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Letter

Non-random distribution of ungulate salt licks relative to distance from North American oceanic margins

Ungulate Salt Licks Relative to Ocean Margins

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ABSTRACT
Aim: Terrestrial deposition of aerosol marine sodium declines with distance from coastlines. Salt deprivation in vertebrate herbivores and salt-seeking behaviors should hence increase with distance inland. We analyze published geospatial data on ungulate-patronized salt licks to test whether they are non-randomly distributed relative to distance from oceans and elevation.
Location: Canada, Alaska, and the contiguous United States.
Taxon: Cetartiodactyla (even-toed ungulates).
Methods: We determined the land area and median elevation of 100 km increments from the North American coast. The null model of the expected number of licks within each interval was determined by the ratio of the interval's land area to the total land area, multiplied by the total number of licks. We asked whether the number of licks further from coastlines was significantly higher than chance. We also assessed whether licks occur disproportionately at higher elevations, comparing the median elevation of observed licks to the median elevation within each interval.
Results: We found a strong positive relationship between salt lick patronage by ungulates and distance from the coast. Licks occurred significantly less often within, and more often beyond, 500 km inland, and at significantly higher elevations than would be expected by chance.
Main conclusions: These findings indicate that the patronage of salt licks is constrained geographically, and that the foraging behavior of ungulates and other phytophagous vertebrate taxa may be influenced over large spatial scales by sodium availability. Salt-seeking behavior varies on a wide biogeographical scale across North America, with concomitant implications for vertebrate herbivore behavior and ecology.

KEYWORDS geophagy, marine sodium deposition, mineral licks, North America, salt licks, ungulates

STATEMENT OF SIGNIFICANCE
We hypothesize that ungulates distant from oceans are more likely to visit salt licks due to an absence of atmospheric marine sodium deposition. We describe salt lick distribution across North America relative to ocean proximity and demonstrate how geographical variation in salt availability may broadly influence animal foraging behavior.

INTRODUCTION

Plant tissues contain sodium at very low concentrations, and herbivores are correspondingly salt-deprived (Cromack et al., 1977; Marschner, 1995; NRC, 2005; Borer et al., 2019). Sodium deprivation has been shown to influence reproduction and survival in ruminants (Church, Smith, Fontenot, & Ralston, 1971), and to be detrimental to population growth in microtine rodents (Aumann & Emlen, 1965). All North American ungulate species have been observed to seek out salt licks (here defined as sites of salt-seeking behavior involving deliberate ingestion of naturally occurring sodium-rich deposits), particularly in the spring and summer months linked to changes in forage profile, lactation, and metabolic demands (e.g., Ayotte, Parker, Arocena, & Gillingham, 2006; Ayotte, Parker, & Gillingham, 2008; Slabach, Corey, Aprille, Starks, & Dane, 2015).

The forage profile of ungulate grazers changes in the spring with the appearance of new grasses, which are disproportionately high in potassium and water (as opposed to drier carbon-rich mature grasses), causing a faster turnover of fluids and increased sodium loss (Blair-West, Coghlan, Denton, Nelson, Orchard, et al., 1968; Weeks & Kirkpatrick, 1976). This exposure induces elevated levels of aldosterone, which functions to retain sodium and purge potassium, but also leads to an accompanying loss in magnesium (which facilitates muscle fiber relaxation), thus potentially causing tetany in addition to diarrhea (Kreulen, 1985; Kaspari, 2020). Consumption of supplemental sodium during this glut of new forage not only prevents the aforementioned imbalances but also aids in the maintenance of the ruminant gut microbiome by facilitating microbial phosphorus cycling (Kaspari, 2020). In browsers, sodium has furthermore been hypothesized to protect the lining of the intestines by inactivating and precipitating tannins (see Freeland, Calcott, & Geiss, 1985; Kaspari, 2020).

Adult females of several ungulate species have been observed frequenting licks disproportionately more than adult males and subadults of both sexes, at periods corresponding to lactation (Heimer, 1973; Singer, 1978; Tankersley & Gasaway, 1983; Atwood & Weeks, 2002; Ayotte, 2004). Sodium requirements are elevated by 40% in lactating reindeer (Staaland, White, Luick, & Holleman, 1980) and the National Research Council (2000) recommends that lactating beef cattle receive 40% more sodium in dietary dry matter than non-lactating cattle.

Although there is a wide range of hypotheses for animal attraction to salt licks, such as attraction to other micronutrients, pH buffering, and as an aid in digestion of secondary plant compounds (Kreulen, 1985), these hypotheses are not mutually exclusive (Ayotte *et al.,* 2006). Despite its relatively low concentrations in the body, and due to a growing appreciation of the disparity between foliar sodium and the physiological requirements of herbivores in the ecological literature, sodium has been proposed as the seventh micronutrient (Kaspari, 2020).

Seasonal sodium deficiency and consequent salt-seeking behavior can also significantly influence ungulate movements and seasonal distribution (Heimer, 1973; Simmons, 1982; Watts & Schemnitz, 1985; Slabach *et al.,* 2015). Close to oceanic coastlines, wide-ranging ungulates may obtain sodium via consumption of algae (e.g., Carlton & Hodder, 2003). Near the oceans, aerosol deposition of marine salts within terrestrial ecosystems promotes their accumulation in freshwater streams, rivers, soils, and on the surface of vegetation (Stallard & Edmond, 1981; NRC, 2005), which results in high environmental availability of sodium. At distances >50–300 km inland, however, environmental salt availability declines dramatically (see continental US in Figure 1; sodium deposition maps in NADP, 2018). In many ant taxa, for example, deliberate salt-seeking behavior becomes more pronounced at greater distances from the oceans, such that this micronutrient at low concentrations becomes preferred relative to much higher concentrations of macronutrients such as carbohydrate and protein (Kaspari, Yanoviak, & Dudley, 2008). Similarly, the occurrence of avian and mammalian salt licks in Amazonian South

America is broadly correlated with environmental sodium availability (Dudley, Kaspari, & Yanoviak, 2012).

Possible geographical and continental-scale consequences of this environmental gradient for salt-seeking behavior by North American vertebrates are unknown, although ungulate mineral licks are widespread across the continent (Jones & Hanson, 1985). We assess here the geographical occurrences of licks collected from a variety of published studies, relative to distances from continental margins, and test the hypothesis that they are located significantly further from coastlines than would be predicted by chance. Additionally we evaluate the elevational distribution of salt licks, as enhanced montane leaching of salts might reduce mineral availability (e.g., Blair-West *et al.,* 1968).

METHODS

Salt lick location data were extracted from 47 studies of ungulates that spanned Canada, Alaska, and the contiguous United States. More than half of the salt licks were documented by Jones and Hanson (1985, p. 73), who collected lick samples through "A circularization of federal, state, and provincial conservation agencies early in 1975 [which] asked that samples be taken when convenient during routine field operations." They presented locality data as "samples that were … selected to represent as wide a geographical range as possible as well as a balanced representation with respect to the species of ungulates that had been reported frequenting the respective lick sites." The other studies confined themselves to localized study areas. Maritime islands (primarily in the Canadian Arctic) were excluded from our analysis; only one island was home to a lick, consumed by *Ovibos moschatus* (muskox), recorded in the Polar Arctic on Ellesmere Island (Tener 1954). Ungulates that were recorded visiting the licks in this study (from high to low frequency) included *Odocoileus spp.* (deer), *Odocoileus virginianus* (white-tailed deer), *Alces alces* (moose), *Cervus canadensis* (elk), *Ovis canadensis* (bighorn sheep), *Oreamnos americanus* (mountain goat), *Ovis dalli* (Dall sheep), *Odocoileus hemionus* (mule deer), *Rangifer tarandus* (caribou), *Bison bison* (bison), and *Antilocapra americana* (pronghorn antelope).

Salt lick locations were processed and analyzed using geospatial software (QGIS version 3.10.4). Locations identified by Jones and Hanson (1985) as "suspected lick" were excluded (11 sites); only confirmed licks were included. Most of Jones and Hanson's locations were specified using Global Positioning System (GPS) coordinates. Some, within the United States, were presented in the format used by the Bureau of Land Management (BLM) and some, in Canada, were in Alberta Township System (ATS) coordinates. To convert these data to GPS coordinates, we used publicly available BLM and ATS GIS data to locate the center of each polygon corresponding to the specified section or township (1 section = 1 sq. mile; 1 township = 36 sq. mile). Many of the remaining studies indicated salt lick locations only on maps or by description of an adjacent natural formation and/or distance from a landmark. In these cases, our specified location is approximate. However, none of these ambiguities affected the classification of licks into distinct 100 km distance classes (see below).

We tested the hypothesis that there is a nominal cutoff (i.e., a threshold of the sodium deposition gradient) beyond which salt licks are disproportionately located. To test this hypothesis independently at various distances, we subdivided the study area into successive 100 km intervals from the coastline (0–100 km, 101–200 km, 201–300 km, etc.) using the "buffer" tool, and calculated the area of land (km^2) of each interval using the "add geometry attributes" tool (after using the "vector intersection" tool to subtract the 1,000 largest water bodies from the study area). Each observed salt lick was classified as lying within one of these distance class layers. We then added these intervals together to test the hypothesis for progressively larger areas, e.g. whether there were disproportionately *fewer* licks in the interval of 0–200 km, and also disproportionately *more* licks within the interval of 201 km–inland. The expected number of licks for each interval was calculated by dividing the interval's land area by the total land area, and then multiplying it by the total number of licks observed. All calculations were conducted within the North American Albers Equal Area Conic map projection. For analysis of elevations within each distance interval (as well as for each individual lick), we used Global Multi-resolution Terrain Elevation Data 2010 (GMTED2010; Danielson & Gesch, 2011), which provides a raster image of median elevations over 7.5 arcsecond spatial intervals. To avoid possible pseudoreplication of spatially clustered lick locations, we drew 50 km radius circles around each observed salt lick and averaged distance and elevation data for licks with overlapping circles, treating these as single licks in our analysis.

We used the chi-square goodness-of-fit test (using the 'chisq.test' function in R; R Core Team, 2020) to determine whether there was a significant difference between the expected and the observed number of licks to either side of each independent distance interval. We used the non-parametric Wilcoxon signed rank test in the 'stats' package in R (R Core Team, 2020) to determine whether there was a significant difference between the median elevation of a given distance interval and the medians of pairwise averages of pair differences for elevations of observed licks within that interval (hereafter referred to as the median of lick elevations).

RESULTS

A total of 345 geographically distinct salt licks was identified (Table S1 in Supporting Information). After averaging data for salt licks within 100 km of one another, 109 distinct lick sites remained (Figure 1; Table S2).

Salt licks were significantly less concentrated within, and more concentrated beyond 100, 200, 300, 400, and 500 km distances from marine coastlines (chi-squared goodness-of-fit, χ^2 (1, N = 109) = 5.2, $P = 0.022$, $\chi^2 = 6.9$, $P = 0.009$, $\chi^2 = 5.8$, $P = 0.016$, $\chi^2 = 6.2$, $P = 0.013$, and $\chi^2 = 4.7$, $P = 0.029$ respectively; Figure 2a).

The median elevation of salt lick sites within the entire study area (786 m) was higher than the median elevation of the total study area (376 m; Wilcoxon signed-rank test, $P < 0.001$). The median elevation of salt lick sites was also significantly higher than the corresponding median elevation for every cumulative range interval toward the marine coastline (e.g., 0–100 km, 0–200 km, 0–300 km, etc.; Figure 2b).

DISCUSSION

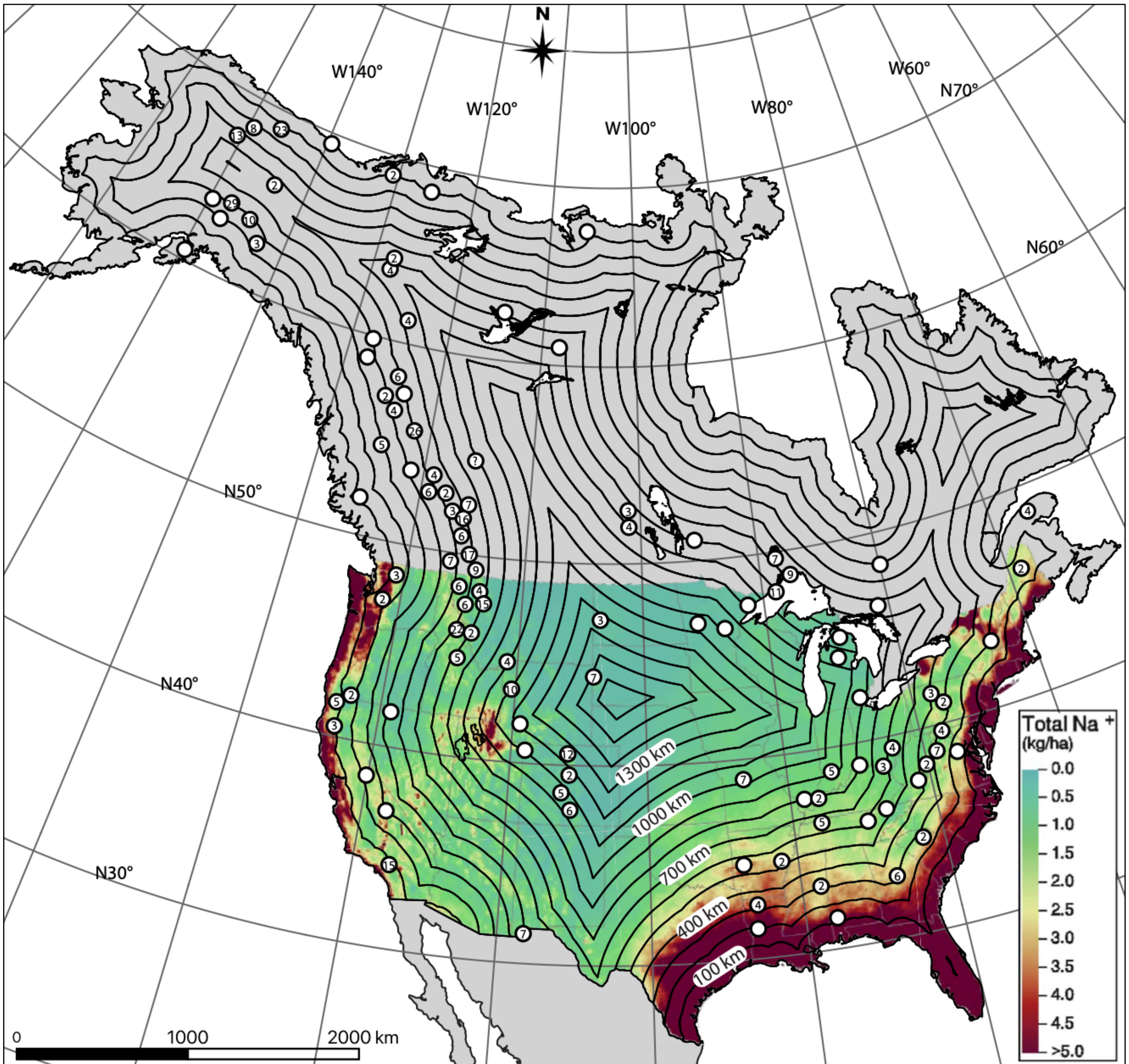

Figure 1. Albers Equal Area Conic projection of the study area in North America, with circles representing ungulate-patronized salt lick sites (see Table S2 in Supporting Information), a georeferenced copy of the National Atmospheric Deposition Program's 2018 total sodium deposition map (NADP 2018) over the continental United States (kg/ha), and lines depicting 100 km increments from the marine coastline. Licks located within 100 km of one another were aggregated into a single location yielding n = 109 sites, represented by circles that contain the number of licks averaged.

Here, we show a strong positive relationship between the recorded occurrences of salt lick patronage by ungulates and their distance from the coast; salt licks occur at significantly lower

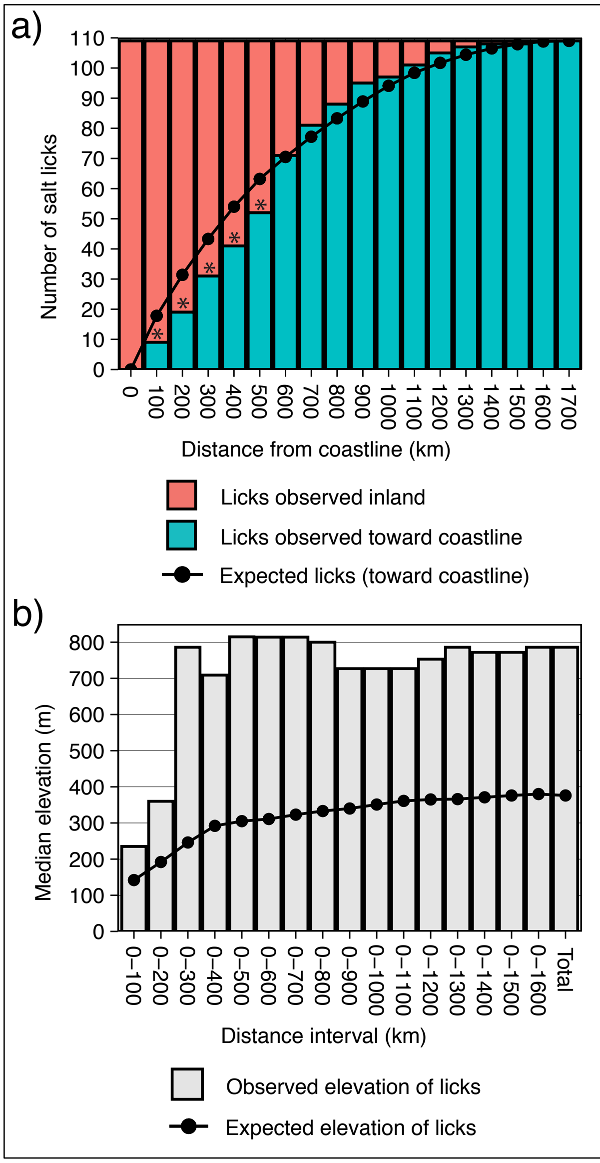

Figure 2
(A) The number of ungulate-patronized salt licks in North America (north of Mexico) in 100 km increments; red bars indicate the proportion of observed salt licks inland and teal bars the number of licks toward marine coastlines. The black line chart indicates the expected number of licks toward marine coastlines, by chance alone. The expected numbers of licks for each interval is determined by the proportion of land area within that interval to the total land area, multiplied by the total number of licks. Asterisks above teal bars mark intervals where the number of observed salt licks significantly differed from the number expected by chance, as indicated by a chi-square goodness-of-fit test.
(B) The median elevations of salt licks within each cumulative 100 km interval from the marine coastline are represented by the bar chart. The median elevation within each corresponding interval is represented by the line graph. Elevation data are from the GMTED2010 topographic dataset (Danielson & Gesch, 2011). All intervals had a significantly higher median elevation of observed licks than the overall median elevation of that interval, as indicated by a Wilcoxon signed-rank test.

frequency within 500 km and at significantly higher frequency beyond 500 km. This relationship illustrates a general pattern in salt-seeking behavioral outcomes as first indicated geographically for ants (Kaspari *et al.,* 2008). Similarly, salt licks visited by ungulates in North America were present at higher elevations than would be expected by chance alone, suggesting an interaction effect between distance from coastlines and elevation across the study area (see Figure 2). In the absence of measurements of sodium availability and consumption rates at study locations, it is not possible to ascribe lick visitation directly to patterns of salt deposition from marine sources. Nonetheless, these findings on a continental scale suggest that sodium deprivation in ungulates is pronounced and motivates salt-seeking behavior.

Ungulates are likely particularly attracted to salt licks at higher elevations because of extremely low concentrations of environmental sodium, resulting from a combination of montane leaching from heavy snowmelt and rainfall with virtually no sodium. Denton (1965) documented significantly lower salivary and urinary sodium levels in cattle grazing on montane pasture, or on flat river pasture heavily irrigated with water containing very little sodium, as compared to montane pasture cattle given sodium supplements or to cattle grazing on lowland control pasture.

Similarly, Blair-West *et al.,* (1968) found that higher elevational sites had lower concentrations of soil and foliar sodium than those at lower elevations.

The geology and geography underpinning the distribution of sodium and its aggregation in the landscape is complex and multifaceted (for examples with respect to specific licks, see Knight & Mudge 1967; Lavelle *et al.,* 2014), and it is beyond the scope of this study to assess whether geologically derived sodium deposits are equally likely to occur within surface features in all distance classes across North America. Salt licks are defined by their patronage, and associated with a variety of physical settings according to the modality of use of their patrons (see Jones & Hanson, 1985). Dry, friable licks may form at the interface of bluff and stream, and are preferred by mountain sheep and goats, but also freely consumed by elk. White-tailed deer and mule deer do not frequent dry licks, but, along with elk, freely consume wet licks, which may be muddy or entirely liquid. For example, licks can span half an acre, resembling a drained pond. They may also occur at the base of tree roots, which apparently concentrate solutes via transpiration, and which ungulates can excavate to a depth of several feet. Complexes of licks may form when sodium deposits are near the surface, or when underground streams carry salts to the surface (e.g., lick runs, found throughout parts of the Midwest and Northeastern United States; Jones & Hanson, 1985). Thus, a null model that incorporates variation in the availability of non-patronized sources of sodium throughout the study range would be extremely difficult to formulate on available information.

Ungulate-frequented salt licks may simply be more evident near roads, rivers, and human settlements (which are primarily concentrated in coastal and lowland regions; see Small & Nicholls, 2003), thus potentially biasing salt lick observations toward these areas. On the other hand, potential salt lick sites near human settlements are more likely to have been anthropogenically disturbed or eliminated. Anthropogenic sources of salt (e.g., winter salting of roads, cattle licks, well sites) may similarly influence patterns of usage by wild ungulates (Jones & Hanson, 1985; NRC, 2005). The latter influence would ostensibly diminish natural salt lick use near coastal lowlands, resulting in an apparently disproportionally high usage of salt licks by ungulates at higher elevations where anthropogenic sources of sodium are less prevalent – as is reflected in our data (see Figure 2b). The interior of North America is also replete with salt pans and salt deserts (Reimold & Queen, 1974), the presence of which may influence ungulate nutritional behavior (e.g., note the presence of the Great Salt Lake relative to atmospheric sodium deposition in Figure 1).

Early efforts at managing ungulate (specifically elk) distributions with artificial salt licks (Case, 1938; Cooney, 1952; Dalke, Beeman, Kindel, Robel, & Williams, 1965) were costly, had limited success, and cast doubt on the working hypothesis that ungulates were motivated by sodium deficiency. Alternative hypotheses proposed that geophagy at salt licks was the result of acquired habit and taste, that it evolved as an instinctive taste association to prevent mineral deficiency prior to an imminent physiological shortfall, and that aggregation by ungulates at natural licks was motivated by social factors elicited by the presence of conspecifics (Knight & Mudge, 1967; Skovlin, Zager, & Johnson, 2002). Walter *et al.* (2010) proposed that difficulties in managing elk on a landscape scale using artificial licks stemmed from a naturally low lick visitation rate, and a necessarily high degree of knowledge of year-round elk movements and forage requirements. Moreover, none of the aforementioned hypotheses exclude physiological deficiency as the primary motivator of this behavior, especially given observed sex differences in lick visitation related to lactation, including for elk (see Introduction).

Cases where populations within the continental interior appear to be thriving without seasonal geophagy may be due to cryptic sources of sodium, such as sodium-enriched springs.

There is no doubt that ungulates have physiological adaptations to delay the necessity of sodium supplementation until it is available seasonally, although the limitations of such adaptations are unknown. Variations in foliar sodium can shore up deficiencies, as herbivores seek out and preferentially consume forage with higher sodium concentrations (Botkin, Jordan, Dominski, Lowendorf, & Hutchinson, 1973). Borer *et al.,* (2019) found that unfenced grassland plots across four continents, treated with fertilizer, showed a disproportionate reduction in abundance of plants higher in foliar sodium relative to fenced plots. They concluded that herbivores preferentially consume plants higher in sodium and may thus historically have selected for a higher abundance of salt-intolerant plant taxa. Other sources of sodium potentially include fungi (which Scharnagl, Scharnagl, & von Wettberg, (2017) called "nature's potato chip"), rotting logs (see Dudley *et al.,* 2012), and bark chewing (Au, Youngentob, Clark, Phillips, & Foley, 2017).

Historically, salt licks may have played a role in shaping ungulate ecology in North America; for example, bison east of the Mississippi created trails from grazing sites to well-known licks in the Appalachian plateau (Jones & Hanson, 1985). The most striking example may be Big Bone Lick, near Cincinnati (>700 km from coastline, and at 151 m elevation), with a wide assemblage of apparently trapped and fossilized vertebrate taxa, including many from the late Pleistocene (Schultz, Tanner, Whitmore, Ray, & Crawford, 1963; Jones & Hanson, 1985). Geophagy at both natural and artificial sodium sites has also been observed in some North American granivorous birds (e.g., Rea, 2017; Sanders & Koch, 2018), which, as herbivorous taxa, are similarly salt-deprived. Thus, large-scale biogeographical variation in the extent of marine salt deposition may affect salt-seeking behavior in a wide variety of wildlife.

Our results indicate that historical patronage of salt licks is constrained geographically, and that foraging behavior of ungulate and other phytophagous taxa may be influenced over large spatial scales by sodium availability. Physiological measures of salt deprivation and intake may illustrate similar geographical patterns, with implications for both fitness and population growth (e.g., Aumann & Emlen, 1965).

DATA AVAILABILITY STATEMENT

Data associated with the GIS analyses used in this study are archived in Dryad (https://doi.org/10.6078/D1CM5S).

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BIOSKETCH

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AUTHOR CONTRIBUTIONS

RD and AEM conceived the study and designed the data analyses. AEM conducted the analyses. RD and AEM wrote the manuscript.