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Physical and Chemical Variables Promote Successful Nesting in High Mountain *Sceloporus* Lizards in Central México

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ABSTRACT: *Sceloporus* (*S. aeneus* and *S. scalaris*) are oviparous sibling lizard species inhabiting high mountain zones (>2700 m) in central México. Females of these species lay their eggs in soil mounds left by burrowing gophers (*Pappogeomys*). Numerous abiotic factors can affect site selection and subsequent development of the lizard embryos, but little is known of the relationship between the optimal physical and chemical variables of the surrounding soil that allow development and successful hatching of the eggs, especially in high-elevation environments. We hypothesized that soil parameters and temperature drive site selections by females seeking nest locations favorable to embryonic development. We recorded differences in the abiotic parameters of soil mounds between dry and rainy seasons, irrespective of whether the mounds contained eggs. Statistical analyses revealed that an environment of high relative humidity and stable temperatures necessary for mound selection as a nesting site were associated with intermediate moisture content, high organic matter content, high values of cation exchange capacity, and relatively high porosity of the soil substrate. Collectively, these values of abiotic soil traits prevent sudden changes in temperature and humidity at the nest depth, providing conditions that promote successful development and hatching. Understanding the relative importance of these abiotic factors in nest site selection by *Sceloporus* should contribute to an understanding of the adaptations of oviparous reptiles that reproduce in different environments.

Key words: Abiotic environment; Eggs; High altitude; Nest; Phrynosomatidae; Soil

HIGH elevation, and the associated conditions of low temperature, oxygen, and humidity, as well as high UV, impose special challenges to reptiles living under these conditions (Navas 2002; Yang et al. 2014; Reguera et al. 2015; Zamora-Camacho et al. 2016). The phrynosomatid lizards *Sceloporus aeneus* and *S. scalaris* are oviparous montane lizards distributed along the Central Volcanic Belt of México, occurring at elevations of up to 3300 m above sea level (asl). Females of these species typically lay their eggs in soil mounds created as a result of tunnel excavation by Merriam's pocket gophers (*Pappogeomys merriami*). Little is known, however, of the characteristics of the soil mounds that make a nesting site more or less attractive, or the abiotic conditions under which the eggs develop and eventually hatch.

In oviparous reptile species, nest temperature and humidity are important to embryonic development, because even slight variations in these factors might cause egg dehydration or premature hatching, or adversely affect the hatchling phenotype. For example, abnormalities in size and body proportions, growth rate, performance during locomotion, brain function, as well as other physical and metabolic disorders, have been correlated with extremes (for the species) in nest temperature or humidity (e.g., Shine 2002; Goodman 2008; Angilletta et al. 2009; Pearson and Warner 2016; Simoniello et al. 2016; Dayananda et al. 2017; Pallotta et al. 2017; Shine et al. 2017; Siviter et al. 2017). Consequently, temperature and humidity of the nest chamber are the abiotic factors that are typically analyzed, for oviparous reptiles in general and especially for montane lizards (Warner and Andrews 2002; Shine 2004). Data on

ambient air temperature and precipitation have also been collected in different studies of reptile nests to correlate abiotic parameters and the stage of development of the eggs therein (Deeming and Ferguson 1991; Shine et al. 1997; García-Collazo et al. 2012). However, these variables are most likely exerting a somewhat indirect influence on embryonic development.

Key factors in the suitability of nests for reptile embryonic development are the characteristics of the surrounding soil, very few of which have been thoroughly examined for any reptile species (e.g., Casas-Andreu 2003). The solid phase of soil consists of three sizes of primary particles of mineral origin: clays (<0.002 mm), silts (0.02–0.05 mm), and sands (>0.05 mm), and an organic fraction composed of organic matter in different grades of alteration (Gee and Bauder 1986; Kay and Angers 2002). The arrangement of primary particles and organic matter in larger units, termed aggregates, determines soil properties such as bulk density and porosity (Chenu and Bruand 2003; Soil Survey Staff 2014). These characteristics are responsible for processes such as gas exchange, the movement of water (Bruckler 2003), and the storage or mineralization of nutrients (Tercé 2003). As such, soil moisture and temperature are the result of the interaction of its physical properties with environmental factors such as solar radiation, precipitation, and vegetative cover (Taylor and Jackson 1986; Fardeau and Stengel 2003). Consequently, soil conditions are likely to be correlated with both lizard nest site selection and normal patterns of embryonic development.

The majority of studies on lizards and their nests in soil have been performed under controlled laboratory conditions, with the goal of revealing the optimal temperature and humidity conditions needed for a successful nesting. In turn, these studies allow extrapolation to the selective forces that might shape behavior of females searching for optimal nesting sites (e.g., Ji et al. 2002; Warner and Andrews 2002;

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Parker and Andrews 2007; Warner and Shine 2008; Angilleta et al. 2009; Du et al. 2010; Warner et al. 2013). The temperature of the soil in which reptile eggs are deposited can alter the eventual phenotypic traits of the adults (Shine et al. 1997), but the principal effect is on developmental time before hatching. We posit that the usual practice of analyzing only seasonal external temperature or rain data, or manipulating only these variables in a laboratory setting, is insufficient to understand fully the process of nest site selection among oviparous reptiles. In this study, we consider the abiotic parameters of the soil that surrounds the eggs when they are laid and how these parameters vary throughout incubation period.

Studies that encompass temperature, moisture, and abiotic parameters of actual nest sites necessarily involve a large number of factors and their interactions, and have rarely been undertaken, with most studies focusing instead on the relatively accessible nests of crocodilians (e.g., Lutz and Dunbar-Cooper 1984; Kofron 1989; Casas-Andreu 2003). Moreover, a sampling constraint of field studies is locating sufficient numbers of nests for analysis (Tinkle 1967; Perry and Dmi'el 1994; Shine 1999). In particular, there have been few field studies addressing nest site selection in squamates (e.g., Bustard 1969; Mautz 1982; Christian and Lawrence 1991), and none from localities above 3000 m asl. Given the limited information about abiotic characteristics of the soil that constitutes nesting sites, the objective of our study was to determine the microclimatic (temperature and moisture) and edaphic characteristics of the soil mounds that influence egg laying by females of two species of *Sceloporus* from high-elevation zones in central México. We hypothesized that soil parameters and temperature might influence nest site selection by female lizards in search of locations that are favorable for embryonic development.

MATERIALS AND METHODS

Sampling Sites

We conducted our study at three localities, two in the State of México and one in the Federal District of México (essentially, the outskirts of México City), along an elevational gradient of 2827–3200 m asl (Table 1). All sites were sampled during the dry season (December–April) and during August of the primary rainy season (June–September) of 2010.

Soil Mound and Nest Measurements

Physicochemical parameters were taken from intact, undisturbed gopher mounds. Soil samples for laboratory analysis were collected simultaneously in each locality. Field measurements taken at each mound included total mound depth from the surface to the bottom, depth of the eggs in mound (from the surface to the uppermost egg in the chamber), and mound circumference. We measured the percentage of moisture in the soil as volumetric water content (VWC) with the use of a SM100 WaterScout type sensor (Spectrum Technologies, Inc). Resistance to penetration was measured with a portable penetrometer (Eijkelkamp®). HOBO temperature recorders (Onset Instruments Co.) were then placed in three locations in and around the mound following the procedures of Andrews (2000): (1) externally at a height of 20 cm above the nest mound surface,

(2) 1 cm below the surface of the nest mound, and (3) 2–3 cm below the mound surface, at the location where the eggs were typically located. Temperature data were recorded via these sensors for 2 d.

For the physical and chemical characterization of the soil mound, samples of ~500 g were taken from each mound. Each sample was placed in a plastic bag and transferred to the Soil Fertility laboratory of the Institute of Geology of the National Autonomous University of México, where the sample was air dried, ground with a mortar and pestle, and then passed through a No. 10 mesh screen (USA Standard ASTM E 11–61) to obtain particles with a mean diameter of 2 mm. We performed analyses of color, texture (proportion of primary particles), real density, apparent density, pH, organic matter, capacity of cation exchange, and interchangeable bases, using methods based on the Official Mexican Standards Catalog (SEMARNAT 2002).

We determined the porosity of unaltered soil samples using the Kubiëna method of petrographic microscopy (Cady et al. 1986; Porta and López-Acevedo 2005). Thin films fixed in epoxy resin were prepared from the samples and photographed. ImagePro Plus (v4, Media Cybernetics, Inc., Rockville, MD) image analyzer was then used to determine the relative abundance of pores. Porosity is expressed as a percentage of the total area (Sustaita-Rivera et al. 2000; Torres-Guerrero et al. 2013).

Statistical Analyses

All statistical analyses were performed with the use of Statgraphics Plus (v5, Statgraphics Technologies, Inc., The Plains, VA), and assessed at a significance level of $\alpha < 0.05$. A principal components analysis (PCA) was used as an exploratory tool to determine the patterns of variation, and identify those variables that contribute to edaphic variation by reducing the dimensionality of the data in different soil samples (McGarigal et al. 2000). Only the principal components with eigenvalues >1.0 were considered for further analysis. We also employed a discriminant function analysis (DFA) with a linear model to determine which variable(s) separated the nest sites by elevation. This analysis is a classification technique used when there are observations of predetermined groups with two or more response variables for each group. This approach also makes possible the combination of variables with different units of measurement (McGarigal et al. 2000; Quinn and Keough 2002).

RESULTS

Frequency of Nest Occurrence

We examined 37 gopher mounds from the three localities to determine lizard egg distribution and depth within mounds (Table 1; Fig. 1). Of these, 13 mounds contained eggs, representing from 20 to 50% of the mounds examined at each site. The eggs of *Sceloporus aeneus* were found in both El Mapa and La Cima locations, and the eggs of only *S. scalaris* were found at El Ocotal (Table 1). The small sample sizes at two of the localities prevented us from detecting any interspecific variation in nest characteristics.

Abiotic Factors of Soil Mounds Containing Eggs

All measured temperatures exhibited circadian variation, with the highest temperatures recorded in the afternoon and

TABLE 1.—Characteristics of the three localities in central México where nest site characteristics for *Sceloporus aeneus* and *Sceloporus scalaris* were measured in 2010. In all cases, datum = WGS84, and the soil type at all three locations was characterized as a combination of andosols and vertisols (Soil Survey Staff 2014).

Parameter	Locality		
	El Mapa	La Cima	El Ocotal
Latitude	19°11'N	19°11'N	19°08'N
Longitude	99°50'W	99°19'W	99°57'W
Elevation (m)	3200	3000	2827
Lizard species present	<i>S. aeneus</i>	<i>S. aeneus</i>	<i>S. scalaris</i>
Number of mounds examined	9	18	10
Number of mounds with eggs	2	9	2
% of mounds containing eggs	22%	50%	20%
Mean number of eggs per mound	6.5	7.4	6.5
Mean egg depth (cm)	2.5	1.9	2.7

the lowest temperatures typically recorded just before sunrise. There were overall variations between locations (e.g., the highest-elevation site had the greatest temperature increase during the afternoon, whereas the lowest site had the smallest temperature interval; Fig. 2). However, the measured aerial, soil surface, and subsurface temperatures were similar across all localities. The surface and air temperatures at the mounds showed greater variation than the temperatures in the middle of the mound, with differences of up to 20°C occurring throughout the day. These differences were especially apparent during brief periods of the day when clouds passed over the mound. At

depths of 2–3 cm below the soil surface (where the majority of eggs were found), the greatest recorded fluctuation in temperature was 3°C (Fig. 2).

Differences in soil characteristics were detected as a function of season only, so we combined the data from the three localities (i.e., no site-specific soil properties). Soils in the study areas are predominantly of the andosol and vertisol types (Soil Survey Staff 2014; World Reference Base 2014). Andosols are young soils formed from volcanic deposits, characterized by being dark in color, with a medium to high content of organic matter, and are considered relatively fertile. In contrast, vertisols are soils with a high clay content (>30%), which usually have a franc-clay texture and high cation exchange capacity, dark color, medium organic matter content, and average fertility (Soil Survey Staff 2014; World Reference Base 2014). Soil samples from the mounds were consistent with the characteristics described for andosols and vertisols: the pH was moderately acidic and there was medium content of organic matter (Table 2). Additionally, the cation exchange capacity was medium to high and, because of the presence of clays, the concentrations of calcium, magnesium, and sodium were low—half that of potassium. There was average resistance to penetration and porosity, which corresponds to the franc-clay texture. The percentage of humidity was consistent with the texture of the soil and the percentage of porosity (SEMARNAT 2002; Porta and López-Acevedo 2005).

When compared to soil mounds lacking eggs, those mounds with *Sceloporus* eggs had a lower penetration

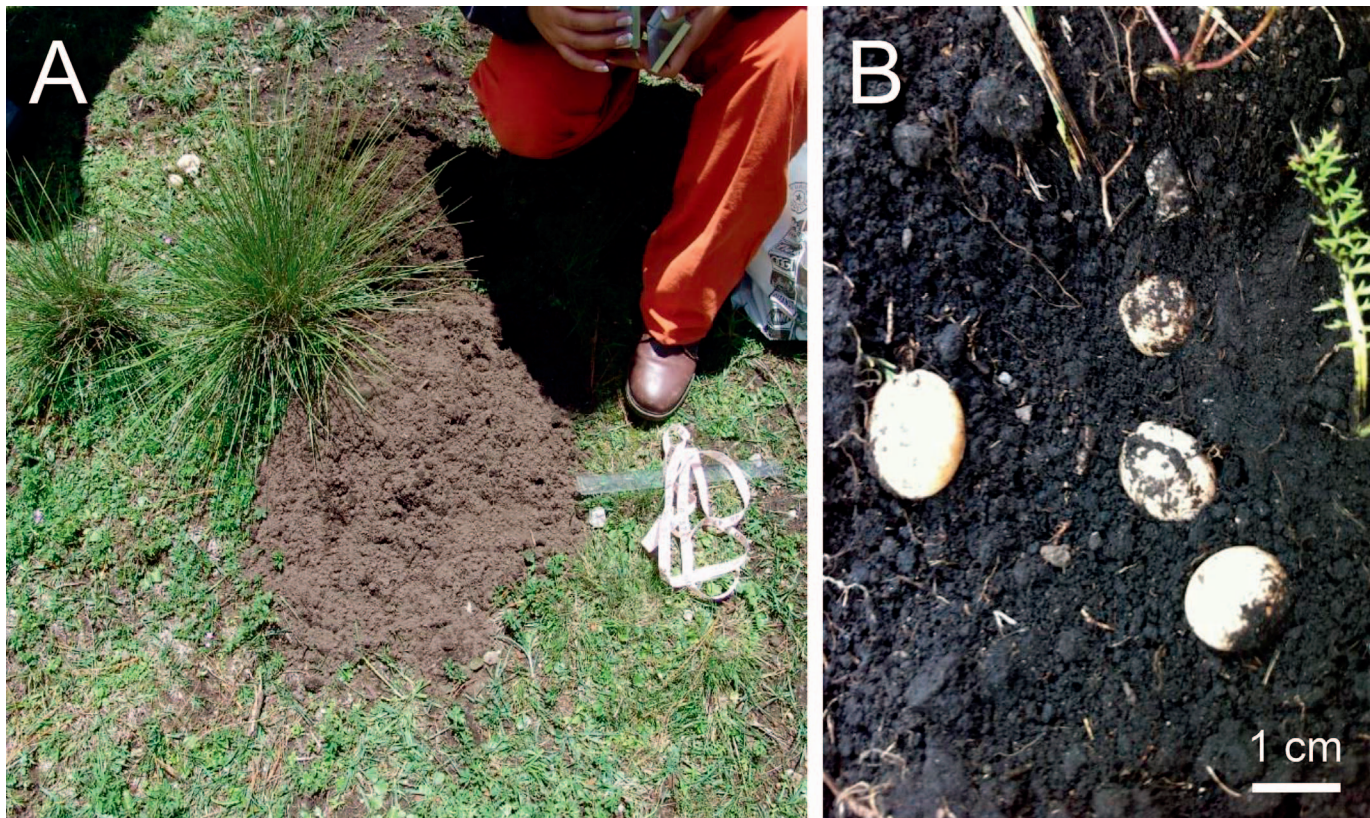


FIG. 1.—A typical nesting site for *Sceloporus* in central México at the El Ocotal site (2827 m above sea level). (A) Gophers (*Pappogeomys merriami*) discard soil from their excavations, forming a soft soil mound in which the lizard eggs are laid. (B) The eggs, typically laid 2–3 cm below the soil surface, have been exposed for this photograph. A color version of this figure is available online.

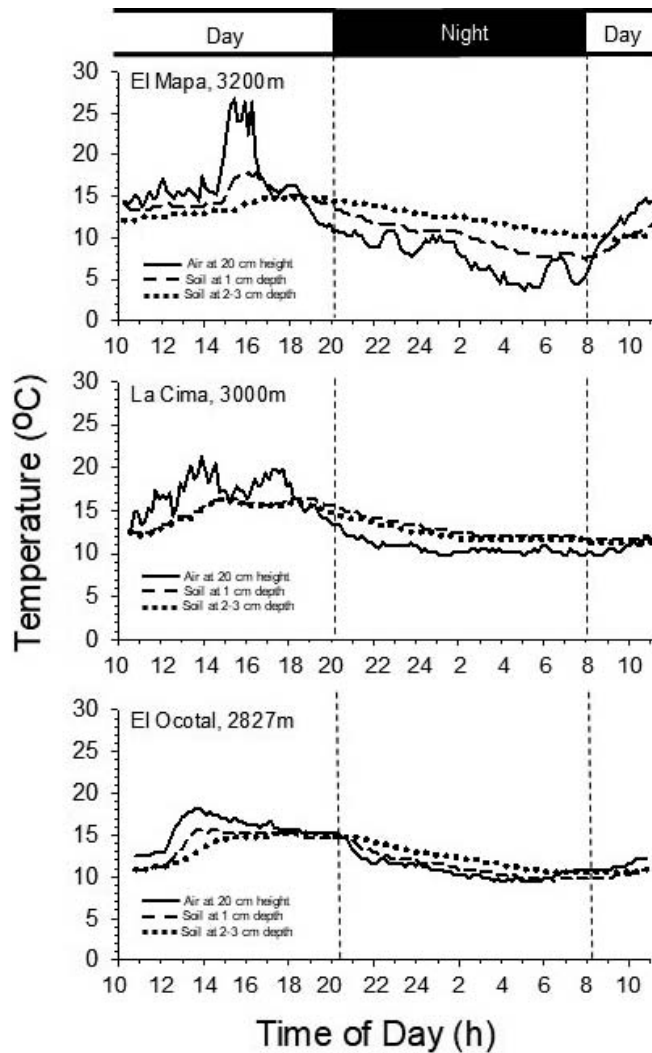


FIG. 2.—Representative temperature measurements in and above gopher mounds containing egg nests over a 24-h period for three nesting sites in central México in 2010: El Mapa, La Cima, and El Ocotal. Note the dampening of temperature fluctuations resulting from the soil layer of the mound.

resistance, and lower calcium, magnesium, and potassium contents. They also showed greater porosity and cation exchange capacity, and higher levels of sodium and organic matter (Table 2; Fig. 3). According to the PCA, the characteristics of the soil that had the greatest influence on the temperature and humidity of the mounds were porosity, organic content, and cation exchange capacity. With respect to precipitation, during the rainy season, the porosity was reduced by more than 50% and the resistance to penetration increased from zero to 2 kg/cm^3 , because of the formation of surface crusts by compaction of fine particles (Klute 1986; Porta and López Acevedo 2005).

Abiotic Correlates of Egg Presence in Nests

The PCA incorporated 13 of our measured variables: 5 representing the physical characteristics of the mounds and 8 related to soil morphology. Three principal components collectively explained 89.4% of the total variance in characteristics of those soil mounds that contained lizard

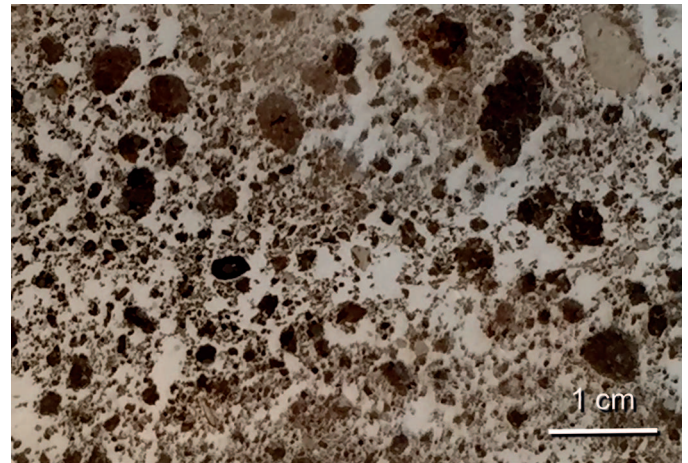


FIG. 3.—A representative epoxy resin thin film of a soil sample from a high-elevation gopher mound in central México. Specific soil color, porosity, and particle size varied with collection site. A color version of this figure is available online.

eggs (Table 3; Fig. 4). The first principal component predicting the presence of eggs in a mound explained the largest amount of variance (65%) and incorporated the variables of nest circumference, porosity, and temperature. Other variables that contributed to egg presence in nests included organic matter, calcium, humidity, and egg depth. The second principal component predicting the presence of eggs in a mound (14% of the remaining variance) incorporated the variables of soil resistance, pH, cation exchange capacity, magnesium, and potassium content (Table 2; Fig. 4).

Discriminant Function Analysis of Abiotic Factors

Discriminant function analysis indicated significant differences between the soil characteristics of mounds at all elevations with and without eggs according to the different seasons of the year. Moreover, sites were 100% correctly classified by the DFA (Tables 4 and 5; Fig. 5). Wilks's λ was significant for both functions, indicating that both contributed to the discrimination between variables (i.e., despite nonhomogenous covariance matrices, the DFA remained robust; Holden and Kelly 2010; Adebajji et al. 2016). The

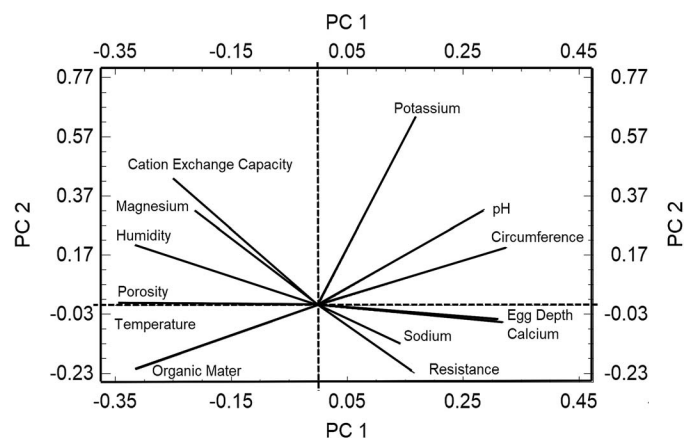


FIG. 4.—Principal components analysis (PCA) of abiotic variables associated with nests containing *Sceloporus* eggs in central México.

TABLE 2.—Mean values (± 1 SE) for physical and chemical characteristics of soil mounds with and without eggs from female spiny lizards (*Sceloporus* spp.) in central México. Differences in values for each mound type, as determined by a two-tailed *t*-test, are indicated in bold font.

Variable	Mounds with eggs <i>n</i> = 13	Mounds without eggs <i>n</i> = 22	<i>P</i>
Nest characteristics			
Mound depth (cm)	12.6 \pm 2.7	13.9 \pm 1.1	NS
Mound circumference (cm)	144.0 \pm 10.2	152.2 \pm 6.4	NS
Soil characteristics			
Resistance (kg · cm ²)	2.6 \pm 0.3	2.2 \pm 0.3	NS
Humidity (%)	31.6 \pm 2.7	26.5 \pm 2.4	NS
Porosity (%)	49.6 \pm 0.5	27.0 \pm 0.6	<0.0001
pH	5.8 \pm 0.1	5.8 \pm 0.1	NS
Organic matter (%)	8.8 \pm 0.6	8.4 \pm 0.6	NS
Cation exchange capacity (cmol · kg ⁻¹)	36.2 \pm 15.7	22.1 \pm 0.9	NS
Ca ⁺⁺ (mg · kg ⁻¹ soil)	1.2 \pm 0.3	4.2 \pm 0.6	<0.0001
Mg ⁺⁺ (mg · kg ⁻¹ soil)	0.9 \pm 0.1	3.4 \pm 0.5	<0.0001
Na ⁺ (mg · kg ⁻¹ soil)	2.1 \pm 0.3	0.8 \pm 0.04	NS
K ⁺ (mg · kg ⁻¹ soil)	0.3 \pm 0.02	0.5 \pm 0.1	NS

coefficients also illustrated the importance of grouping soil mound samples as a function of season within the DFA (Table 6).

DISCUSSION

Rationale for Combining Site Data

This study is among the first to quantify a suite of abiotic characteristics of the soil in which oviparous lizards lay their eggs, and the first for a lizard laying eggs at such high elevation. We choose to combine data from the three localities and the two lizard species based on three patterns in our data. First, the soil type (a mixture of andosols and vertisols) was the same at all three localities (Table 1). Moreover, some of the soil characteristics that we measured are more dependent upon external conditions (climate, vegetation) than on the genesis of the soil. Second, precipitation levels and temperatures at the three localities during any given season are relatively homogenous, as evidenced from climate data for the 10 yr that preceded sampling (A. Velázquez-Rodríguez, personal observation).

TABLE 3.—Principal component analysis for physical and chemical characteristics of the soil mounds in which *Sceloporus* eggs were found in central México. Principal component values outside the range of -0.3 to 0.3 (i.e., those factors that influenced nest sites selection) are indicated in bold font.

	Principal component (PC)		
	PC 1	PC 2	PC 3
Nest characteristics			
Egg depth	0.30	-0.05	-0.06
Nest circumference	0.32	0.19	0.07
Soil characteristics			
Resistance	0.16	-0.22	-0.63
Humidity	-0.31	0.20	0.04
Porosity	-0.34	-0.00	0.00
pH	0.28	0.32	-0.05
Organic matter	-0.31	-0.21	0.21
Cation exchange capacity	-0.24	0.42	0.22
Ca ⁺⁺	0.31	-0.05	0.26
Mg ⁺⁺	-0.21	0.31	-0.53
Na ⁺	0.14	-0.12	0.35
K ⁺	0.16	0.63	0.03
Temperature	-0.34	0.00	0.00
Analysis characteristics			
Eigenvalue	8.47	1.82	1.32
% of variance explained	65.2	14.0	10.1

The differences in soil conditions at the three localities arise from seasonal changes, not differences between sites within a given season. Third, the focal species in this study are sister taxa that (a) occur in areas having the same climatic conditions, (b) share reproductive phenology, and (c) establish their nests in substrates with edaphically homogenous characteristics.

Nest Characteristics Associated with Egg Presence

The main characteristics of the soil that influenced nest selection were porosity, cation exchange capacity, interchangeable ion content, and organic matter content. All of these properties are directly related to moisture content and soil temperature (SEMARNAT 2002; Porta and López-Acevedo 2005). A similar pattern is apparent in crocodylans (e.g., Casas-Andreu 2003), wherein embryos depend on the temperature of the nest microenvironment for development to proceed naturally (Deeming and Ferguson 1991; Andrews et al. 1999; Birchard 2004; Bicego et al. 2007; Molina and Leynaud 2017).

Soils with porosity values greater than 40% are correlated with moisture percentages greater than 30%. Additionally, empty interstitial spaces characteristic of porous soils facilitate gas exchange and infiltration, which prevents waterlogging and hypoxia within the soil mounds (Danielson and Sutherland 1986; Topp et al. 1996; SEMARNAT 2002; Porta and López-Acevedo 2005; Lipiec et al. 2006). On the

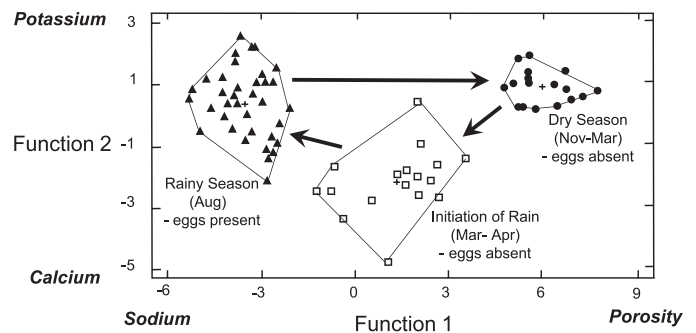


FIG. 5.—Discriminant function analysis (DFA) for mounds with and without eggs of *Sceloporus* in central México in 2010. The soil characteristics are different in mounds containing eggs in the rainy season when compared to mounds lacking eggs during the dry season and in the beginning of the rainy season.

TABLE 4.—Test statistics for the discriminant function analysis presented in Fig. 5.

	Discriminant function (DF)	
	DF1	DF2
Eigenvalues	17.78	2.37
Relative percentage	88.2	11.8
Canonical correlation	0.973	0.839
Wilks's lambda	0.016	0.297
Chi-square statistic	219.9	64.4
df	22	10
Significance level	$P < 0.00001$	$P < 0.00001$

other hand, a high content of organic matter guarantees an increase in soil temperature compared to surface and temperature, because the exothermic decay of the organic compounds from microbial metabolism releases heat (Abu-Hamdeh and Reeder 2000; Peltre et al. 2013; Paz and Etchevers 2016).

Lizard embryos within small eggs have little capacity for thermoregulation and there is no parental care. Consequently, these embryos are dependent upon ambient temperatures remaining within tolerable limits. Our results indicated relatively large fluctuations of temperature external to the soil mound (superficial and air temperature) at all three localities. However, soil temperature within the mounds showed much less fluctuation than the soil surface or air temperatures. We suggest that the soil mounds function as incubators, creating a relatively stable microenvironment for embryonic development when compared with abiotic surface conditions (Andrews et al. 1999; Deeming 2004; Doody et al. 2009).

Collectively, the physical and chemical characteristics of the soil mounds impact most of the oviparous species within the *S. scalaris* species complex, which is distributed primarily at high-elevation sites within central México (Smith and Taylor 1966). These conditions appear to exert selective pressures on these species to lay their eggs in mounds that provide better microclimatic conditions for embryo development (Rodríguez-Romero 1999). Essentially, the soil mounds buffer the extreme climatic effects (low temperatures and humidities) that are characteristic of high-elevation environments, even at subtropical latitudes.

Previous studies have shown that abiotic characteristics affect reptile nest selection and embryonic development (e.g., Ji et al. 2002; Parker and Andrews 2007; Angilletta et al. 2009; Warner et al. 2013). None of these, however, have analyzed the edaphic microclimatic properties necessary to maintain an active movement of gas and water, along with the thermal energy necessary for the embryonic development of oviparous species. Microclimatic conditions (mainly temperature and water vapor) in the substrate of a soil mound constructed by gopher activity are typically lower than ambient air, but scant attention has been paid to this

TABLE 6.—Coefficients of the discriminant function analysis for characteristics of nest sites of *Sceloporus* as a function of season. For each discriminant function (DF), all negative values are presented before positive values and, within each grouping, values are presented in decreasing order of importance.

DF 1	
Porosity	-1.20
pH	-0.53
Calcium	-0.30
Egg depth	-0.19
Temperature	0.50
Sodium	0.22
Potassium	0.22
Organic matter	0.18
Magnesium	0.17
Cation exchange capacity	0.12
Humidity	0.06
DF2	
Potassium	-0.52
Cation exchange capacity	-0.41
pH	-0.13
Humidity	0.77
Calcium	0.70
Egg depth	0.51
Organic matter	0.47
Magnesium	0.30
Temperature	0.24
Sodium	0.13
Porosity	0.12

topic (e.g., Ackerman et al. 1985). Two studies indicated optimal conditions of temperature and water vapor pressure that permit the development of reptile embryos (Ackerman et al. 1985; Birchard 2004). Both of these studies, however, indicated the need for additional research to measure changes in ion active transport, nest heat transfer, and preferred temperature to avoid accelerated or delayed emergence of embryos. Our results indicate the potential importance of organic matter content in the soil in which eggs are laid. This is likely the result of organic matter affecting soil color, porosity, pH, and soil moisture. Additionally, organic material will progressively decompose by microbial action, which can help maintain the operative temperature for proper embryonic development (Andrews et al. 1999).

The high capacity of cation exchange is characteristic of andosols and vertisols, as a result of the high content of organic and inorganic colloids that they possess, as well as the content of interchangeable ions (Porta and López-Acevedo 2005). Moreover, the decrease in calcium, magnesium, and potassium ions that occurs in nests with eggs could be related to shell and egg membrane permeability to solutes that can be important nutrients for embryos (Ackerman and Lott 2004; Deeming 2004; Castaños et al. 2009).

Finally, we note that egg laying in *S. aeneus* and *S. scalaris* is temporally confined to the peak of the rainy season (at our study site, primarily August; Fig. 5). There are major

TABLE 5.—Classification table for discriminant function analysis of nests for high-elevation *Sceloporus* recorded in central México as a function of season in 2010.

Season	Sample size (n)	Beginning of rainy season	Dry season	Rainy season
Beginning of rainy season	17	17 (100.0%)	0 (0.0%)	0 (0.0%)
Dry season	17	0 (0.0%)	17 (100.0%)	0 (0.0%)
Rainy season	27	0 (0.0%)	0 (0.0%)	27 (100.0%)

seasonal differences in mound characteristics involving primarily sodium content and porosity that probably drive egg laying in these species. It would be interesting to determine whether or not exceptionally wet dry seasons, or exceptionally dry wet seasons, would produce any shifts in the timing of oviposition, or the survivorship of embryos developing in mountain environments.

In summary, we have described the temperature profile and several physico-chemical characteristics of soil mounds that appear to influence site selection for egg laying by female sceloporine lizards. These soil characteristics correlate reliably with the structure of the soil mounds, and might influence nest site selection in *Sceloporus* lizards at high elevations. Studies of soil science and its application in different environments, in both temperate and tropical climates, should reveal the roles that abiotic parameters have in conferring stability to the thermal and moisture profiles in the nests of oviparous reptiles. Furthermore, details about the abiotic factors involved in nest site selection will increase our understanding about the reproductive strategies that oviparous reptiles employ in different elevations and habitats.

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RÉSUMEN: Las lagartijas ovíparas que habitan zonas de alta montaña (>2700 m) en el centro de México experimentan situaciones extremas de oxígeno, temperatura y humedad. Dos especies hermanas de *Sceloporus* (*S. aeneus* y *S. scalaris*) colocan sus huevos a 2–3 cm de profundidad en los montículos de tierra que dejan las tuzas (*Pappogeomys*) al construir sus madrigueras. Numerosos factores abióticos pueden direccionar la selección del sitio de oviposición y el desarrollo embrionario posterior; sin embargo, poco se conoce sobre la relación entre las variables físicas y químicas óptimas del suelo circundante, que permiten el desarrollo y la exitosa eclosión de los huevos de lacertilios, especialmente en entornos desafiantes de alta montaña. Nuestra hipótesis es que los parámetros del suelo y la temperatura promueven la selección del sitio por las hembras, quienes buscan nidos con características favorables para el desarrollo embrionario. Los resultados indican que hubo diferencias entre la estación seca y la de lluvias, independientemente de la presencia de huevos. Los análisis revelados que se requiere un ambiente de alta humedad relativa y temperatura estable, para la selección de montículos como sitios de anidación; éstos se asociaron con valores intermedios de humedad, alto contenido de materia orgánica, capacidad de intercambio catiónico alta y valores altos de porosidad. Estas características, en conjunto, evitan cambios repentinos en la temperatura y la humedad en donde se localizan los huevos lo que proporciona condiciones adecuadas para un desarrollo exitoso y la eclosión de los embriones. La comprensión

de la importancia relativa de estos y otros factores abióticos involucrados en la selección del sitio de anidación para las especies del grupo *Sceloporus*, permitirá entender las adaptaciones de la reproducción de reptiles ovíparos en diferentes condiciones climáticas.

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