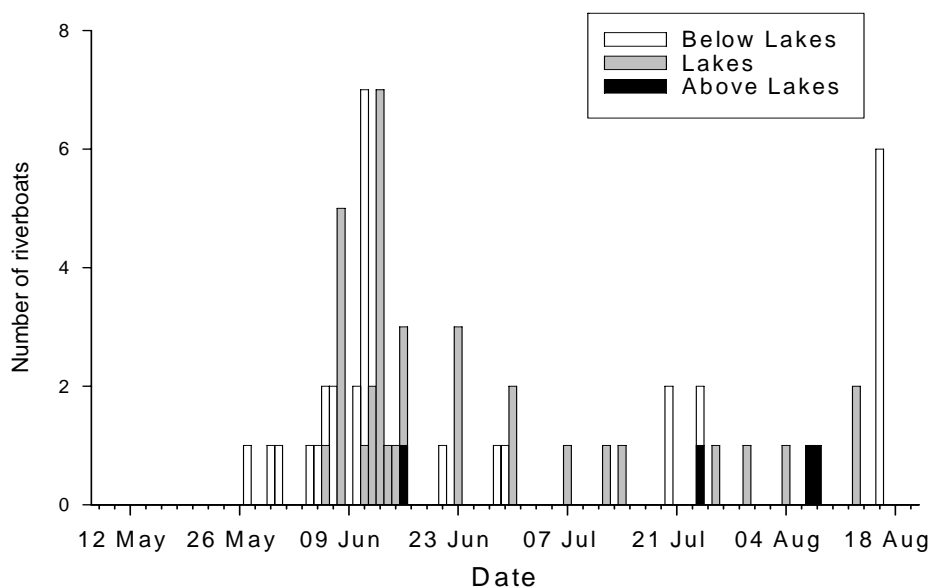


Figure 4.1. Observed riverboat presence in the Tuchodi watershed (above Childers Creek confluence), May – August 2002.

several alternative possibilities for lick use (nocturnal use, very early spring use, or use of smaller licks in the area). Radiocollaring individuals would provide valuable information on frequency of lick use by each ungulate species, and may provide insights into ‘new’ licks. Multiple field seasons would confirm whether peak timing of lick use among years was consistent, and longer field seasons might assess the potential impact of hunter presence on lick use. Although data might also be gained from remote trail cameras, the scope of this information is limited. Our understanding of the niche requirements involving the use of licks by four different ungulates species was advanced more by maintaining crews in the Tuchodi watershed for a continuous field season.

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Appendix A: Attendance by ungulate species and sexes at wet and dry licks in the Tuchodi watershed, May – August 2002.

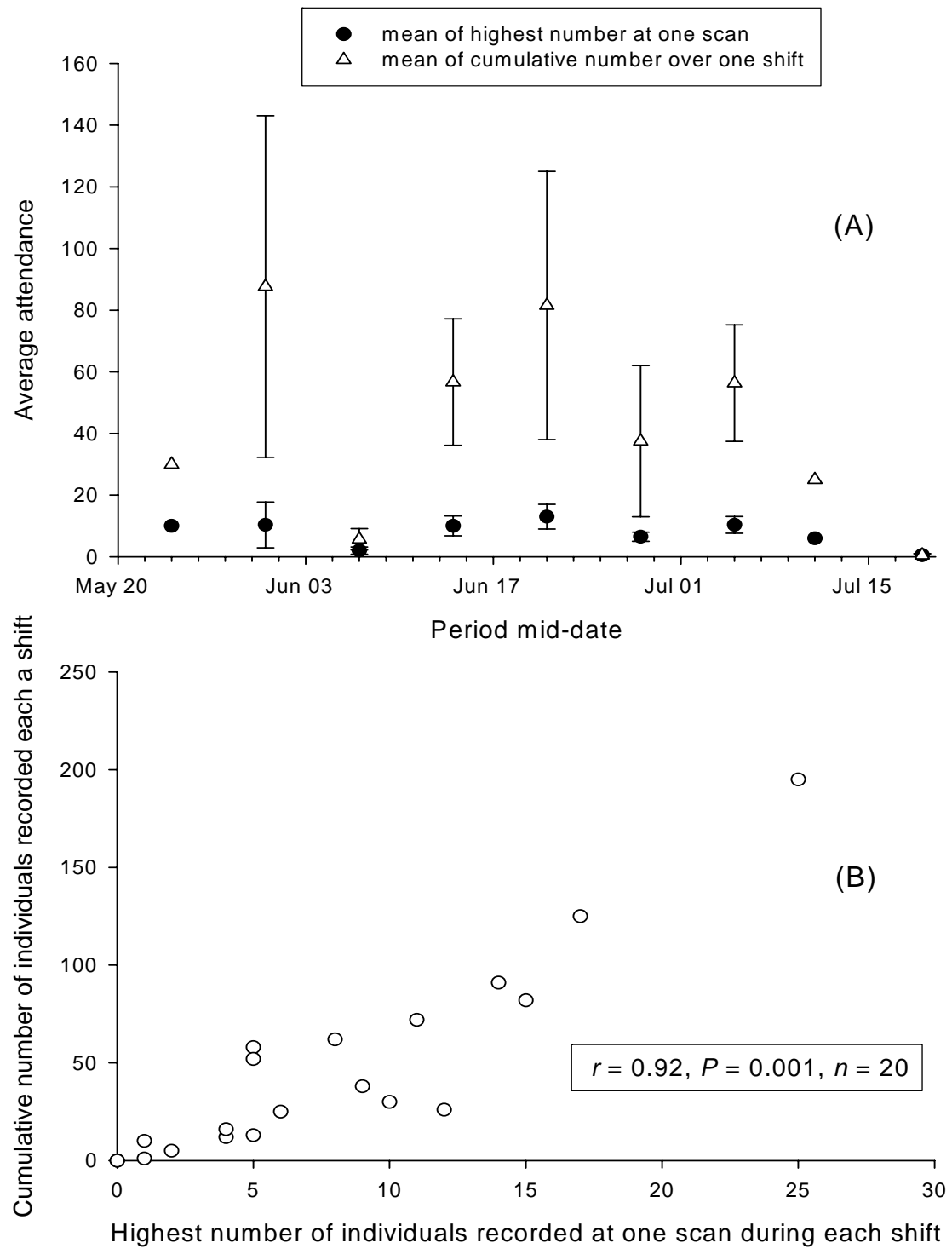


Figure A.1. Attendance ($\bar{X} \pm SE$) by female elk at Childers lick (May – August 2002), as measured by two indices of use (cumulative number of individuals observed during each 6-h shift, and the highest number of individuals observed at one scan during that shift) averaged over consecutive shifts (A), and the relationship between the two indices during each shift (B).

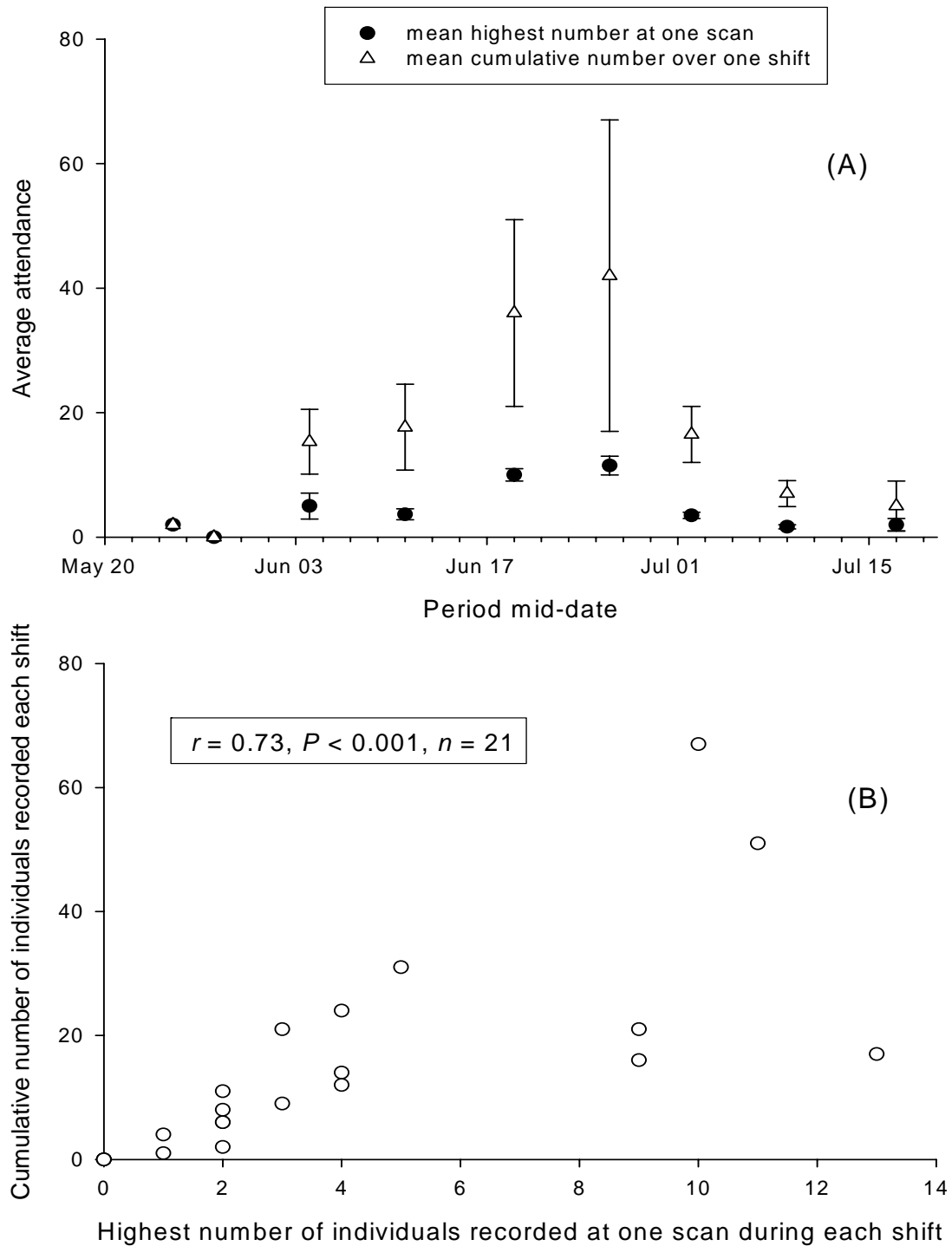


Figure A.2. Attendance ($\bar{X} \pm SE$) by female elk at Dead dog lick (May – August 2002), as measured by two indices of use (cumulative number of individuals observed during each 6-h shift, and the highest number of individuals observed at one scan during that shift) averaged over consecutive shifts (A), and the relationship between the two indices during each shift (B).

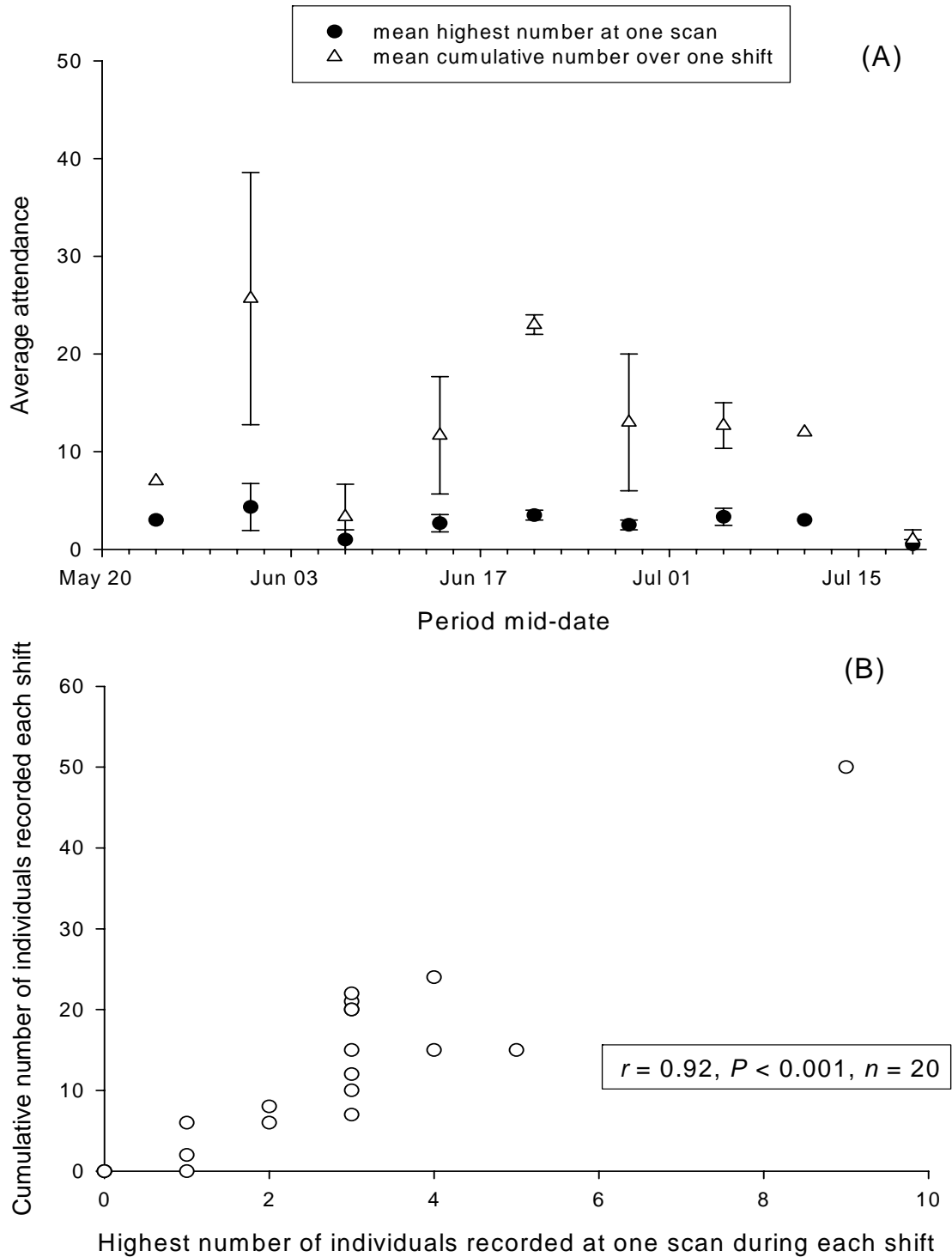


Figure A.3. Attendance ($\bar{X} \pm SE$) by male elk at Childers lick (May – August 2002), as measured by two indices of use (cumulative number of individuals observed during each 6-h shift, and the highest number of individuals observed at one scan during that shift) averaged over consecutive shifts (A), and the relationship between the two indices during each shift (B).

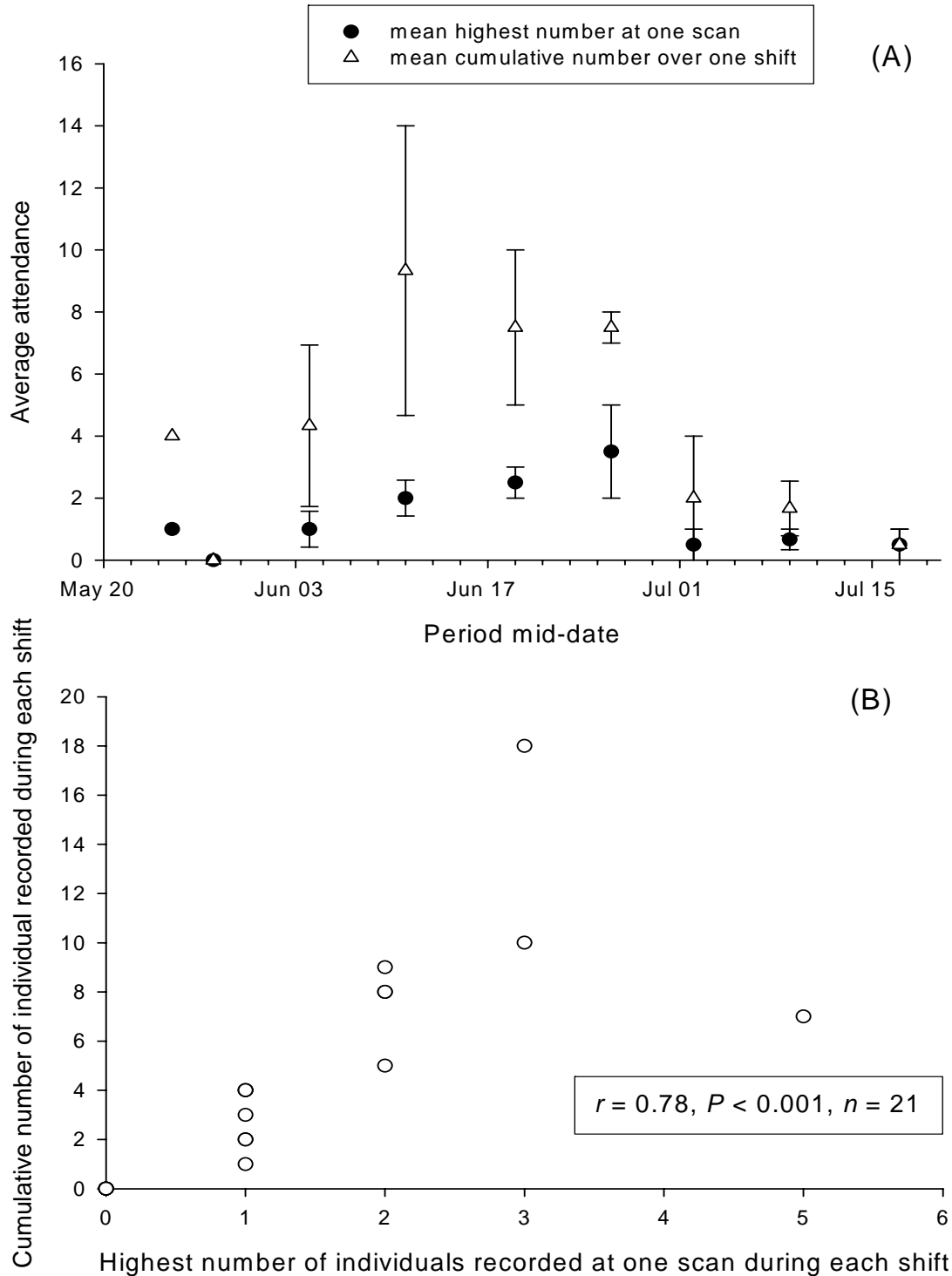


Figure A.4. Attendance ($\bar{X} \pm SE$) by male elk at Dead dog lick (May – August 2002), as measured by two indices of use (cumulative number of individuals observed during each 6-h shift, and the highest number of individuals observed at one scan during that shift) averaged over consecutive shifts (A), and the relationship between the two indices during each shift (B).

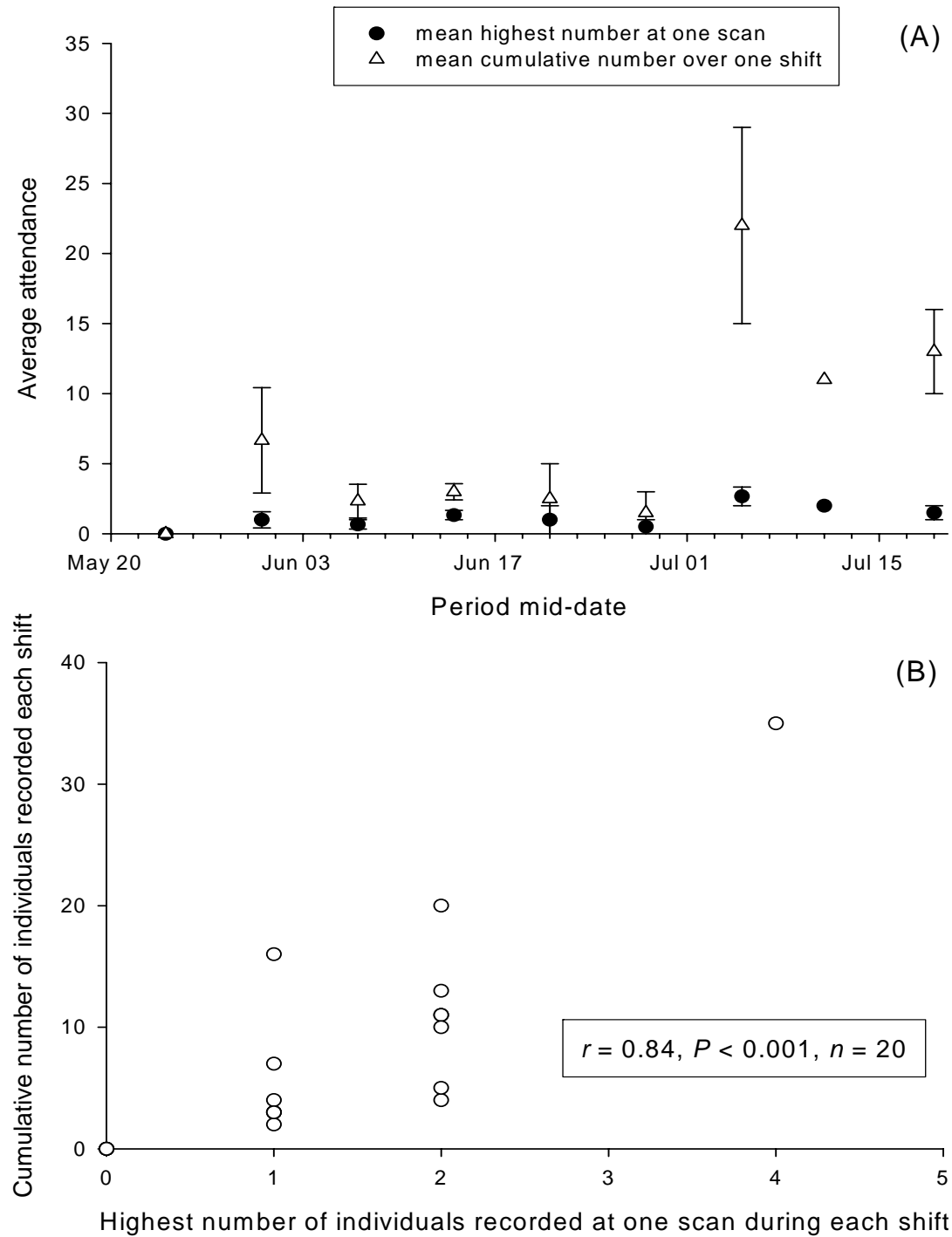


Figure A.5. Attendance ($\bar{X} \pm SE$) by female moose at Childers lick (May – August 2002), as measured by two indices of use (cumulative number of individuals observed during each 6-h shift, and the highest number of individuals observed at one scan during that shift) averaged over consecutive shifts (A), and the relationship between the two indices during each shift (B).

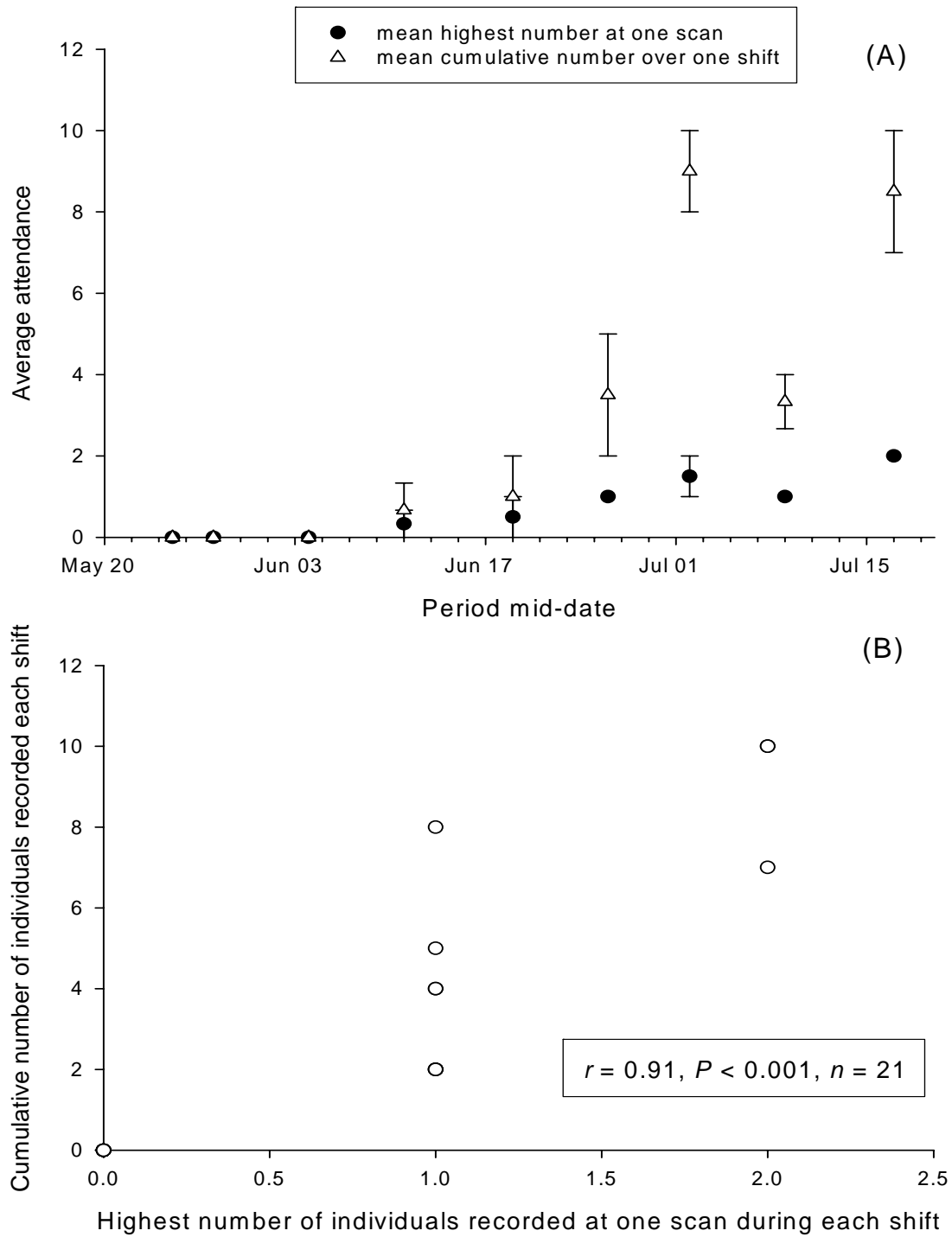


Figure A.6. Attendance ($\bar{X} \pm SE$) by female moose at Dead dog lick (May – August 2002), as measured by two indices of use (cumulative number of individuals observed during each 6-h shift, and the highest number of individuals observed at one scan during that shift) averaged over consecutive shifts (A), and the relationship between the two indices during each shift (B).

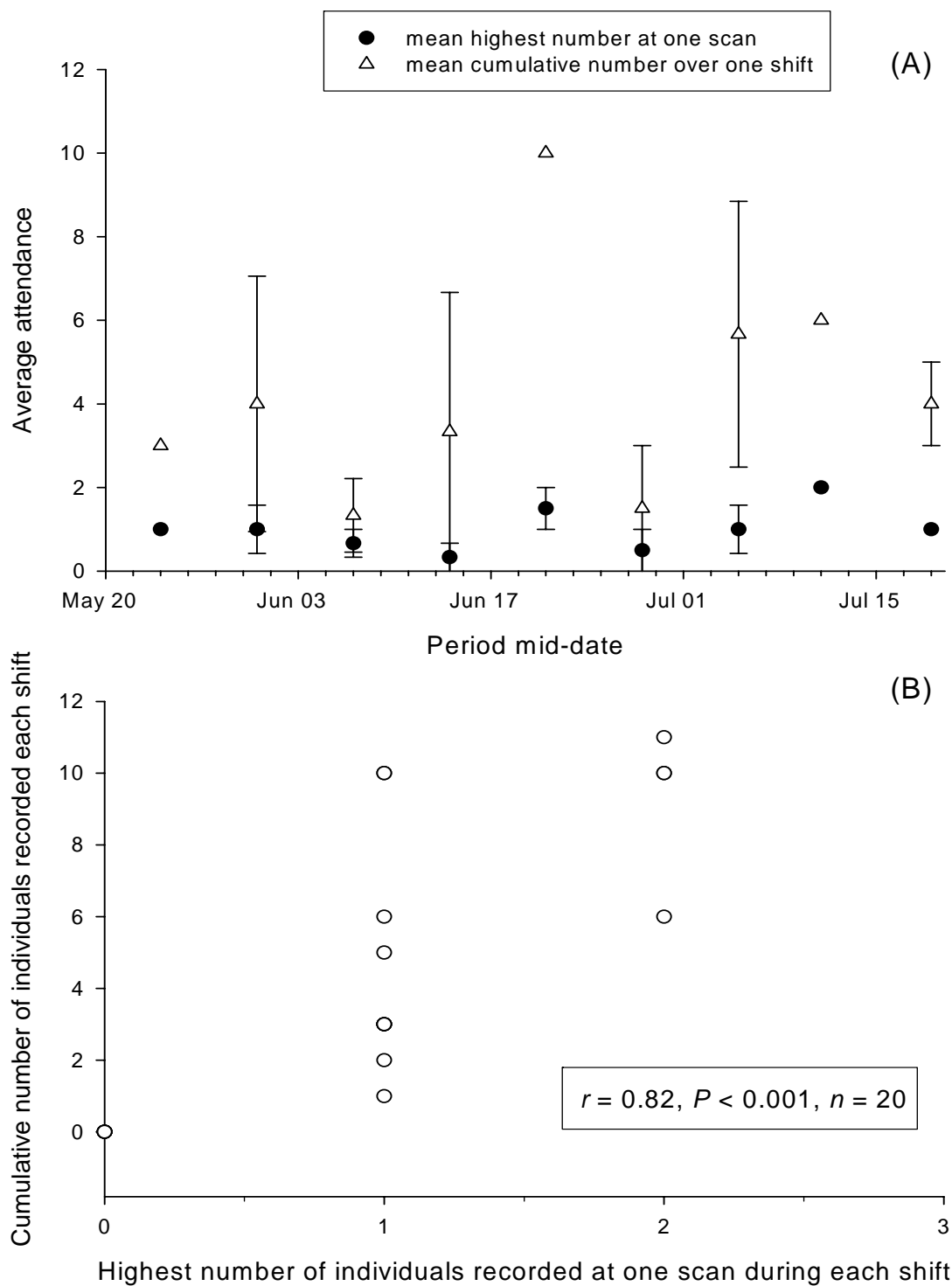


Figure A.7. Attendance ($\bar{X} \pm SE$) by male moose at Childers lick (May – August 2002), as measured by two indices of use (cumulative number of individuals observed during each 6-h shift, and the highest number of individuals observed at one scan during that shift) averaged over consecutive shifts (A), and the relationship between the two indices during each shift (B).

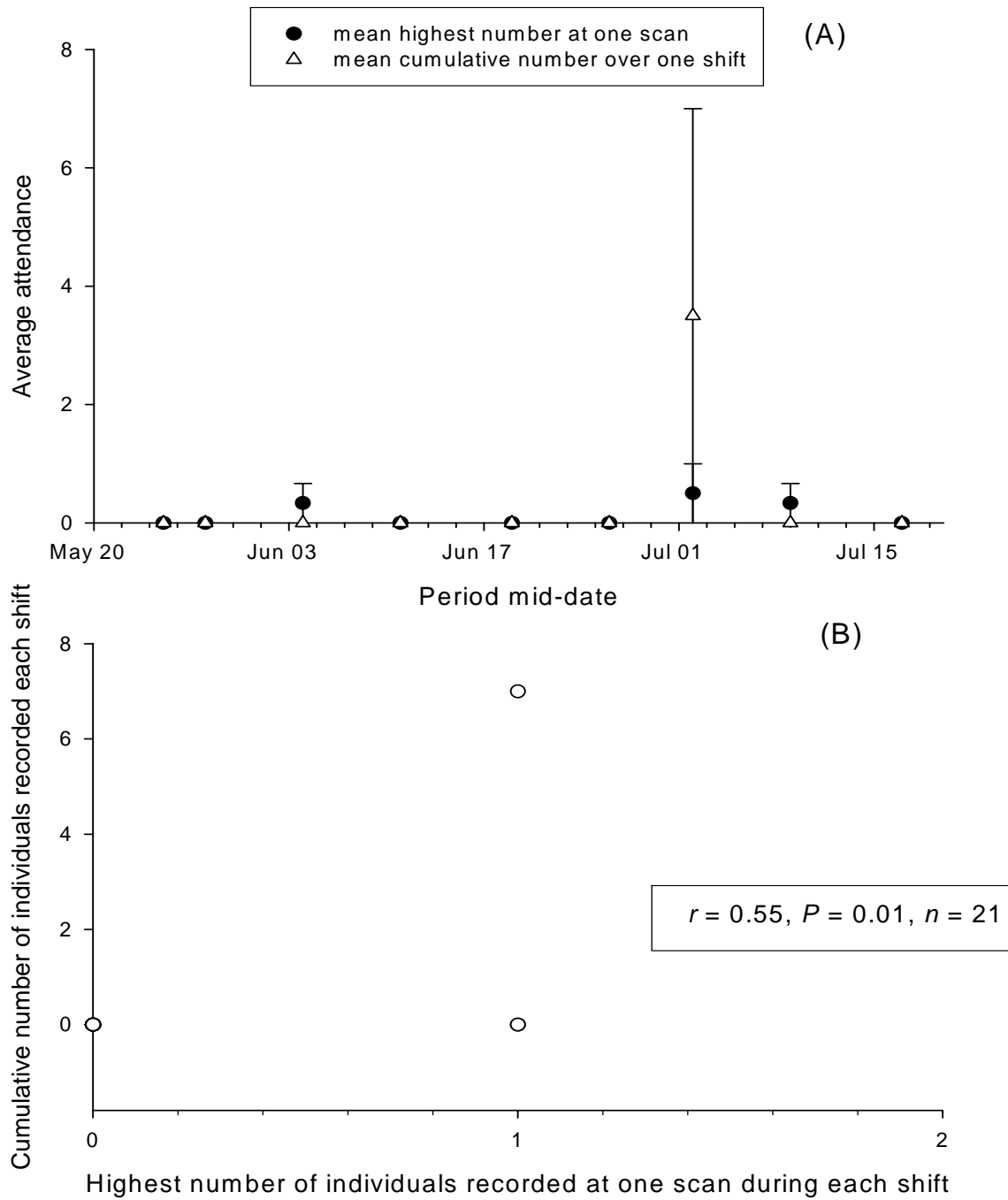


Figure A.8. Attendance ($\bar{X} \pm SE$) by male moose at Dead dog lick (May – August 2002), as measured by two indices of use (cumulative number of individuals observed during each 6-h shift, and the highest number of individuals observed at one scan during that shift) averaged over consecutive shifts (A), and the relationship between the two indices during each shift (B).

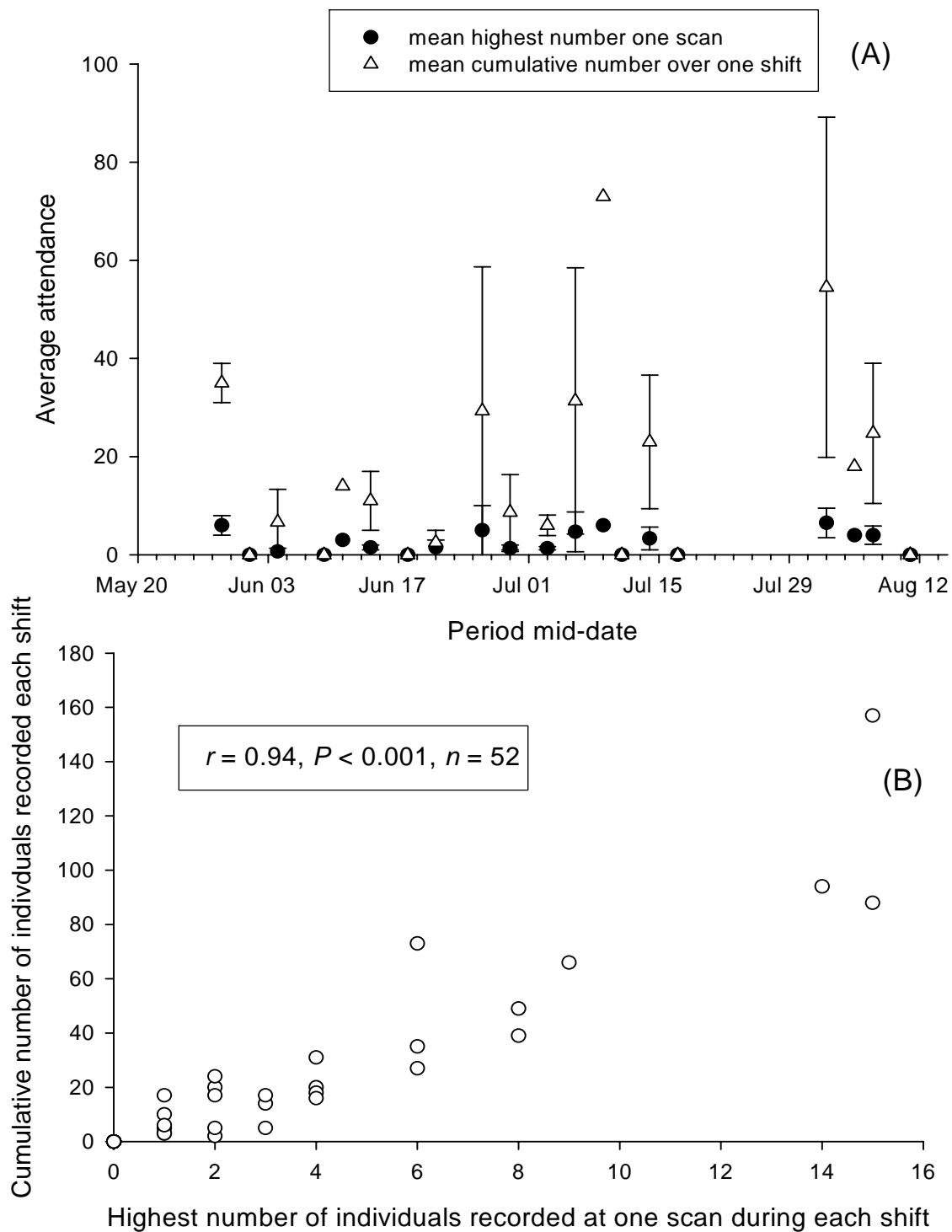


Figure A.9. Attendance ($\bar{X} \pm SE$) by Stone's sheep at dry licks (May – August 2002), as measured by two indices of use (cumulative number of individuals observed during each 6-h shift, and the highest number of individuals observed at one scan during that shift) averaged over consecutive shifts (A), and the relationship between the two indices during each shift (B).

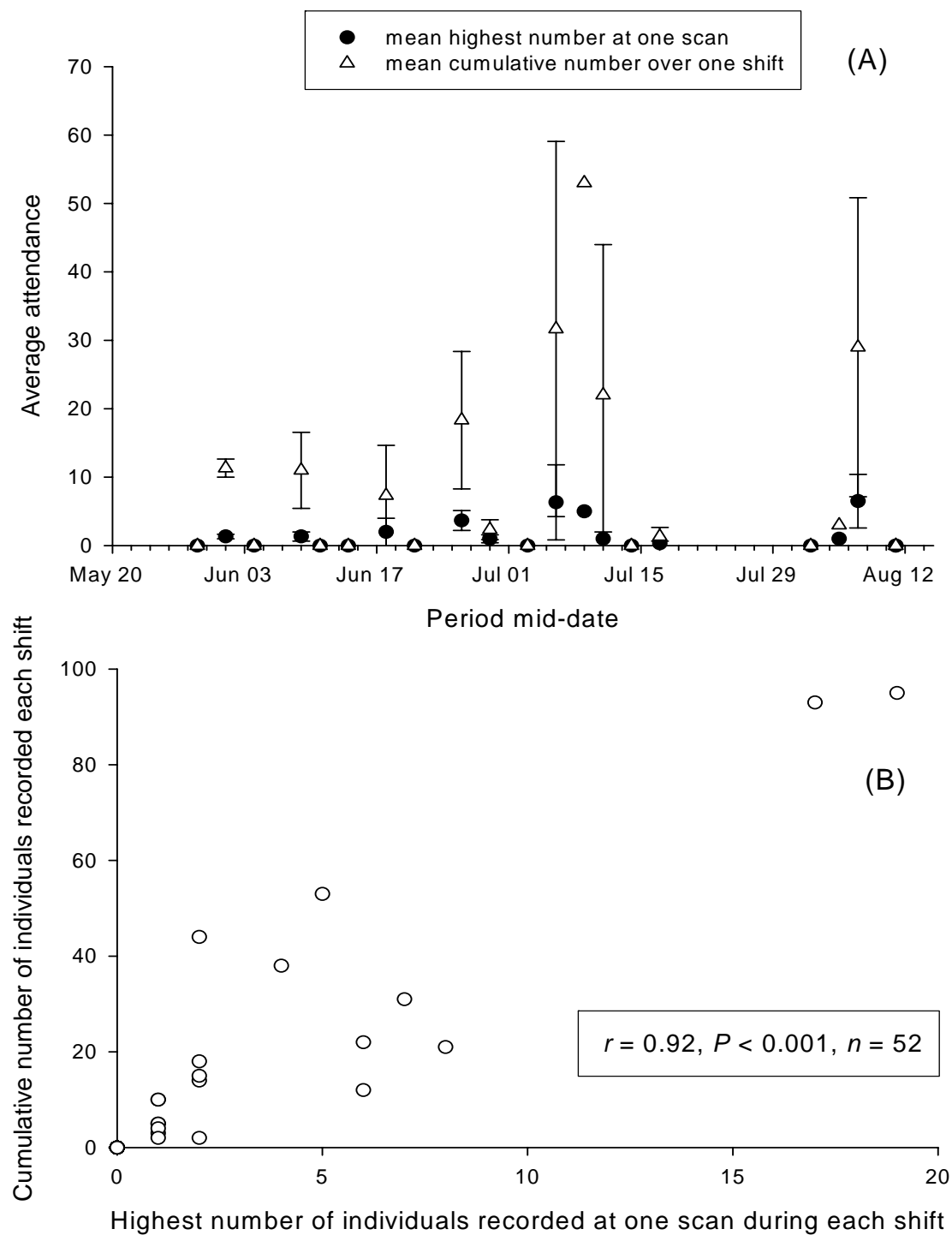


Figure A.10. Attendance ($\bar{X} \pm SE$) by mountain goats at dry licks (May – August 2002), as measured by two indices of use (cumulative number of individuals observed during each 6-h shift, and the highest number of individuals observed at one scan during that shift) averaged over consecutive shifts (A), and the relationship between the two indices during each shift (B).

Appendix B: Species-specific daily attendance at wet and dry licks in relation to precipitation days in the Turchodi watershed, May – August 2002.

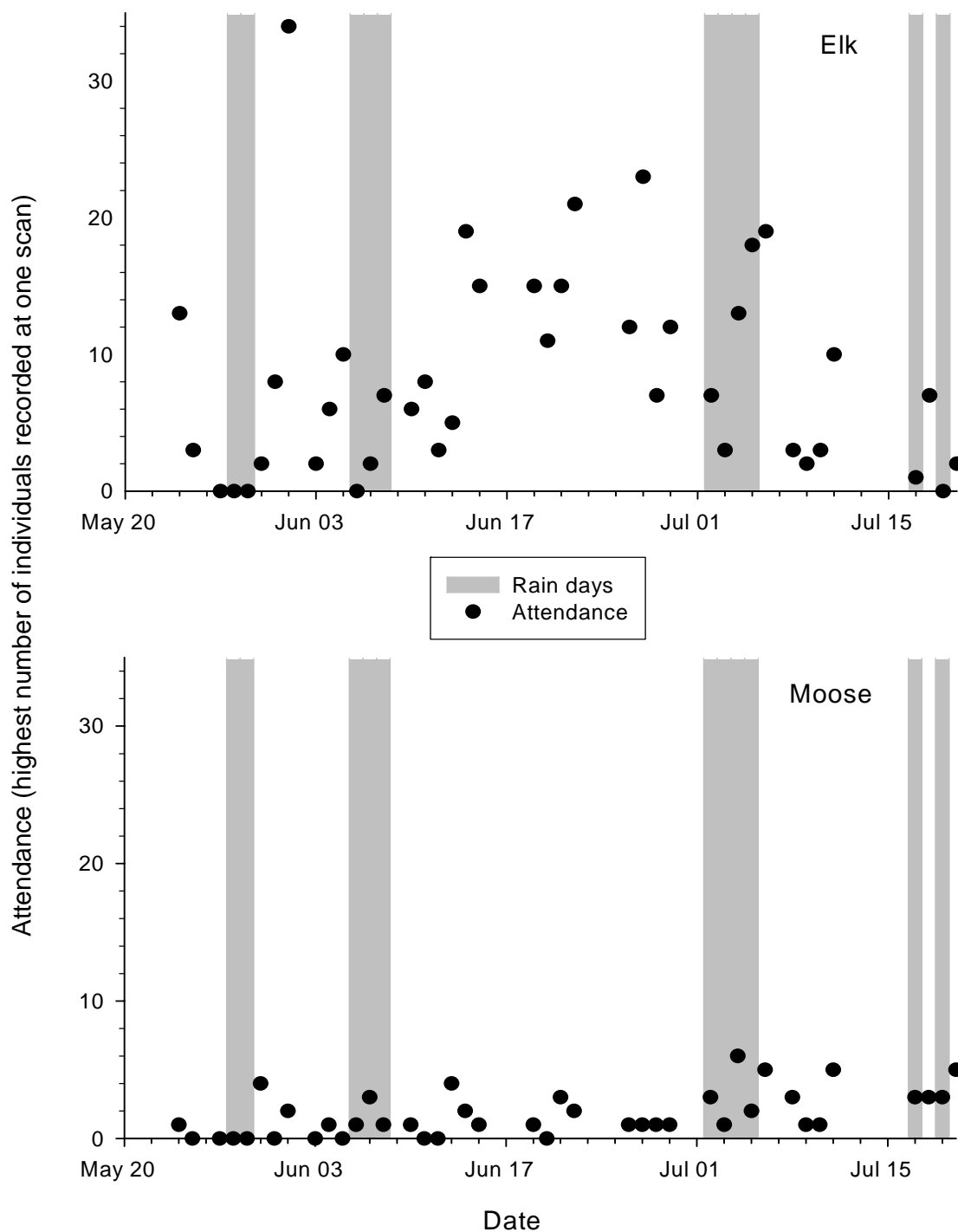


Figure B.1. Daily attendance by elk and moose as indexed by the highest number of individuals observed at one scan, in relation to precipitation recorded by observers at each of two wet licks (Childers and Dead dog) in the Tuchodi watershed, BC.

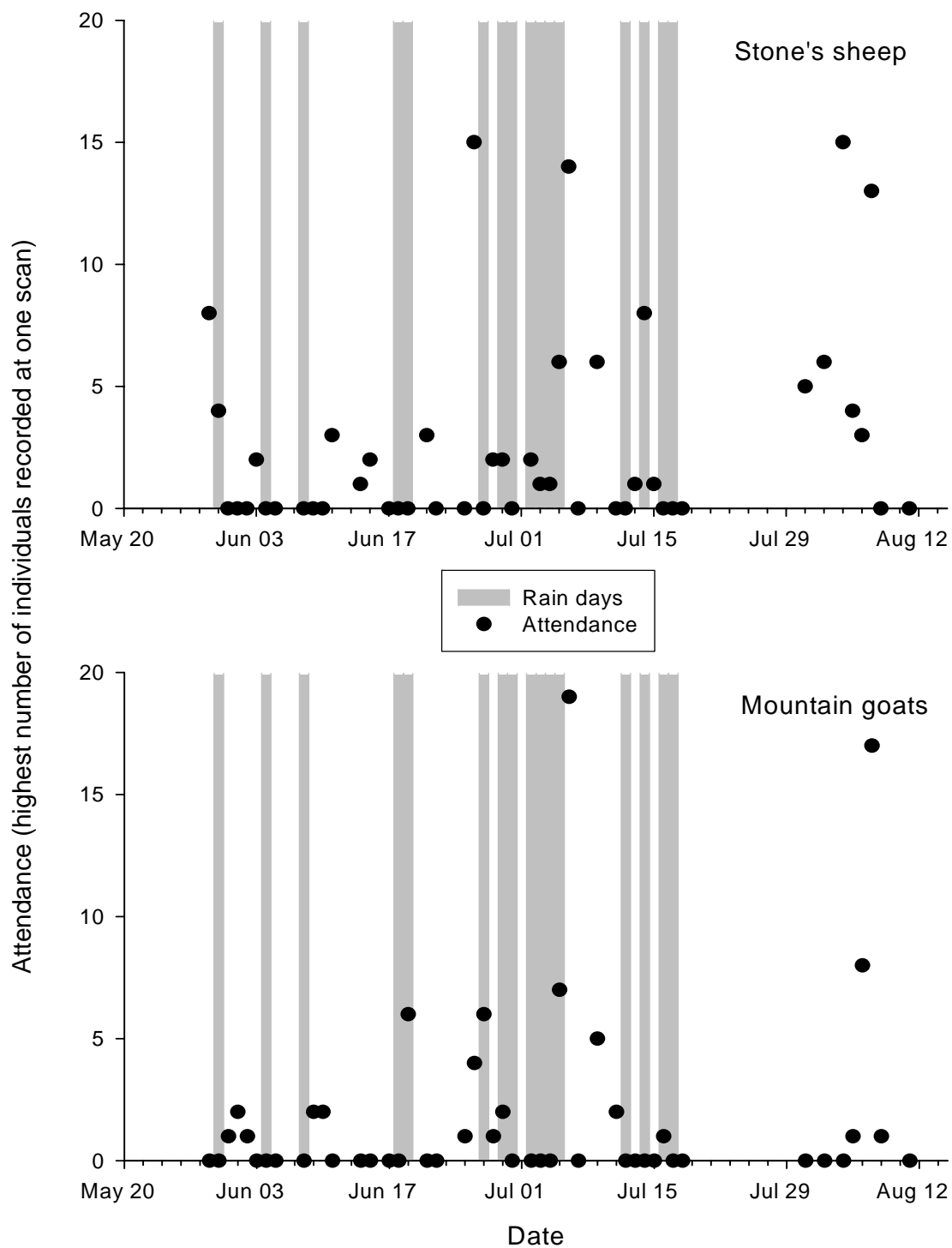


Figure B.2. Daily attendance by Stone's sheep and mountain goats as indexed by the highest number of individuals observed at one scan, in relation to precipitation recorded by observers at each of three licks (Upriver, Standard, and Lac-a-nookie) in the Tuchodi watershed, BC.

Appendix C: Hourly variation in the use of trails by Stone's sheep and mountain goats photographed approaching and leaving two dry licks in the Tuchodi watershed, May – August 2002.

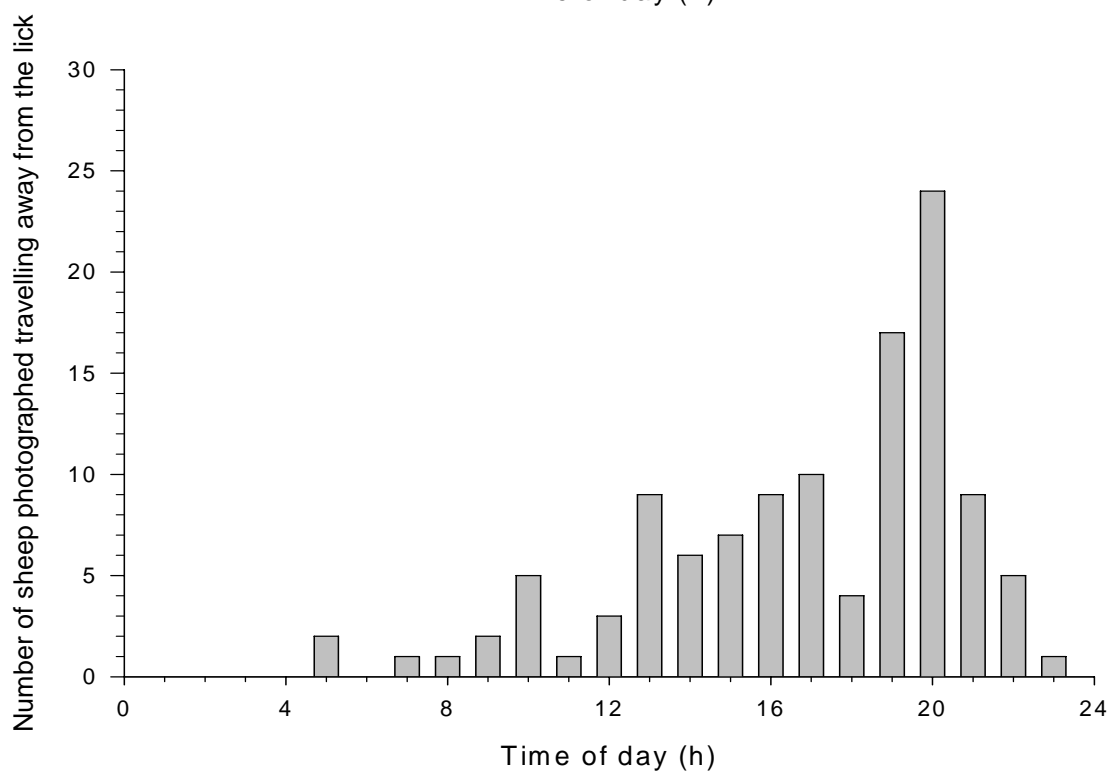
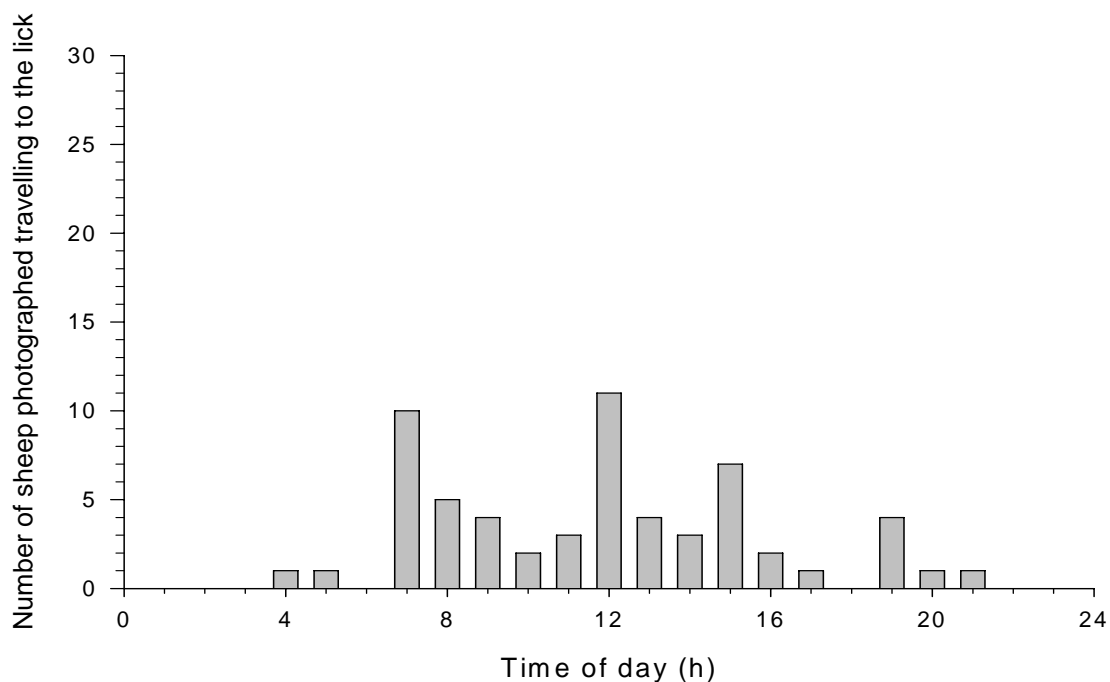


Figure C.1. Photographs from two remote trail cameras recording Stone's sheep traveling to (top) and away (bottom) from two dry licks (Lac-a-nookie and Standard). Hourly distributions were similar at both licks.

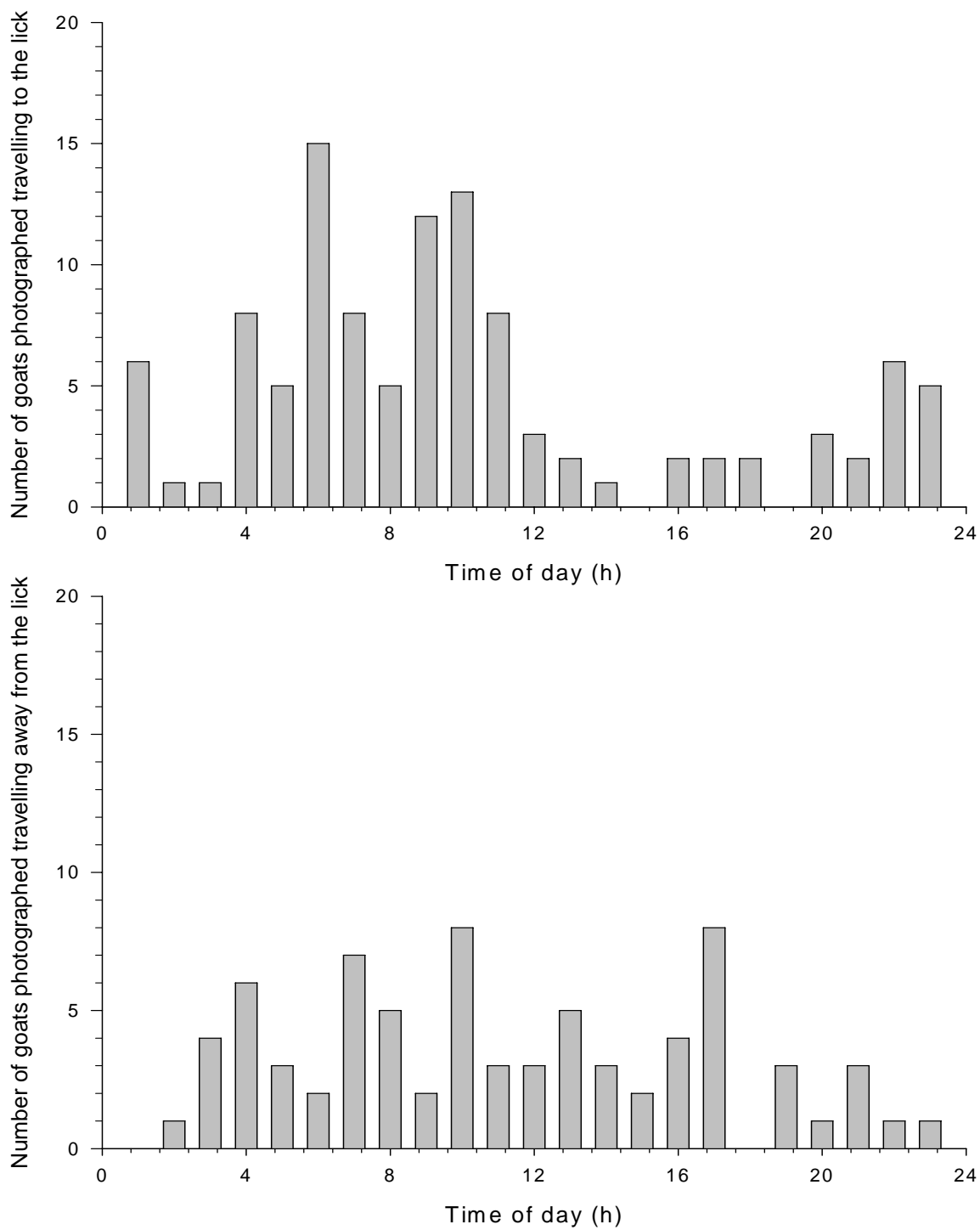


Figure C.2. Photographs from two remote trail cameras recording mountain goats traveling to (top) and away (bottom) from two dry licks (Lac-a-nookie and Standard). Hourly distributions were similar at both licks.

Appendix D: An example of the overview maps used to direct soil sampling efforts following behavioural observations (Tuchodi watershed, May – July 2002).

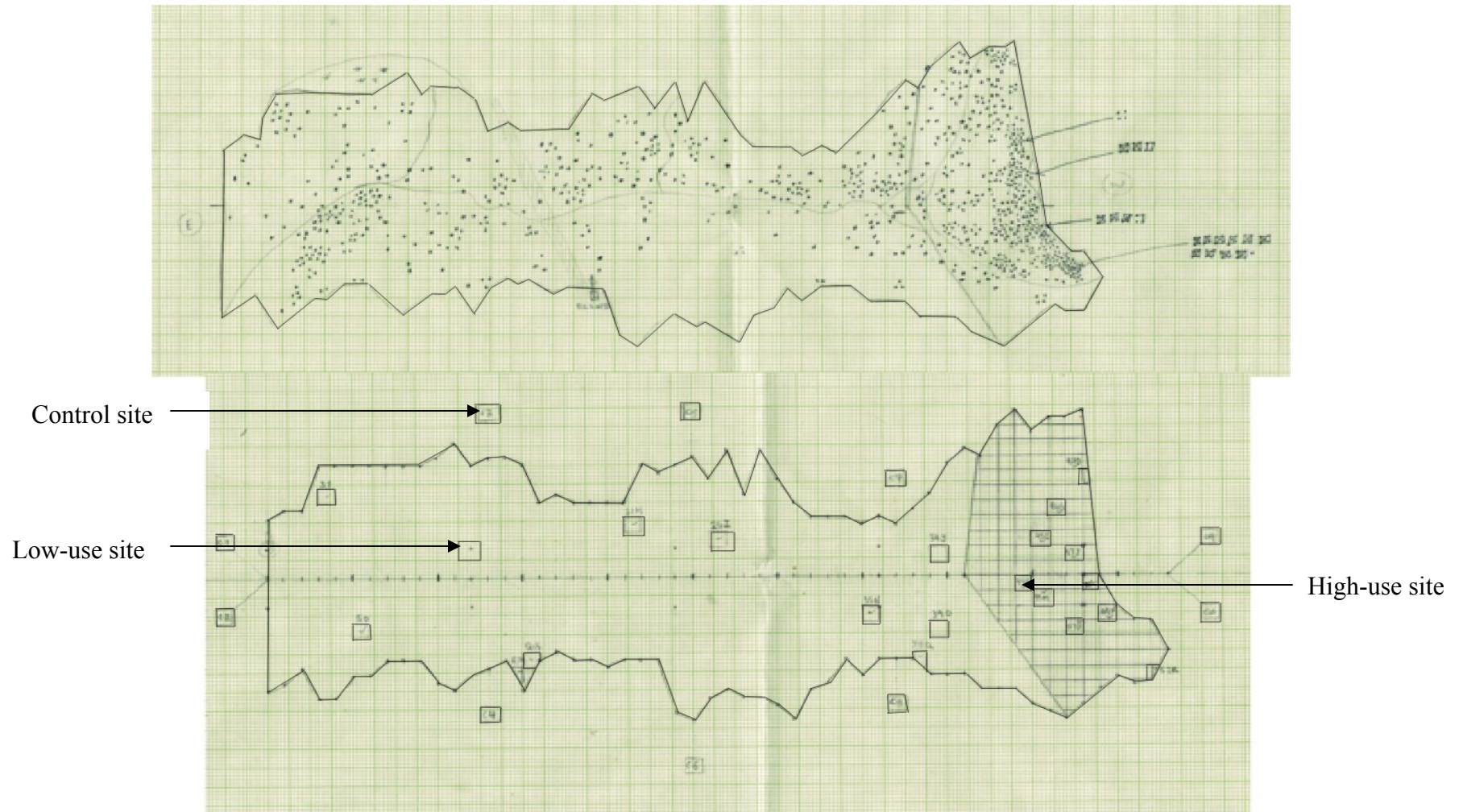


Figure D.1. An example of the overview maps drawn of each lick (Childers lick is shown). The top map was used to plot all locations of animals observed at the lick. The bottom map was then used to delineate high- and low-use areas, and randomly select 10 sites for sampling. Control sites were 10 m beyond the boundary of the lick and evenly distributed around its perimeter.

Appendix E. Relationships between soil analysis methods (pH 2.5 and pH 7) used to extract cations.

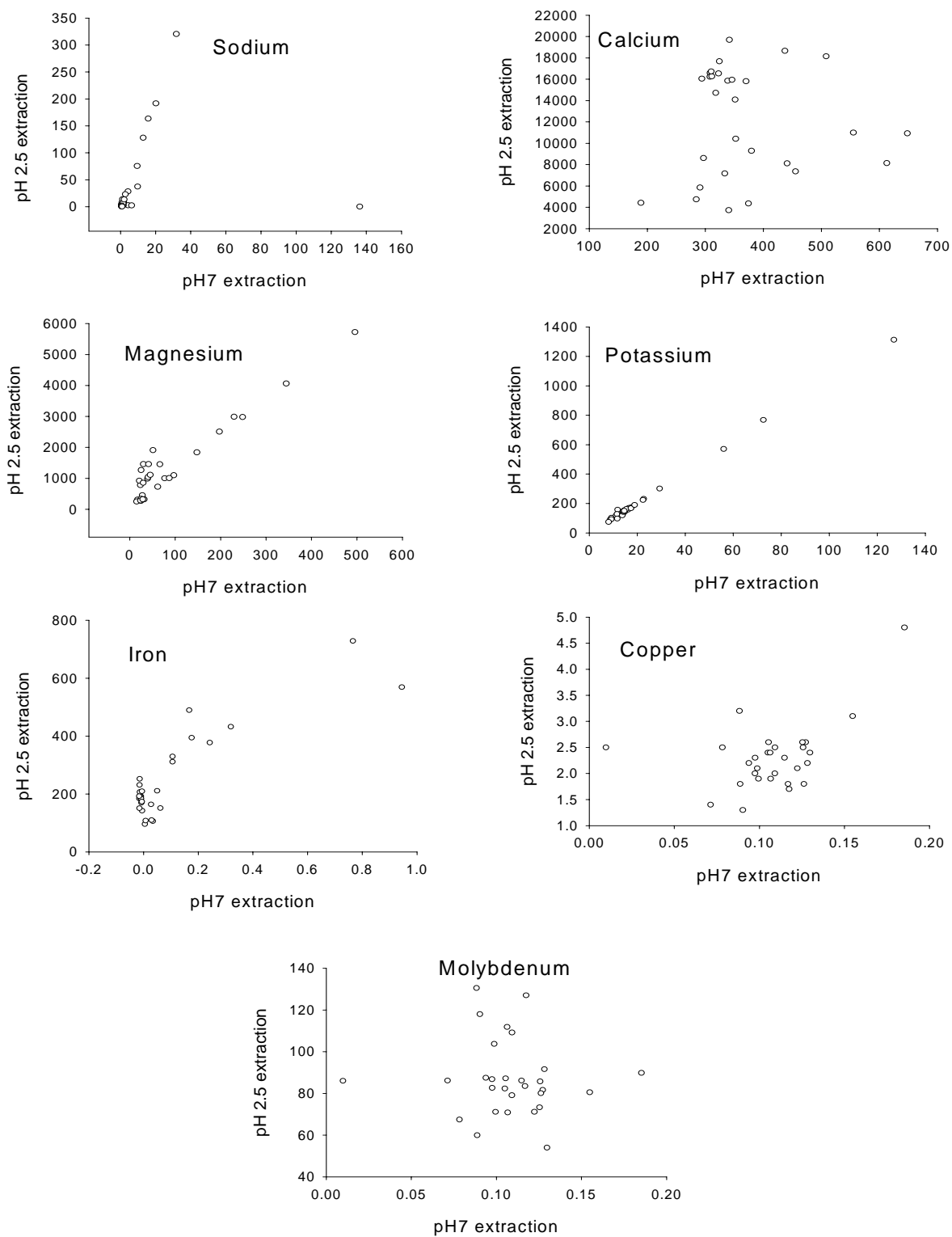


Figure E.1. Comparison of results (ppm) from two methods of cation extraction (Mehlich III at pH 2.5, and ammonium acetate at pH 7) for soil samples collected at a dry lick (Lac-a-nookie) in the Tuchodi watershed, July 2002.

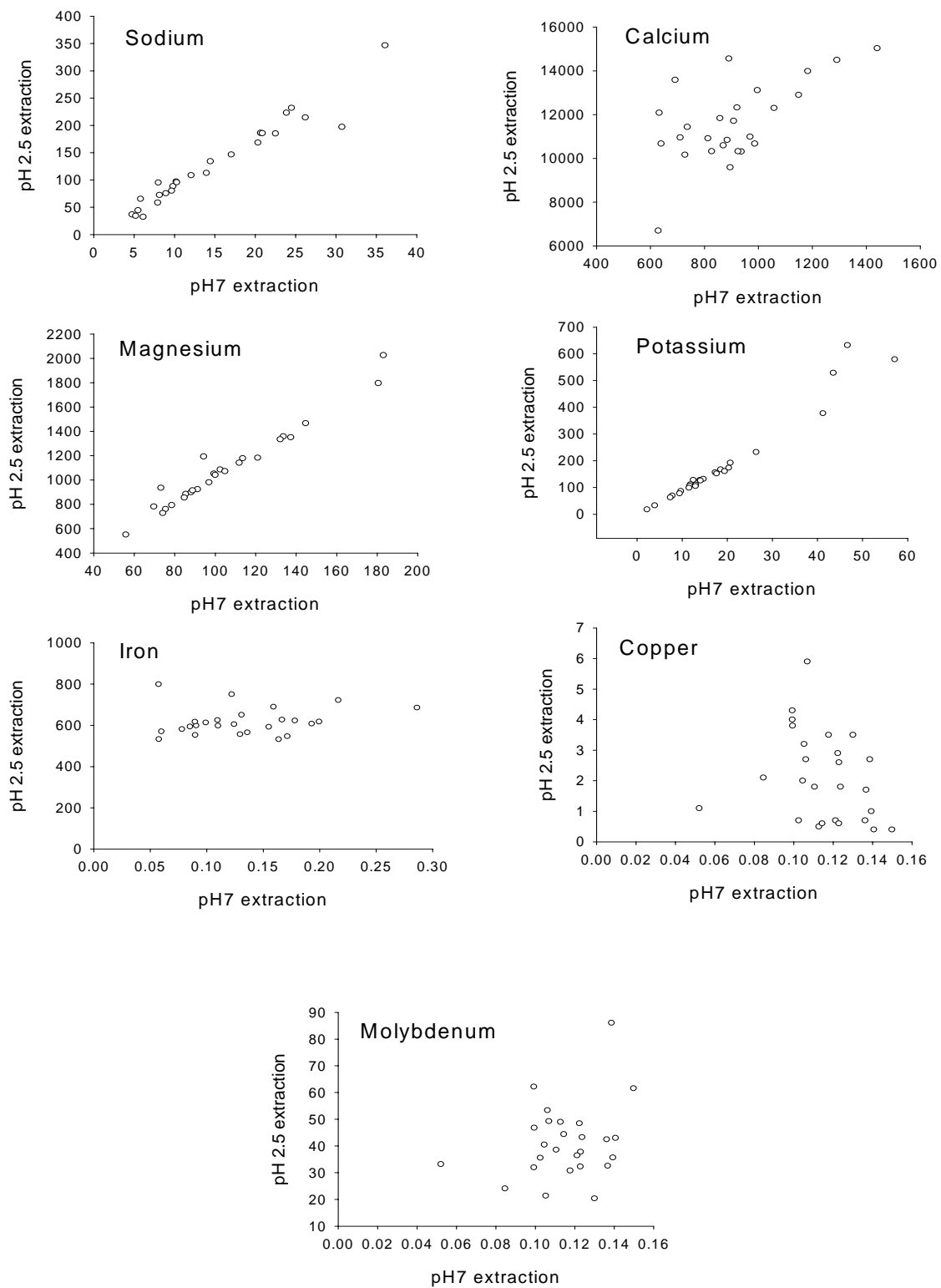


Figure E.2. Comparison of results (ppm) from two methods of cation extraction (Mehlich III at pH 2.5, and ammonium acetate at pH 7) for soil samples collected at a wet lick (Childers) in the Tuchodi watershed, July 2002.

Appendix F. Average concentrations of soil components in samples collected from high-use, low-use, and control sites at six licks in the Tuchodi watershed, BC (2002).

Table F.1. Average concentrations ($\bar{X} \pm SD$) of soil components in samples collected from high-use, low-use, and control sites at three wet licks in the Tuchodi watershed, BC (2002). Sample sizes are included in parentheses.

Soil components	Childers lick			Dead dog lick			Grizzly lick	
	High-use (10)	Low-use (10)	Control (9)	High-use (10)	Low-use (10)	Control (10)	Lick (10)	Control (9)
Na (ppm)	153 ± 53.5	131 ± 3.1	77.8 ± 0.05	110 ± 44.6	98.1 ± 41.1	21.4 ± 10.3	79.9 ± 33.6	51.8 ± 34.2
Mg (ppm)	902 ± 80.9	1127 ± 41.5	1179 ± 46.2	667 ± 93.9	606 ± 15.4	696 ± 324	1052 ± 262	1479 ± 983
Ca (ppm)	10603 ± 753	11676 ± 265	12721 ± 7612	4561 ± 734	4394 ± 1325	10463 ± 1908	6290 ± 1736	8391 ± 2051
K (ppm)	116 ± 65.5	113 ± 105	280 ± 27.9	179 ± 84.4	158 ± 38.5	219 ± 109	75.4 ± 26.5	229 ± 253
P (ppm)	10.4 ± 5.2	8.9 ± 3.0	33.2 ± 33.8	5.9 ± 1.1	5.8 ± 2.3	21.5 ± 20.7	2.4 ± 2.4	29 ± 49.3
Sulfate (ppm)	2112 ± 418	9039 ± 39.1	8674 ± 5018	369 ± 135	390 ± 193	79.7 ± 99.0	394 ± 435	140 ± 142
Fe (ppm)	661 ± 82.7	591 ± 46.6	575 ± 30.4	651 ± 75.6	678 ± 77.7	537 ± 64.5	710 ± 124	546 ± 132
Cu (ppm)	0.73 ± 0.38	2.4 ± 0.18	3.4 ± 1.2	2.9 ± 2.2	2.3 ± 1.7	5.1 ± 2.1	2.7 ± 1.7	4.0 ± 1.3
Mn (ppm)	41.3 ± 9.0	31.6 ± 8.1	48.9 ± 18.1	40.2 ± 10.5	48.8 ± 6.6	44.1 ± 18.7	44.4 ± 24.6	69.2 ± 24.8
Zn (ppm)	13.2 ± 1.4	20.6 ± 6.8	45.2 ± 27.7	21.9 ± 3.2	21.6 ± 3.4	33.2 ± 7.7	25.1 ± 9.5	46.8 ± 48.6
Carbonate (%)	18.5 ± 5.3	19.0 ± 7.0	9.7 ± 3.0	13.9 ± 3.2	17.6 ± 3.1	13.6 ± 5.0	34.2 ± 3.8	28.4 ± 8.5
C (%)	13.0 ± 4.0	15.5 ± 4.9	31.4 ± 12.6	9.0 ± 2.3	7.6 ± 1.2	15.0 ± 8.6	10.2 ± 2.9	15.9 ± 8.9
N (%)	0.49 ± 0.16	0.88 ± 0.28	1.4 ± 0.42	0.39 ± 0.12	0.32 ± 0.05	0.74 ± 0.37	0.44 ± 0.17	0.79 ± 0.52
CEC (cmol(+)/kg)	15.5 ± 3.9	58.3 ± 116	41.7 ± 13.3	14.5 ± 4.9	10.6 ± 1.7	23.8 ± 5.6	11.3 ± 5.4	21.2 ± 12.3

Table F.2. Average concentrations ($\bar{X} \pm SD$) of soil components (ppm) in samples collected from high-use, low-use, and control sites at three dry licks in the Tuchodi watershed, BC (2002). Sample sizes are included in parentheses.

Soil components	Lac-a-nookie lick			Standard lick			Upriver lick		
	High-use (9)	Low-use (10)	Control (11)	High-use (10)	Low-use (11)	Control (10)	High-use (10)	Low-use (10)	Control (10)
Na (ppm)	107±104	16.4±31.7	13.3±29.3	60.4±61.5	13.9±18.4	15.1±18.4	118±57.5	11.9±14.9	11.9±5.8
Mg (ppm)	2653±1498	995±467	677±512	3225±5227	883±345	634±262	1713±1465	599±359	671±231
Ca (ppm)	15419±3579	14617±3657	7141±2568	13067±3954	1334±4188	10125±1554	10372±2161	10709±3141	8211±1728
K (ppm)	418±402	139±28.7	143±50.5	145±46.5	119±27.2	155±36.2	232±113	75.8±53.7	313±274
P (ppm)	45.9±52.3	51.6±52.1	8.6±4.6	0.39±0.99	1.6±2.6	6.0±3.7	2.4±2.9	2.4±2.5	17.7±17.9
Sulfate (ppm)	2463±2308	57.9±99.6	8.5±5.9	3187±7094	92.9±157	5.2±1.4	304±367	43.5±53.1	31.1±38.1
Fe (ppm)	170±44.4	183±42.0	373±182	181±31.1	152±38.9	261±145	188±52.9	159±72.1	196±71.8
Cu (ppm)	2.7±0.88	2.2±0.38	2.1±0.49	2.0±0.89	2.3±0.50	2.3±0.36	3.1±0.69	3.1±0.85	2.9±0.49
Mn (ppm)	79.1±11.3	81.1±6.7	98.9±23.1	79.4±20.3	78.5±16.6	92.0±17.8	57.6±12.7	63.4±11.4	77.1±6.8
Zn (ppm)	1.2±0.29	1.1±0.31	2.2±1.1	1.1±0.46	1.2±0.24	4.2±4.2	4.0±1.6	4.5±1.8	13.8±7.9
Carbonate (%)	28.9±1.2	26.1±6.4	11.3±6.8	30.1±9.5	29.4±7.3	20.3±5.9	20.3±1.3	22.2±2.7	17.8±1.8
C (%)	3.6±0.28	3.4±0.75	5.9±2.7	3.3±1.0	3.8±0.88	6.5±2.1	3.5±0.47	4.4±1.4	8.4±2.9
N (%)	0.03±0.02	0.04±0.03	0.25±0.11	0.02±0.01	0.05±0.04	0.24±0.10	0.10±0.03	0.13±0.08	0.31±0.09
CEC (cmol+)/kg)	1.3±0.38	1.4±0.86	9.1±4.9	1.2±0.88	2.1±1.4	10.0±4.3	3.5±1.9	3.6±2.3	10.2±4.7

Appendix G. X-ray diffraction scans of soil samples from a high-use and a control site at one wet lick and one dry lick in the Tuchodi watershed, BC (2002).

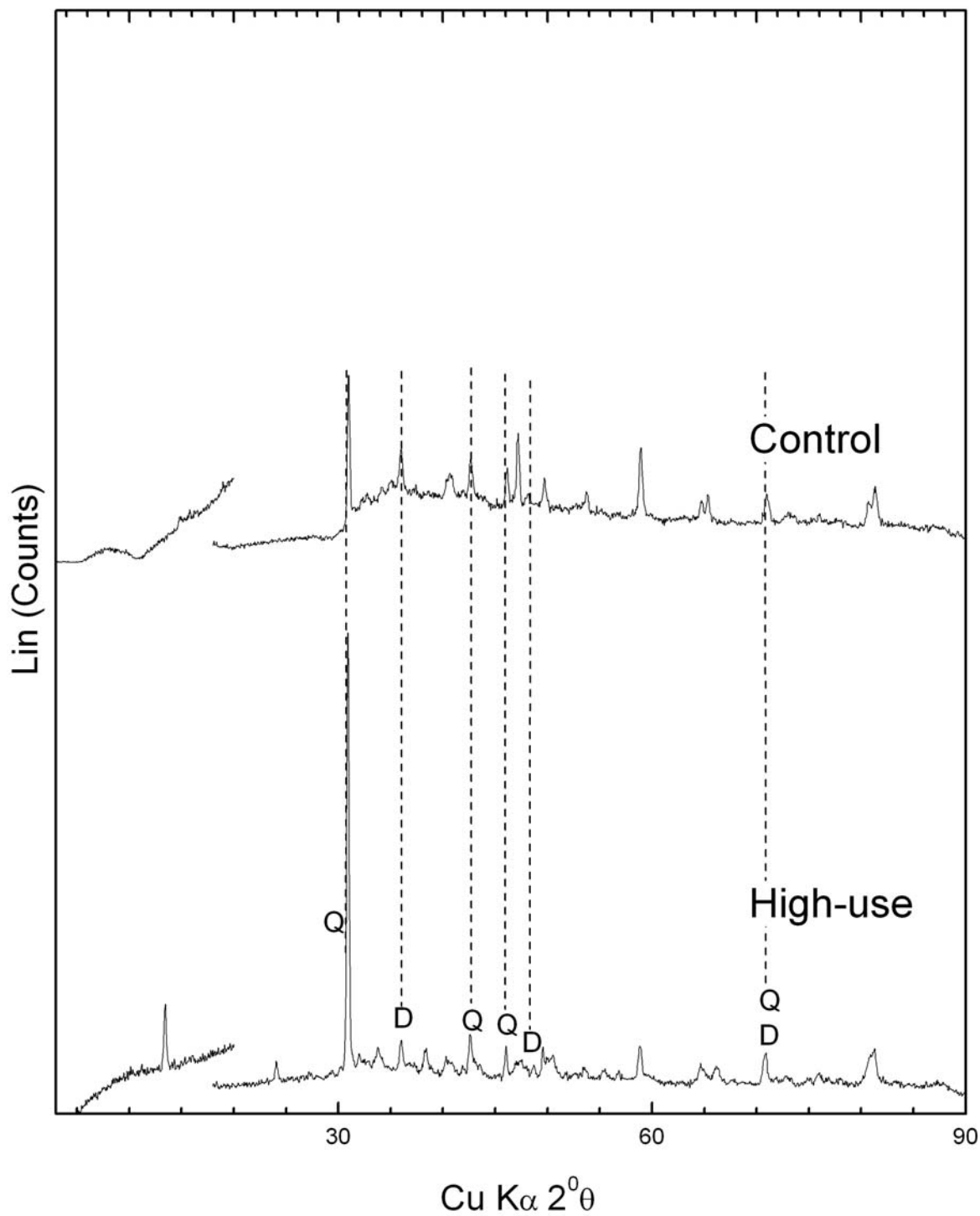


Figure G.1. X-ray diffraction scans of one high-use and one control soil sample from a wet lick (Childers) in the Tuchodi watershed, BC. (2002). The y-axis is a measure of radiation and the x-axis is the angle x-rays diffract off of the sample. The presence of quartz (Q) and dolomite (D) was detected in both samples.

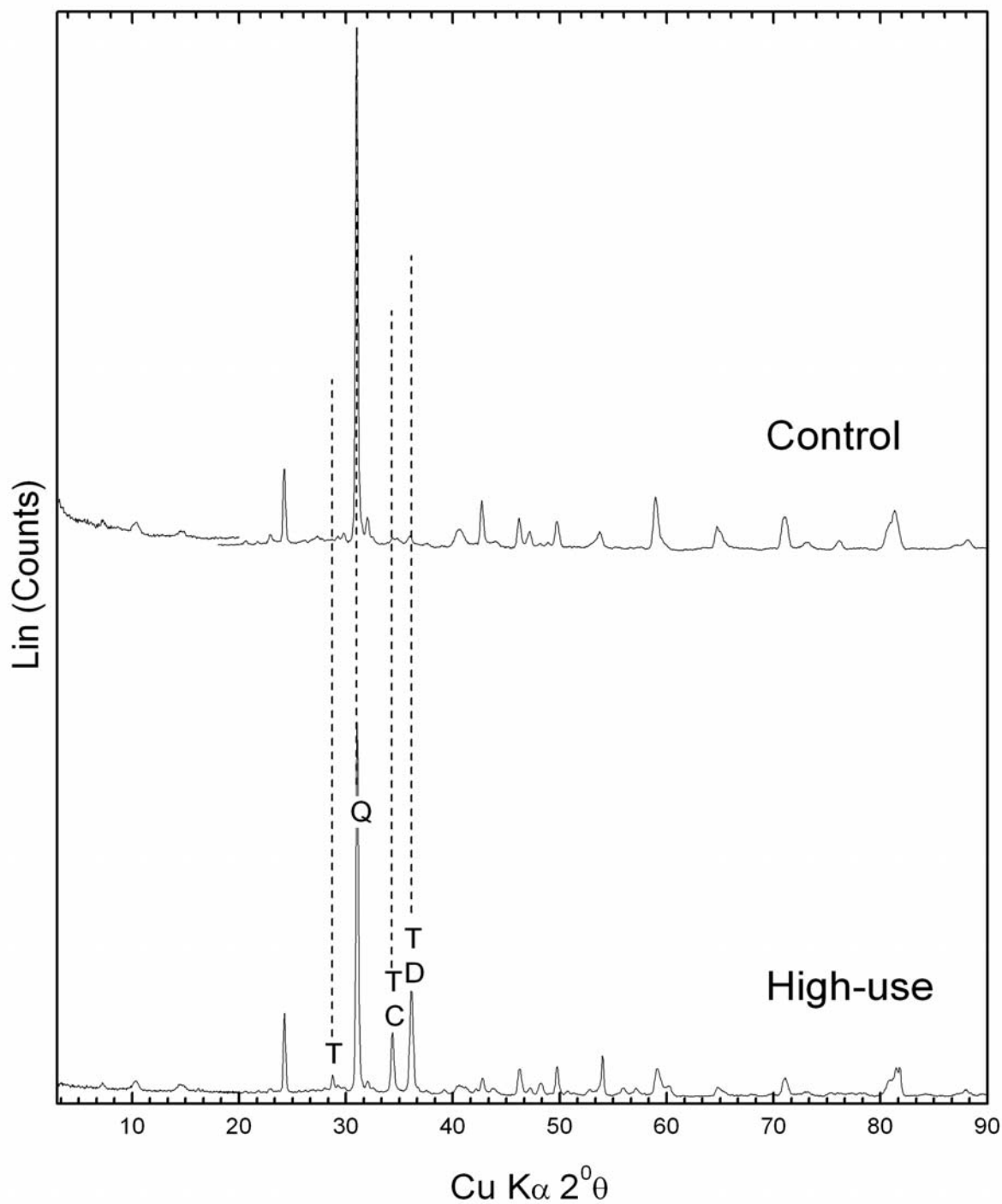


Figure G.2. X-ray diffraction scans of one high-use and one control soil sample from a dry lick (Lac-a-nookie) in the Tuchodi watershed, BC. (2002). The y-axis is a measure of radiation and the x-axis is the angle x-rays diffract off of the sample. Presence of the sodium sulfate mineral tamarugite (T), and the carbonate minerals calcite (C) and dolomite (D) was detected in the high-use sample but not in the control. Quartz (Q) was detected in both samples.

Appendix H. Average concentrations of elements in water samples collected from inflow, outflow, and control sites at two wet licks in the Tuchodi watershed, BC (2002).

Table H.1. Average concentrations ($\bar{X} \pm SD$) of elements (ppm) in water samples collected from inflow, outflow, and control sites (all $n = 3$) at two wet licks in the Tuchodi watershed, BC (2002).

Elements	Childers lick			Dead dog lick		
	In	Out	Control	In	Out	Control
Na	22.121 ± 27.246	35.964 ± 0.221	2.048 ± 0.048	239.723 ± 10.247	6.775 ± 0.261	4.283 ± 0.015
Mg	44.724 ± 7.280	46.602 ± 0.259	21.107 ± 0.288	107.837 ± 17.615	42.379 ± 0.269	36.971 ± 0.239
Ca	157.06 ± 2.720	145.129 ± 0.831	54.560 ± 1.588	223.135 ± 37.156	105.947 ± 0.454	97.730 ± 0.422
K	1.411 ± 0.996	2.291 ± 1.410	0.669 ± 0.104	7.461 ± 4.319	0.819 ± 0.105	0.780 ± 0.057
Fe	1.344 ± 1.754	1.127 ± 0.515	0.0420 ± 0.049	0.049 ± 0.035	0.121 ± 0.006	0.025 ± 0.001
Cu	0.001 ± 0.000	0.001 ± 0.000	0.001 ± 0.003	0.000 ± 0.001	0.001 ± 0.001	0.001 ± 0.002
Mn	0.128 ± 0.092	0.075 ± 0.000	0.010 ± 0.019	0.268 ± 0.268	0.000 ± 0.001	0.000 ± 0.000
Zn	0.004 ± 0.007	0.009 ± 0.003	0.001 ± 0.002	0.014 ± 0.011	0.000 ± 0.003	0.003 ± 0.001
Mo	0.042 ± 0.000	0.047 ± 0.005	0.019 ± 0.002	0.105 ± 0.011	0.042 ± 0.006	0.029 ± 0.007
Co	0.003 ± 0.004	0.0001 ± 0.002	0.001 ± 0.005	0.000 ± 0.004	0.001 ± 0.002	0.001 ± 0.002

Appendix I. Average elemental compositions of diets used by four ungulate species June – August 2002, Tuchodi watershed, BC.

Table I.1. Average elemental concentrations ($\bar{X} \pm \text{SD}$, ppm) in estimated diets of elk and moose in the Tuchodi watershed, BC. Dietary estimations are based on samples of six primary forage species. Collections (sample sizes in parentheses) were made in spring (early June), early summer (early/mid July), and summer (late July/early August) 2002.

Elements	Elk			Moose		
	Spring (1)	Early summer (3)	Summer (3)	Spring (3)	Early summer (3)	Summer (3)
Na	58.1	36.5 ± 2.2	34.7 ± 12.4	22.8	24.4 ± 17.9	36.2 ± 10.9
Mg	1187	2066 ± 68.8	1512 ± 802	1679	1947 ± 456	2280 ± 305
Ca	4562	10014 ± 1783	5803 ± 3734	11345	8208 ± 3261	8195 ± 635
K	23942	16923 ± 2407	14051 ± 6663	10096	17577 ± 9668	11331 ± 1745
P	2466	2527 ± 364	1443 ± 486	2913	3487 ± 1782	2101 ± 342
Fe	58.4	3935 ± 3964	199 ± 292	126	98.8 ± 66.1	46.9 ± 17.9
Cu	9.2	8.9 ± 1.3	4.9 ± 2.3	10.9	7.8 ± 1.9	5.8 ± 1.3
Mn	23.8	53.6 ± 10.4	21.2 ± 3.9	67.4	82.2 ± 106.7	106.1 ± 56.3
Mo	10.2	6.4 ± 2.3	0.41 ± 0.62	0.27	0.08 ± 0.07	0.18 ± 0.20
Co	0.34	0.97 ± 0.88	0.34 ± 0.19	0.99	0.96 ± 0.03	0.63 ± 0.25
Zn	46.6	89.1 ± 42.9	27.3 ± 16.7	154	135 ± 72.2	214 ± 79.9

Table I.2. Average elemental concentrations ($\bar{X} \pm SD$, ppm) in estimated diets of Stone's sheep and mountain goats in the Tuchodi watershed, BC. Dietary estimations are based on samples of six primary forage species. Collections (sample sizes in parentheses) were made in spring (early June), early summer (early/mid July), and summer (late July/early August) 2002.

Elements	Stone's sheep			Mountain goats		
	Spring (3)	Early summer (3)	Summer (3)	Spring (3)	Early summer (3)	Summer (3)
Na	67.5 ± 16.7	47.6 ± 2.6	45.9 ± 4.5	50.3 ± 9.7	85.9 ± 37.4	48.8 ± 32.4
Mg	1656 ± 479	2773 ± 924	2576 ± 649	3614 ± 559	3935 ± 2437	6221 ± 2188
Ca	5536 ± 1083	10867 ± 666	10205 ± 746	12359 ± 7017	14197 ± 8963	30194 ± 9942
K	18950 ± 8574	15950 ± 4089	16828 ± 1890	20914 ± 4732	12193 ± 4051	15459 ± 4034
P	2061 ± 734	1147 ± 175	1284 ± 212	3309 ± 961	1387 ± 493	1319 ± 444
Fe	207 ± 107	353 ± 306	321 ± 270	205 ± 137	728 ± 365	338 ± 412
Cu	6.4 ± 2.0	5.0 ± 0.89	6.2 ± 2.4	10.9 ± 2.3	11.8 ± 2.1	7.8 ± 4.9
Mn	69.9 ± 41.7	53.8 ± 5.7	67.9 ± 17.9	114 ± 36.4	94.8 ± 11.6	208 ± 107
Mo	0.00 ± 0.00	1.3 ± 0.29	1.9 ± 0.65	0.14 ± 0.22	0.27 ± 0.34	0.99 ± 0.44
Co	0.51 ± 0.08	0.78 ± 0.19	0.27 ± 0.12	0.72 ± 0.26	0.77 ± 0.21	0.13 ± 0.18
Zn	25.2 ± 7.9	18.6 ± 6.4	22.1 ± 5.8	31.5 ± 6.0	25.1 ± 4.2	20.5 ± 11.4