Geographic variation in trace mineral concentrations in blood of mule deer from the Mojave Desert, California, USA

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FULL RESEARCH ARTICLE

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Abstract

Minerals are important nutrients and are essential components of the diets of animals. Nutritional requirements or minimum concentrations of minerals for nutritional health are largely unknown for the majority of large, free-ranging herbivores. We investigated concentrations of 9 trace minerals in mule deer (*Odocoileus hemionus*) inhabiting 3 distinct geographic areas—Cima Dome, New York Mountains, and the Mid Hills—in the eastern Mojave Desert, San Bernardino Co., California from 2008 to 2016. These areas differed in vegetative communities, topography, water availability, and fire histories. Telemetered mule deer demonstrated high fidelity to each of these areas, and movement by those individuals between study areas was not detected. During our investigation, overall differences occurred in mean concentrations of magnesium ($P < 0.001$), calcium ($P = 0.022$), phosphorus ($P = 0.023$), potassium ($P = 0.042$), and selenium ($P < 0.001$) among the 3 geographic areas. Among years, differences occurred in concentrations of the trace elements investigated in the New York Mountains with the exceptions of magnesium and potassium; at Cima Dome with the exceptions of iron, sodium, potassium, and selenium; and in the Mid Hills with the exceptions of magnesium and zinc. A positive upward trend existed between selenium concentration in the New York Mountains and the year of sample collection ($P < 0.05$), and a similar—albeit not significant—upward trend was discernible in the Mid Hills, but no such relationship was apparent at Cima Dome. These results emphasize the importance of investigating micronutrient status of mule deer on a local scale and temporally and add to the sparse information available on trace mineral concentrations in mule deer. Despite limited samples (≤165), we make available for the first time reference values for mule deer inhabiting the Mojave Desert, to serve as a baseline against which to measure responses to future environmental perturbations or for comparison with deer occupying other disparate ecosystems, and further contribute to the derivation of reference values for mule deer in general.

Key words: California, geographic variation, macronutrients, micronutrients, Mojave Desert, mule deer, nutrition, *Odocoileus hemionus*, temporal variation, trace minerals

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Introduction

Minerals are important nutrients in the body, but represent a small fraction of total composition, usually < 5% (Robbins 1993; Barboza et al. 2009). Mineral requirements or levels of toxicity for animals may vary with age, sex, species, season, growth stage, and reproductive state of individuals (Kalinsinska 2019), but actual requirements for most species of wildlife have not yet been determined (Robbins 1993; Barboza et al. 2009). Although other nutrients including sources of protein and energy are of primary interest with respect to body condition, deficiencies of minerals are important and can affect fertility, productivity, and survival (Robbins 1993). Minerals also play important roles in disease resistance, antler growth or strength, recruitment, and vital rates of large herbivorous mammals (French et al. 1956; Bowyer 1983; Flueck 1991; Failla 2003; O’Hara et al. 2001; Johnson et al. 2007). As a result, mineral concentrations often vary among tissues or organs responsible for the multitude of physiological processes in the bodies of animals (Barboza et al. 2009).

Despite their importance to animal health, some minerals can be toxic or otherwise harmful if they are overabundant in the diet or in animal tissues (McDowell 2003; Pond et al. 2005; Radostits et al. 2007; Duffy et al. 2009; Hernandez et al. 2017; Herrada et al. 2024; Bedouet et al. 2025). Indeed, at the population level, mineral deficiencies or toxicities may both be overlooked and attributed to other factors such as food shortage, parasites, infectious agents, or even severe weather (Robbins 1993). In the absence of information pertaining to mineral concentrations in wildlife, it is impossible for managers to ascertain if those levels are adequate, deficient, or toxic (Kalisinska 2019). As a result, the potential for micronutrient levels to affect individual animals or entire populations remains speculative.

In a classic example illustrating the importance of trace minerals, antlers of tule elk (*Cervus canadensis nannodes*) occupying the Owens Valley in Inyo County, California develop normally in size and conformation but long have been known to break easily during the mating season when males compete for breeding opportunities (McCullough 1969). Although overall forage quality is an important contributor to antler quality, bone fragility has been associated with mineral imbalances (French et al. 1956;

Underwood 1977; Gogan et al. 1988; Bleich 1990; Robbins 1993). This observation is particularly true in tule elk, which generate great interest among hunters and non-hunters alike, and are valued highly for aesthetic, recreational, and economic reasons. A very high proportion of males inhabiting the Owens Valley exhibited broken antler tines (82%), and 36% had broken main beams shortly after the onset of rut (Johnson et al. 2005). McCullough (1969) attributed the high proportion of males exhibiting broken antlers to a probable mineral imbalance involving inadequate amounts of calcium, but not phosphorus, which was confirmed many decades later by Johnson et al. (2007).

Mule deer (*Odocoileus hemionus*) are popular big game animals and also generate tremendous interest among the general public. Mule deer are widely distributed across western North America (Heffelfinger and Latch 2023; Jensen et al. 2023), but little is known is known about mineral nutrition despite the widespread distribution of that species. Although numerous authors have investigated trace element concentrations in white-tailed deer (*Odocoileus virginianus*), similar contributions to the literature on mule deer since that of Anderson (1981) are few. The information presented herein augments the few data currently available (Anderson 1981; Anderson and Medin 1982; DelGiudice et al. 1990; Zimmerman et al. 2008; Myers et al. 2015; Roug et al. 2015) for mule deer, and most of which were subject to the limitations associated with small sample sizes (Friedrichs et al. 2012; **Appendix I**). As a result, information presented herein is of particular value (Myers et al. 2015).

In this paper, we describe concentrations of 9 trace elements (the micro-minerals iron, copper, zinc, and selenium, and macro-minerals calcium, magnesium, phosphorus, potassium, and sodium) in the blood of mule deer occupying three distinct geographic regions of the Mojave Desert wherein those cervids occupy a variety of habitats. Fidelity to these habitat types in which deer were captured and the lack of movement among the three regions of the study area, strong selection for the habitat types represented by each region, and differing landforms and vegetation among the three regions (Bush 2015; McKee et al. 2015; Heffelfinger et al. 2018) provided the opportunity to (1) evaluate trace mineral concentrations in the blood of adult female mule deer on a local basis; (2) test for differences in blood parameters among animals sampled from populations occupying 3 Mojave Desert vegetation types; and (3) provide reference values for mule deer occupying the Mojave Desert using data that are not conflated with results from other disparate systems.

Methods

Study Area

Our study area was located in the eastern Mojave Desert, San Bernardino County, California, and was bounded on the north and south by U.S. Interstate Highways 15 and 40, respectively, on the west by Kelbaker Rd., and on the east by the California-Nevada state line, wherein we investigated mule deer ecology from 2008 to 2016 (Bush 2015; McKee et al. 2015; Heffelfinger et al. 2018, 2020). Vegetation assemblages representative of the Great Basin, Mojave, and Sonoran deserts create heterogeneity across the landscape (Thomas et al. 2004), which is characterized by distinct, rugged, mountain ranges separated by bajadas, playas, or dunes, and elevations range from 270 m to 2,400 m (Thorne et al. 1981; McKee et al. 2015). The study area lies within a legislatively defined area administered by the National Park Service (NPS) known as the Mojave National Preserve (**Fig. 1**; Pauli and Bleich 1999). Climate is xeric and representative of the Mojave Desert in general, and is characterized by high summer temperatures and limited annual precipitation that is bimodal with peaks during winter and summer seasons (Hereford et al. 2004), although inter-annual and spatial variation in precipitation both are substantial (Rundel and Gibson 1996). Elevation and landform play important roles in determining precipitation and temperature on a local basis in the eastern Mojave Desert (Bleich 2017), contributing further to heterogeneity of vegetation and affecting forage quality, forage availability, or both (Bleich et al. 1992, 1997). Moreover, concentrations of trace elements in forage species have been shown to vary across the region (Bleich et al. 2017).

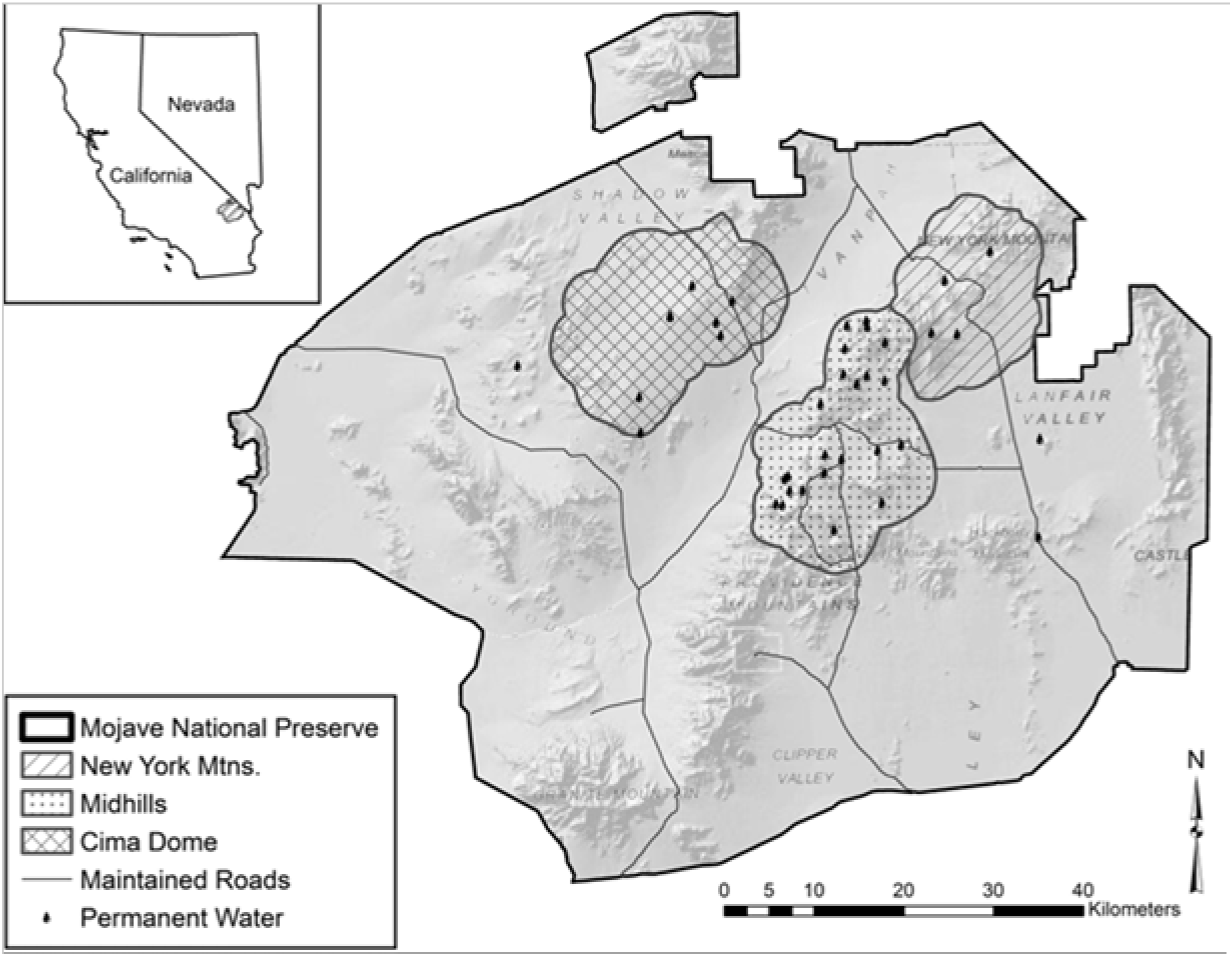

Figure 1. Three study areas were located in Mojave National Preserve, San Bernardino Co., California, and are identified as the New York Mountains, Cima Dome, and the Mid Hills. Telemetered mule deer did not move among these three areas during 2008–2016. Figure adapted from Heffelfinger et al. 2020.

We identified 3 distinct geographic regions of the eastern Mojave Desert as the New York Mountains (35°17′ N, 115°15′ W), Cima Dome (35°18′ N, 115°35′ W), and the Mid Hills (35°07′ N, 115°25′W). Each of these areas was inhabited by mule deer (Bleich and Pauli 1999; Bush 2015; McKee et al. 2015; Heffelfinger et al. 2018) and characterized by distinctive topography, habitat type, and availability of water (Figs. 1 and 2). Vegetation in the New York Mountains was dominated by pinyon-juniper (*Pinus* spp. – *Juniperus osteosperma*) woodland at upper elevations and desert scrub at lower elevations (McKee et al. 2015; Heffelfinger et al. 2018). Vegetation at Cima Dome was dominated by Joshua tree (*Yucca brevifolia*) woodland, and vegetation in the Mid Hills was pinyon pine-juniper woodland that experienced a massive (285 km^2) conflagration 3 years prior to the onset of our investigation (Casebier 2005). As a result of that fire, vegetation within the burn was dominated by globemallow (*Sphaeralcea* spp.), bitterbrush (*Purshia* sp.), and desert almond (*Prunus fasciculata*) during our research. Surface water available to mule deer occurred at a mean density of 0.01 sources/km^2 in the New York Mountains, 0.02 sources/km^2 at Cima Dome, and 0.08 sources/km^2 in the Mid Hills (McKee et al. 2015).

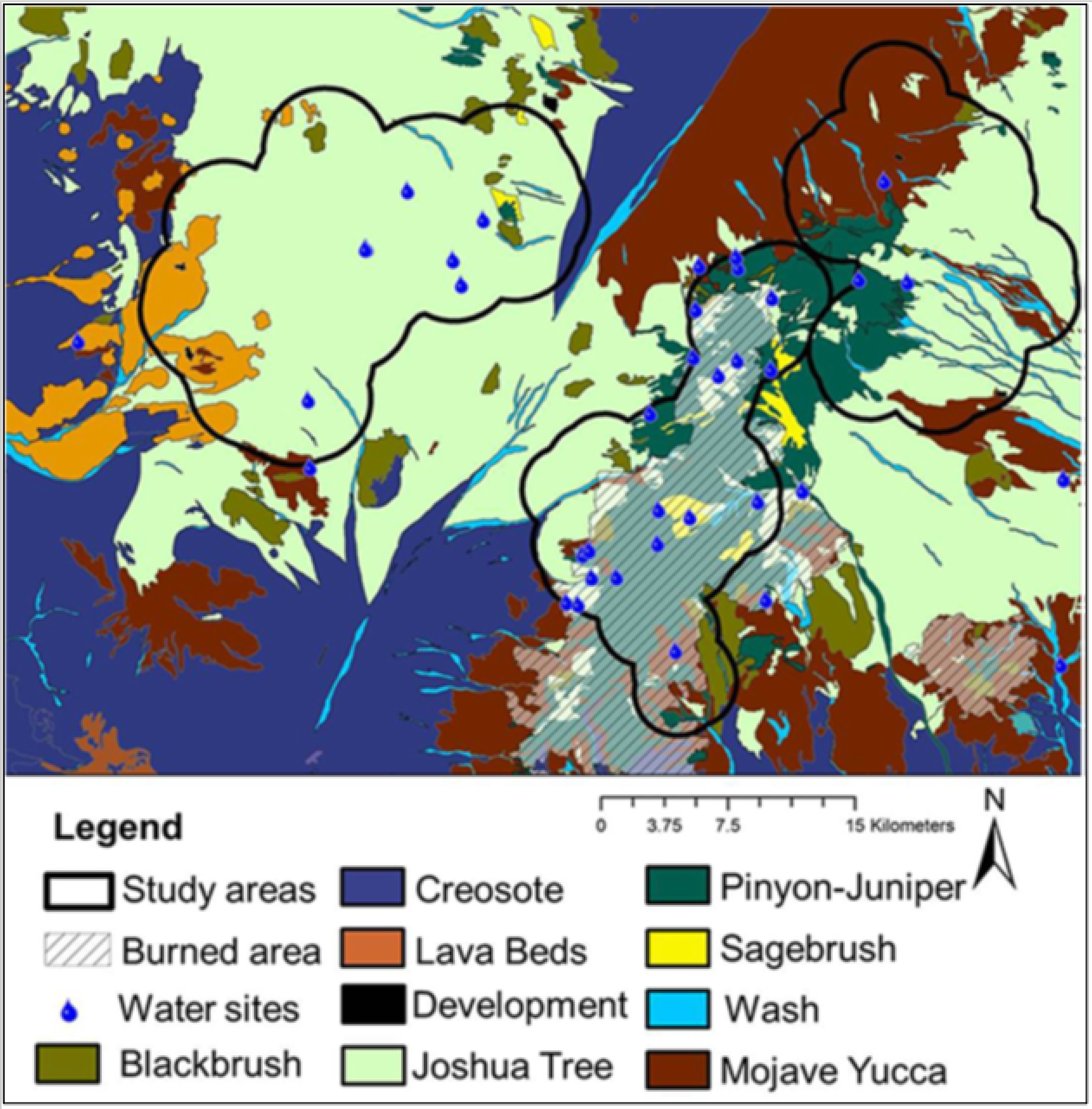

Figure 2. Distribution of vegetation types and developed areas occurring at Cima Dome (upper left polygon), in the New York Mountains (upper right polygon), and the Mid Hills (lower center polygon), in each of the 3 study areas in Mojave National Preserve, San Bernardino County, California.

Sample Collection

We used a helicopter and net-gun to capture mule deer (Krausman et al. 1985). Most animals were transported to a central processing area where morphometrics were determined, and biological samples were collected. From 2013 to 2016, we also measured nutritional condition of adult females (Monteith et al. 2013) using standard protocols developed and validated for mule deer (Stephenson et al. 2002; Cook et al. 2007, 2010), and we used ultrasonography to ascertain pregnancy (Stephenson et al. 1995). Several individuals processed in the field because of the distance from the location of capture to the processing area were not examined for pregnancy or body condition. Regardless of processing location, all animals were fitted with a Global Positioning System (GPS) telemetry collar (Wildlife GPS Datalogger, Sirtrack, Havelock North, New Zealand; McKee et al. 2015). Animals processed at a central area were transported back to the capture location prior to being released, and all animals processed in the field were released at the site of capture.

We collected blood by jugular venipuncture using a 25-mm, 18-gauge needle and a 60-ml syringe. We placed whole blood from each deer in a trace element EDTA collection tube for selenium analysis; an additional sample was placed in an additive-free trace element collection tube to be analyzed for calcium, copper, iron, magnesium, phosphorus, potassium, sodium, and zinc. Those samples were centrifuged for ~12 minutes at ~1,750×g the day of collection, after which we transferred the serum to a new trace element collection tube. Samples then were placed on ice and kept refrigerated until delivered to the California Animal Health and Food Safety Laboratory at the University of California, Davis where samples were prepared and analyzed for the elements of interest using inductively coupled plasma-atomic emission spectrometry (Poppenga et al. 2012). Reporting limits were 2.0 and 0.1 mEq/l for sodium and potassium, respectively; 2 ppm for calcium; 1 ppm for phosphorus and magnesium; 0.2 ppm for iron; 0.05 ppm for zinc and copper; and 0.010 ppm for selenium.

All procedures were approved by the Institutional Animal Care and Use Committee at the University of Nevada, Reno (IACUC Protocol #00538). Additionally, methods were in keeping with guidelines established by the American Society of Mammalogists for research on wild mammals (Gannon et al. 2007; Sikes et al. 2011, 2016), and followed capture and handling procedures developed by the California Department of Fish and Game (CDFG 2007).

Statistical Analyses

We collected samples during late winter (i.e., late February or early March) from deer occupying three distinct areas and over a period of up to nine years, and composited analytical results from the three geographic areas across years to obtain an overall estimate for each trace mineral representative of the entire study area (i.e., the eastern Mojave Desert). We explored the potential for differences in trace element concentrations among areas, and also among years of sample collection within each of the 3 areas. We used one-way Analysis of Variance (ANOVA) to test for an overall difference ($\alpha = 0.05$) among mean values of analytes for deer occupying the New York Mountains, Cima Dome, or the Mid Hills. Similarly, we used one-way ANOVA to test for differences among mean values of analytes among years within each of those geographic areas. If mean values of analytes differed among areas, we relied on Tukey’s HSD to make pairwise comparisons (Zar 2010). In addition, we used Spearman’s Rank Correlation Coefficient to examine relationships between concentrations of selenium—the only element with a sufficiently long data stream (9 years)—and year of collection for the New York Mountains and Cima Dome—neither of which had experienced large wildfires for at least several decades—as well as the Mid Hills, which had experienced a massive wildfire three years prior to the onset of our investigation.

We composited analytical results from the three geographic areas across years and used Reference

Value Advisor (Greffre et al. 2011)—an Excel Spreadsheet add-in—to evaluate each variable for distribution and outliers, to calculate descriptive statistics, and to establish reference values for mule deer occupying the eastern Mojave Desert. Reference Value Advisor used Tukey's Test to flag outliers and confirmed them with the Dixon-Reed Test (Greffre et al. 2011). These are the first data on trace mineral concentrations from mule deer occupying the Mojave Desert and, with one exception, we had no compelling reason to exclude suspect data (Greffre et al. 2009). With respect to potassium, we excluded results for 11 samples ($\bar{x}$ = 19.45 mEq/L, range 12–44) collected consecutively on a single day from two of the geographic areas, and that likely represented pseudohyperkalemia when compared to results for all other samples collected during our investigation ($\bar{x}$ = 5.16 mEq/L, range 3.8–7.9). Pseudohyperkalemia is an elevation of potassium in blood serum and frequently results from improper collection, handling, or storage of a sample, but does not represent the level of potassium *in vivo* (De Rosales et al. 2017).

Results

We obtained blood from 194 mule deer captured in the New York Mountains (n = 66), at Cima Dome (n = 59), or in the Mid Hills (n = 69) during winter from 2008 to 2016. Differences occurred in mean concentrations of magnesium ($F_{2,92}$ = 10.07, $P < 0.001$), calcium ($F_{2,92}$ = 3.95, $P = 0.022$), phosphorus ($F_{2,91}$ = 3.92, $P = 0.023$), potassium ($F_{2,81}$ = 3.29, $P = 0.042$), and selenium ($F_{2,162}$ = 25.85, $P < 0.001$) among the New York Mountains, Cima Dome, and the Mid Hills (**Table 1**). Among years, differences occurred in concentrations of all trace elements in the New York Mountains with the exceptions of magnesium and potassium (**Table 2**); at Cima Dome with the exceptions of iron, potassium, and selenium (**Table 3**); and in the Mid Hills with the exceptions of magnesium and zinc (**Table 4**). In the New York Mountains a positive upward trend existed between selenium concentration and the year of collection (n = 6, $r_s = 0.893$, $P < 0.05$), and a similar—albeit not significant—upward trend was discernible in the Mid Hills (n = 6, $r_s = 0.309$); no such relationship was apparent at Cima Dome (n = 6, $r_s = 0.058$). Reference values for analytes from all three areas and all years combined are presented in **Table 5**.

Table 1. ANOVA results comparing concentrations of 9 analytes for female mule deer (*Odocoileus hemionus* ssp.) occupying three distinct regions of the eastern Mojave Desert, mean (± SE) of all sampling years combined, in Mojave National Preserve, San Bernardino County, California, 2008–2016. Where ANOVA identified significant differences among the 3 areas, Tukeys HSD revealed pairwise differences in mean concentrations of magnesium, phosphorus, calcium, and selenium, which are indicated by differing superscripts ('a' and 'b'). Mean values for potassium exclude samples from 11 deer in which potassium concentrations were substantially elevated and likely represented pseudohyperkalemia (De Rosales et al. 2017), as explained in the text.

Analyte (units)	ANOVA Results	New York Mtns	Cima Dome	Mid Hills
Fe (ppm)	$F_{2,92}$ = 2.01, P = 0.140	1.81 ± 0.124	1.53 ± 0.081	1.70 ± 0.074
Mg (ppm)	$F_{2,92}$ = 10.07, P < 0.001	36.31^{a} ± 0.690	32.52^{b} ± 0.963	31.97^{b} ± 0.610
Zn (ppm)	$F_{2,92}$ = 2.16, P = 0.121	1.17 ± 0.121	0.86 ± 0.063	1.05 ± 0.106
Cu (ppm)	$F_{2,92}$ = 2.59, P = 0.080	1.07 ± 0.088	0.94 ± 0.078	0.84 ± 0.050

Analyte (units)	ANOVA Results	New York Mtns	Cima Dome	Mid Hills
Ca (ppm)	$F_{2,92}$ = 3.95, P = 0.022	95.0^{a} ± 2.334	85.45^{b} ± 2.664	85.50^{b} ± 3.180
P (ppm)	$F_{2,91}$ = 3.92, P = 0.023	62.28^{a} ± 2.620	48.55^{b} ± 3.750	59.91 ± 4.227
Na (mEq/L)	$F_{2,92}$ = 1.34, P = 0.267	158.13 ± 2.436	153.79 ± 1.884	154.71 ± 1.477
K (mEq/L)	$F_{2,81}$ = 3.29, P = 0.042	5.45 ± 0.197	4.92 ± 0.148	4.89 ± 0.160
Se (ppm)	$F_{2,162}$ = 25.85, P < 0.001	0.215^{a} ± 0.0102	0.137^{b} ±0.0080	0.208^{a} ± 0.0066

Table 2. Means (±SE) from analysis of variance (ANOVA test statistic and p-value) for 9 trace minerals in female mule deer compared among years in the New York Mountains in Mojave National Preserve, San Bernardino County, California, 2008–2016. (Note: no data for 2010 and 2013)

Analyte (units)	ANOVA	P	2008	2009	2011	2012	2014	2015	2016
Iron (ppm)	$F_{3,28}$ = 3.39	0.032	1.29 ± 0.131	2.35 ± 0.286	1.63 ± 0.181	1.86 ± 0.222	—	—	—
Magnesium (ppm)	$F_{3,28}$ = 1.01	0.403	33.60 ± 1.208	37.25 ± 1.532	36.50 ± 1.164	36.31 ± 0.690	—	—	—
Zinc (ppm)	$F_{3,28}$ = 9.34	<0.001	0.54 ± 0.084	1.85 ± 0.286	1.24 ± 0.135	0.71 ± 0.053	—	—	—
Copper (ppm)	$F_{3,28}$ = 6.97	0.002	0.66 ± 0.045	1.23 ± 0.171	1.38 ± 0.140	0.67 ± 0.059	—	—	—
Calcium (ppm)	$F_{3,28}$ = 7.44	<0.001	95.20 ± 0.482	93.25 ± 1.645	87.17 ± 3.688	110.28 ± 4.063	—	—	—
Phosphorus (ppm)	$F_{3,28}$ = 4.86	<0.008	73.20 ± 6.514	59.75 ± 2.590	53.42 ± 4.389	72.57 ± 4.116	—	—	—
Sodium (mEq/L)	$F_{3,28}$ = 5.51	0.004	150.00 ± 3.162	147.50 ± 5.261	166.67 ± 3.760	161.43 ± 1.429	—	—	—
Potassium (mEq/L)	$F_{2,21}$ = 1.7	0.207	5.16 ± 0.244	—	5.26 ± 0.246	6.00 ± 0.468	—	—	—
Selenium (ppm)	$F_{5,52}$ = 3.04	0.018	0.16 ± 0.017	—	0.17 ± 0.010	0.22 ± 0.064	0.23 ± 0.019	0.22 ± 0.032	0.27 ± 0.021

Table 3. Means (±SE) from analysis of variance (ANOVA statistic and p-value) for 9 trace minerals in blood of female mule deer compared among years at Cima Dome in Mojave National Preserve, San

Bernardino County, California, 2008–2016. (Note: no data for 2010 and 2013)

Analyte (units)	**ANOVA**	**P**	**2008**	**2009**	**2011**	**2012**	**2014**	**2015**	**2016**
Iron (ppm)	$F_{3,25}$ = 0.95	0.432	1.50 ± 0.167	1.41 ± 0.114	1.73 ± 0.191	1.45 ± 0.132	—	—	—
Magnesium (ppm)	$F_{3,25}$ = 7.18	0.002	28.83 ± 0.910	29.80 ± 0.940	36.78 ± 1.862	35.25 ± 2.056	—	—	—
Zinc (ppm)	$F_{3,25}$ = 8.50	< 0.001	0.51 ± 0.034	0.87 ± 0.112	1.16 ± 0.070	0.73 ± 0.083	—	—	—
Copper (ppm)	$F_{3,25}$ = 19.45	< 0.001	0.73 ± 0.045	0.75 ± 0.057	1.46 ± 0.125	0.60 ± 0.040	—	—	—
Calcium (ppm)	$F_{3,25}$ = 8.29	< 0.001	89.00 ± 1.366	82.60 ± 3.015	76.44 ± 5.135	107.50 ± 2.500	—	—	—
Phosphorus (ppm)	$F_{3,25}$ = 8.25	< 0.001	45.00 ± 5.780	40.60 ± 3.509	44.33 ± 6.784	83.25 ± 5.121	—	—	—
Sodium (mEq/L)	$F_{3,25}$ = 12.68	< 0.001	146.67 ± 2.108	147.00 ± 2.134	163.33 ± 2.887	160.00 ± 0.000	—	—	—
Potassium (mEq/L)	$F_{3,25}$ = 1.88	0.159	4.55 ± 0.184	4.70 ± 0.148	5.16 ± 0.393	5.53 ± 0.184	—	—	—
Selenium (ppm)	$F_{5,43}$ = 1.00	0.431	0.18 ± 0.055	—	0.11 ± 0.015	0.13 ± 0.018	0.12 ± 0.016	0.15 ± 0.012	0.15 ± 0.015

Table 4. Means (±SE) from analysis of variance (ANOVA statistic and p-value) for 9 trace minerals in female mule deer compared among years in the Mid Hills in Mojave National Preserve, San Bernardino County, California, 2008–2016. (Note: no data for 2010 and 2013)

Analyte (units)	**ANOVA**	**P**	**2008**	**2009**	**2011**	**2012**	**2014**	**2015**	**2016**
Iron (ppm)	$F_{3,30}$ = 8.38	< 0.001	1.64 ± 0.173	1.34 ± 0.076	1.94 ± 0.101	2.08 ± 0.120	—	—	—
Magnesium (ppm)	$F_{3,30}$ = 1.60	0.21	31.29 ± 1.782	30.45 ± 0.790	33.36 ± 1.170	33.20 ± 0.583	—	—	—
Zinc (ppm)	$F_{3,30}$ = 2.8	0.057	0.54 ± 0.033	1.23 ± 0.146	1.26 ± 0.242	0.94 ± 0.218	—	—	—
Copper (ppm)	$F_{3,30}$ = 33.46	< 0.001	0.63 ± 0.037	0.72 ± 0.040	1.20 ± 0.060	0.62 ± 0.016	—	—	—

Analyte (units)	ANOVA	P	2008	2009	2011	2012	2014	2015	2016
Calcium (ppm)	$F_{3,30}$ = 30.01	< 0.001	90.00 ± 2.093	87.091 ± 2.226	67.18 ± 4.251	116.00 ± 2.450	—	—	—
Phosphorus (ppm)	$F_{3,29}$ = 5.97	< 0.003	55.86 ± 8.362	57.27 ± 6.093	48.5 ± 7.032	94.20 ± 4.862	—	—	—
Sodium (mEq/L)	$F_{3,30}$ = 6.49	< 0.002	150.00 ± 0	150.00 ± 1.907	158.18 ± 2.960	164.00 ± 2.450	—	—	—
Potassium (mEq/L)	$F_{3,27}$ = 4.63	0.01	5.61 ± 0.466	4.39 ± 0.136	4.57 ± 0.178	5.40 ± 0.324	—	—	—
Selenium (ppm)	$F_{5,52}$ = 3.92	< 0.005	0.12 ± 0.016	—	0.21 ± 0.018	0.20 ± 0.035	0.21 ± 0.017	0.21 ± 0.009	0.20 ± 0.008

Table 5. Descriptive statistics, reference intervals, and 90% confidence intervals for lower and upper confidence limits determined for female mule deer (*Odocoileus hemionus*) in Mojave National Preserve, San Bernardino County, California, 2008–2016.

Analyte (units)	n	Mean	SD	Median	Range	Reference Interval	90% CI Lower	90% CI Upper
Iron (ppm)	95	1.68	0.544	1.60	0.6–3.7	0.714–3.160	0.600–0.960	2.662–3.700
Magnesium (ppm)	95	33.6	4.60	33.0	23–47	25.8–46.0	23.0–27.0	41.0–47.0
Zinc (ppm)	95	1.03	0.581	0.880	0.38 –3.50	0.410–3.000	0.380–0.460	2.100–4.500
Copper (ppm)	95	0.95	0.417	0.81	0.46–2.70	0.500–2.760	0.467–0.503	1.756–2.337
Calcium (ppm)	95	88.7	16.10	89.0	32–120	59.4–120.0	32.0–62.6	116.0–120.0
Phosphorus (ppm)	94	56.36	21.260	54.50	8.9–100.0	20.13–100.0	8.90–26.0	97.25–100.0
Sodium (mEq/L)	95	155.6	11.10	160.0	120–200	140.0–180.0	120.0–140.0	170.0–200.0
Potassium (mEq/L)[a]	84	5.06	0.910	4.85	3.7–7.9	3.71–7.65	3.70–4.10	6.80–7.90
Selenium (ppm)	165	0.186	0.7250	0.180	0.05–0.50	0.078–0.368	0.050–0.091	0.300–0.500

[a] Excludes samples from 11 deer suspected of pseudohyperkalemia in 2009; see text for details.

Discussion

Although mule deer have been studied extensively across their range, trace mineral concentrations rarely have been reported, thereby enhancing the utility of our results (Myers et al. 2015). Indeed, few authors have provided such information (**Appendix I**), and reference intervals of trace elements in blood (**Table 5**) previously have not been reported for mule deer (Myers et al. 2015) or for the majority of wild species. Ours is the first effort to generate reference values for trace minerals in the blood of mule deer and were derived at a localized scale. Thus, readers should interpret our results in the context of those available for other North American cervids or domestic livestock, and acknowledge the limitations associated with that approach (Myers et al. 2015).

Data presented herein provided the opportunity to compare values for mule deer occupying three distinct habitat types within the Mojave Desert (**Table 1**). Mean values of iron, zinc, copper, and sodium did not differ among the three areas and were similar to those for other populations of mule deer for which limited information is available (Oliver et al. 2000; **Appendix I**), as well as for white-tailed deer (*Odocoileus virginianus* ssp.) and domestic livestock (Kie et al. 1983; Puls 1994; Chitwood et al. 2013). Mean values for magnesium, calcium, phosphorus, potassium, and selenium differed among the three areas but, with the exception of phosphorus, generally were within the ranges of values available in the literature (**Appendix I**). Mean levels of phosphorus were low relative to ranges previously reported for mule deer (**Appendix I**), which was unanticipated given the recent fire in the Mid Hills and the role of fire in recycling that essential nutrient (Butler et al. 2018).

Despite differences in mean concentration of potassium in blood of mule deer occupying the Mid Hills ($\bar{x} = 5.61$ mEq/l) and those occurring at Cima Dome ($\bar{x} = 4.55$ mEq/l), both values were within the ranges of values reported for mule deer elsewhere (**Appendix I**). A difference also existed in the concentrations of magnesium in mule deer occupying the New York Mountains ($\bar{x} = 33.6$ ppm) and those occupying Cima Dome (28.83 ppm), but those values also were within the ranges of magnesium reported previously for that taxon (**Appendix I**). The low values at Cima Dome may have reflected differences in substrate chemistry when compared to the Mid Hills or the New York Mountains. Additionally, the recent fire in the Mid Hills may have resulted in a temporary increase in concentrations of potassium in vegetation (Ohr and Bragg 1985). Moreover, biomass of preferred forage may have increased after the fire; although total mineral mass is generally not affected by fire, availability of some minerals on xeric sites is temporarily increased because of release from litter or from standing perennial plant material (Merrill et al. 1980). Finally, we cannot rule out the potential for a sample size effect, which may become less apparent with additional sampling.

Similar to results reported by earlier investigators (Anderson and Medin 1982; Myers et al. 2015; Roug et al. 2015), we found annual differences among the populations sampled, among locations (**Table 1**) or among years, but on a much smaller geographic scale (**Tables 2–4**). Seasonal variation in mineral concentrations is known to occur (Borch-Iohnsen and Nilssen 1987; Staaland and Hove 2000), and our samples were obtained during the same period each year. That alone, however, may not rule out within-year seasonal effects of localized precipitation on plant productivity and resultant declines or increases in forage availability. It is possible that our findings reflect individual variation within each of the three populations we investigated rather than covarying with annual precipitation or other climatological factors. Nevertheless, herbivores derive minerals from the forage consumed and the concentrations of minerals in vegetation—or combined with osteophagy (Krausman and Bissonette 1977; Bowyer 1983; Warrick and Krausman 1986; Keating 1989) or geophagy (Holl and Bleich 1987; Ayotte et al. 2006) potentially to supplement uptake of minerals—and that ultimately is a function of edaphic factors dependent on the underlying geology of the area in question (Van Soest 1994). The geological substrate did not change in any of the areas we investigated.

Differences between fire histories in the New York Mountains, at Cima Dome—neither of which had burned in recent decades—and the Mid Hills could provide insight into differences in selenium concentrations among deer occupying each of those areas, but wildfire has been shown to play only a minor role in selenium availability (Burton et al. 2016). Although plant succession was ongoing in the Mid Hills throughout our investigation and there was a general upward trend in selenium concentrations in mule deer over 9 years, this relationship likely is not readily explained by fire history. Further, a stronger and significant upward trend in selenium concentration occurred among deer inhabiting the New York Mountains (r_s = 0.893), an area that was not impacted by wildfire, and there was virtually no relationship between selenium concentration and time at Cima Dome (r_s = 0.058), neither of which had experienced recent conflagrations. Thus, multiple local factors likely influence results and, as emphasized previously (Pierce and Bleich 2003, Bleich et al. 2019), demonstrates the value of sampling at scales that reflect differing ecological or temporal settings (**Appendix I**).

Despite increasing interest in nutrition and its importance to population performance (Monteith et al. 2023), information on geographic or temporal variation in mineral content of various forage species remains poorly researched (Bleich et al. 2017). Variability in habitat selection by mule deer in the eastern Mojave Desert provided the opportunity to explore that question and add to the scant information available on trace elements in the blood of this widely distributed cervid. Environmental change—whether the result of stochastic events such as fire or extreme weather, long-term responses of vegetation to increased atmospheric CO_2 (Hamerlynck et al. 2000), climate change (Hantson et al. 2021), seasonal variation in rainfall (Greene et al. 1987, Sprinkle et al. 2000), seasonal changes in plant phenology (Staaland and Hove 2000), or the result of pollution from a variety of sources—singly or collectively has the potential to alter soil chemistry and resulting levels of micro-minerals or macro-minerals in soils, forage, or in wildlife itself (Harrison and Dyer 1984; Flueck 1991; Basanta et al. 2002; Garcia-Marco and Gonzalez-Prieto 2008; Duffy et al. 2009). Moreover, the large wildfire in the Mid Hills (Casebier 2005) just prior to the onset of our investigation, and additional wildfires at Cima Dome (McAuliffe 2021) and in the New York Mountains (Thornton 2023) shortly after our investigation ended, recently have altered the composition of vegetation across extensive portions of our study areas. These events provide heretofore unprecedented opportunities for continuing investigations of vegetation succession, its effect on the chemical composition of mule deer forage, and trace element concentrations among mule deer occupying a variety of habitat types across a xeric desert ecosystem; as yet, those opportunities have not been realized.

Nutritional requirements are not well understood for most species of wildlife (Robbins 1993; Johnson et al. 2007; Barboza et al. 2009), but mule deer are among the most widely distributed ungulates native to North America (MDWG 2004; Heffelfinger and Latch 2023; Jensen et al. 2023). Rather than assuming that information or descriptive statistics from a single location are representative across the range of this taxon, differences among geographic areas or populations should be anticipated (Pierce and Bleich 2003). It would be useful if a range of values or thresholds for deficiency (or toxicity) of mineral concentrations for mule deer were established (Myers et al. 2015) for use as baselines against which to compare changes resulting from environmental perturbations (Duffy et al. 2009), or as precursors to a lowered immune response and its potential for population-level effects of disease (Downs and Stewart 2014). Additionally, a better understanding of mineral availability and metabolism, and their roles in population ecology of large herbivores would be of value (Flynn et al. 1977; Robbins et al. 1985; Frank et al. 1994; O'Hara et al. 2001; Barboza et al. 2003). Such information also will help in determining the relevance of these elements in the overall health of local populations (Myers et al. 2015), and population biology—especially in the form of life-history investigations—is among the most promising areas of micronutrient ecology, in that variation in clutch size and body size of offspring may be a function of ecosystem biogeochemistry (Kaspari 2021). Indeed, long-term screening will advance understanding of population-level and individual-animal concentrations of trace elements in the context of population health (Poppenga et al. 2012), geographic location (Bleich et al. 2017), or environmental conditions (Pierce and Bleich 2003).

Many environmental factors affect mineral concentrations in forage consumed by large herbivores (Staaland and Hove 2000; Staaland and White 2001; Poppenga et al. 2012; Bleich et al. 2017). Among these are landscape features (Kozakiewicz et al. 2018), differences in elemental concentrations in substrate (Carlisle and Cleveland 1958; Hunt 1966; Lisk 1972; Van Soest 1994; Banuelos and Ajwa 1999), seasonal variation in rainfall (Greene et al. 1987; Sprinkle et al. 2000), moisture content of forage (Holl and Bleich 1987), diet at the time of sample collection (Johnson et al. 2007; Rosen et al. 2009; Bleich et al. 2017; Myers et al. 2015), and demographic characteristics (Pollock 2005). Further, handling and processing of samples (Ellervik and Vaught 2015), capture techniques (Kock et al. 1987), or other environmental stressors (Gartner et al. 1965; Duffy et al. 2009) also may influence analytical results.

Results reported herein add to the paucity of existing information on trace element concentrations in mule deer and emphasize the value of detailed sampling under a variety of ecological conditions, both spatially and temporally (Kie et al. 1983; Chitwood et al. 2013), and the importance of long-term monitoring of populations (Monteith et al. 2023). Deficiencies in trace minerals may be widespread, but the incidence of such underestimated because subclinical forms of deficiency can occur and go unnoticed or be attributed to other factors (Robbins 1993; Barboza et al. 2003; Radostits et al. 2007:1698–1699). Additionally, our findings emphasize the value of detailed sampling at multiple locations within the distribution of any particular species (Pierce et al. 2003; Bleich et al. 2019) and is information that may be useful when evaluating future conservation objectives (Reeves et al. 2024). Consistent with the recommendation of Anderson and Medin (1982), we encourage investigators to continue to add to our understanding of mineral content of forage, its effect on large, native herbivores—mule deer in particular—and to further explore variation in trace element concentrations among populations of this widely distributed species.

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