
EVAPORATIVE WATER LOSS OF SOME HABITAT-RESTRICTED MEXICAN LIZARD SPECIES

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Abstract.—Water relations of terrestrial ectotherms are influenced by a number of environmental factors and physiological constraints. Whereas macroenvironment undoubtedly plays a role in determining such relations, microenvironmental conditions are likely to be of even greater importance for habitat specialist species. The aim of this study was to examine the habitat- and size-related patterns of evaporative water loss (EWL) of eight Mexican endemic lizards: *Anolis barkeri* (Barker's Anole), *A. gadovii* (Gadow's Anole), *Lepidophyma gaigeae* (Gaige's Tropical Night Lizard), *L. inagoi* (Tierra Colorada Tropical Night Lizard), *L. pajapanense* (Pajapan Tropical Night Lizard), *Phyllodactylus delcampoi* (Del Campo's Leaf-toed Gecko), *Sceloporus stejnegeri* (Stejneger's Blackcollar Spiny Lizard), and *Xenosaurus newmanorum* (Newman's Knob-scaled Lizard), all of which are restricted to humid habitats or microhabitats. The species studied exhibited considerably high rates of EWL, even in comparison to other mesic environment squamates. Although the relationship between EWL and habitat aridity was not very strong, this pattern might be influenced by the highly specialized and secretive habits of some of these lizards. Based on these results, we argue that the marked habitat specificity of the species studied can be explained, at least partially, by their high EWL rates, suggesting that microenvironmental conditions are of major importance for the water relations of these lizards.

Key Words.—*Anolis*; dehydration; ecophysiology; *Lepidophyma*; microhabitat; *Phyllodactylus*; *Sceloporus*; *Xenosaurus*

INTRODUCTION

For terrestrial animals, water balance is a key physiological feature that allows them to survive in environments of varying degrees of humidity (Dmi'el 2001). This process involves the search, gather, preservation, storage, and use of water through both behavioral and physiological mechanisms (Minnich 1982; Willmer et al. 2005). A particularly important osmoregulatory issue these organisms face is dehydration due to evaporation (Schmidt-Nielsen 1969). Even in reptiles, which stand out for having different adaptations for life on land (e.g., dry skin, excretion of uric acid, cloacal reabsorption of water, and presence of salt glands), evaporative water loss (EWL) can account for considerable amounts of water lost to the environment (Bentley and Schmidt-Nielsen 1966; Schmidt-Nielsen 1969; Mautz 1982a, b).

Evaporative water loss rates of reptiles are influenced by a number of biological factors such as scale morphology (Soulé and Kerfoot 1972; Calsbeek et al. 2006; Wegener et al. 2014), epidermal lipid content (Roberts and Lillywhite 1980), respiratory metabolism (Snyder 1975; Mautz 1982a), and peripheral vasodilation or vasoconstriction (Mautz 1982b; Dmi'el 2001). Body size is another key driver of EWL rates, as smaller organisms tend to have proportionally more exposed surface area (i.e., higher surface to volume ratios), which increases cutaneous evaporative water loss; on the other hand, larger organisms usually have proportionally less exposed surface area (i.e., lower surface to volume ratios), leading to less pronounced rates of cutaneous water loss (Mautz 1982b; Parker 2014). All these intrinsic factors result in intra- and interspecific differences (Mautz 1982b), which are in turn related to physical or environmental factors to



FIGURE 1. Habitat of the endemic lizards studied at the four localities sampled in Mexico. (A) Los Tuxtlas, Veracruz (Tropical Rainforest) habitat for *Anolis barkeri* (Barker’s Anole) and *Lepidophyma pajapanense* (Pajapan Tropical Night Lizard); (B) Palo Gordo, Guerrero (Tropical Semideciduous Forest) habitat for *A. gadovii* (Gadow’s Anole), *L. inagoi* (Tierra Colorada Tropical Night Lizard), *Phyllodactylus delcampoi* (Del Campo’s Leaf-toed Gecko), and *Sceloporus stejnegeri* (Stejneger’s Blackcollar Spiny Lizard); (C) Jalpan de Serra, Querétaro (Tropical Deciduous Forest) habitat for *L. gaigeae* (Gauge’s Tropical Night Lizard); (D) Xilitla, San Luis Potosí (Tropical Montane Cloud Forest) habitat for *Xenosaurus newmanorum* (Newman’s Knob-scaled Lizard). (Photographed by Adán Bautista-del Moral and David Alejandro Brindis-Badillo).

which organisms are exposed, including temperature, humidity, and wind speed (Mautz 1982b). Humidity, or water vapor density, is directly related to EWL (Willmer et al. 2005), and some studies have found a positive relationship between EWL of lizards and mean annual precipitation (Acevedo 2009). Indeed, species from xeric (arid) environments have significantly lower EWL rates than species from mesic (more humid) environments (Bentley and Schmidt-Nielsen 1966; Mautz 1982a, b), even when phylogenetic relationships are considered (Dmi’el 2001; Cox and Cox 2015).

Physiological requirements and constraints, such as water physiology, can help explain habitat preferences and current distributions of species, identify possible threats to their persistence, and help estimate the effects of environmental changes, both natural and anthropogenic (Neilson 2002; Kearney and Porter 2004; Seebacher and Franklin 2012). Lizards are suitable models to study the implications of habitat and microhabitat use on physiological parameters, as they are often dependent on particular environmental factors (Smith and Ballinger 2001). For habitat specialist species, like those restricted to humid microenvironments, this

dependence is even stronger, and could be related to a lower tolerance to dehydration or reduced capacities for water conservation (Neilson 2002; Nava 2004). Furthermore, EWL rates do not always correlate to broad scale climate conditions but, rather, with microclimate differences (Mautz 1982b). Hence, the aim of this study was to examine the patterns of EWL of eight Mexican endemic habitat-restricted lizards in relation to their habitat preferences (accounting for effects of body size) and discuss if EWL could be an underlying factor in determining their marked habitat specificity.

MATERIALS AND METHODS

Study organisms and sites.—We obtained data on eight species of lizards from four localities (Fig. 1) in México: (1) Los Tuxtlas, Veracruz (Tropical Rainforest; 180 m elevation); (2) Palo Gordo, in the Tierra Colorada area of Guerrero (Tropical Semideciduous Forest; 165 m elevation); (3) Jalpan de Serra, Querétaro (Tropical Deciduous Forest; 1,015 m elevation), and (4) Xilitla, San Luis Potosí (Tropical Montane Cloud forest; 687 m elevation). Except for Los Tuxtlas, which was sampled

TABLE 1. Environmental conditions at the four localities sampled for evaporative water loss of eight endemic lizards in Mexico. Climatic variables are from WorldClim (Fick and Hijmans, 2017). Habitat aridity index (Q) was calculated according to Tieleman et al. (2002). Abbreviations of headings are Elev. = elevation, MAP = mean annual precipitation, MAT = mean annual temperature, MMTWM = mean maximum temperature of warmest month, MMTCM = mean minimum temperature of coldest month, and HAI = habitat aridity index.

Locality	Vegetation	Elev. (m)	MAP (mm)	MAT (° C)	MMTWM (° C)	MMTCM (° C)	HAI (Q)
Los Tuxtlas, Veracruz	Tropical rainforest	180	3268	24.5	32.3	17.1	4,352.23
Palo Gordo, Guerrero	Tropical semideciduous forest	165	1,342	27.5	36.8	18.3	1,356.23
Jalpan de Serra, Querétaro	Tropical deciduous forest	1,015	861	21.2	33	8.5	8,46.82
Xilitla, San Luis Potosí	Tropical montane cloud forest	687	2,260	22.5	33.3	10.4	2,258.35

in 2016, we obtained data from the remaining study sites in 2017. In both years, we conducted samplings between September and November (after the end of the rainy season).

We selected the species for this study based on their restriction to specific habitats and microhabitats, where microenvironmental conditions (temperature and humidity) are relatively homogeneous in comparison to surrounding environments and yet different from each other (Table 1). Based on such characteristics, we hypothesized that most of these species are probably stenohydric (i.e., able to tolerate only a narrow range of moisture levels; Morris 1992), according to the conditions of their habitat. The model species (Fig. 2) were the following: (1) *Anolis barkeri* (Barker's Anole: Dactyloidae), a semiaquatic lizard restricted to shaded rivers and streams in Tropical Rainforest of Los Tuxtlas, Isthmus of Tehuantepec, and Sierra Madre de Chiapas, from sea level to 500 m (Meyer 1968; Heras Lara and Villarreal Benítez 2000; Birt et al. 2001); (2) *Anolis gadovii* (Gadow's Anole: Dactyloidae), found on large boulders and slides of huge granite rocks of the Tierra Colorada area, from 269–600 m (Fitch and Henderson 1976); (3) *Lepidophyma gaegeae* (Gaege's Tropical Night Lizard: Xantusiidae), which occurs in limestone crevices in different vegetation types such as Pine-oak Forests, scrubs, and Tropical Deciduous Forests in the Sierra Madre Oriental in Queretaro and Hidalgo States, from 720 to more than 2,500 m (Bezy and Camarillo 2002); (4) *Lepidophyma inagoi* (Tierra Colorada Tropical Night Lizard: Xantusiidae), microendemic to the Tierra Colorada region in the state of Guerrero, where it is found only in caves formed by large boulders of granitic rocks in Tropical Semideciduous Forest (Palacios-Aguilar et al. 2018); (5) *Lepidophyma pajapanense* (Pajapan Tropical Night Lizard: Xantusiidae), found in tree buttresses and rock crevices of the rainforest of Los Tuxtlas region and near Coatzacoalcos River, from sea level to about 1,500 m (Bezy and Camarillo 2002); (6) *Phyllodactylus delcampoi* (Del Campo's Leaf-toed Gecko: Phyllodactylidae), known only from the region of

Tierra Colorada, in the state of Guerrero, where occupies rock crevices and caves formed by the large boulders of granitic rock in Tropical Semideciduous Forest (Dixon 1964); (7) *Sceloporus stejnegeri* (Stejneger's Blackcollar Spiny Lizard: Phrynosomatidae), another species restricted to the Tierra Colorada area and found only on granite boulders at an altitudinal range of 50–1,400 m (Smith 1942; Pérez-Ramos and Saldaña-de la Riva 2008); and (8) *Xenosaurus newmanorum* (Newman's Knob-scaled Lizard: Xenosauridae), a crevice-dweller lizard distributed in the Tropical Montane Cloud Forests and coffee plantations of Xilitla, San Luis Potosí, and Pisaflores, Hidalgo, from 389 to around 1,100 m elevation (Lemos-Espinal et al. 1998; Lara-Tufiño et al. 2017). Most of these species are listed in at least one category of risk according to International Union for Conservation of Nature (IUCN) criteria and to the Mexican Endangered Species Act (Appendix).

We directly captured lizards either by noosing or by hand, and then took them to facilities near the study sites to perform the pertinent experiments under controlled conditions. When possible, we attempted to collect individuals of different sizes to address mass-specific water loss. We did not use injured or recently autotomized individuals for the experiments.

Laboratory work.—We housed lizards in plastic terraria of different sizes depending on the species, filled with moistened peat moss and dry leaves and kept at a room temperature of about 26° C for 2 d before tests. This temperature is within the documented selected (preferred) temperature range or field body temperatures of these lizards or closely related species from similar habitats (Lemos-Espinal et al. 1998; Birt 2001; Domínguez-Bahena and Florentino-Melchor 2014; Florentino 2015; Arenas-Moreno et al. 2018). To minimize the chances of water loss through defecation during the tests, we fasted individuals for 48 h before the experiments, but we provided them with water *ad libitum* (Neilson 2002).



FIGURE 2. Species of endemic lizards studied in Mexico. (A) *Anolis barkeri* (Barker's Anole); (B) *A. gadovii* (Gadow's Anole); (C) *Lepidophyma gaigeae* (Gaige's Tropical Night Lizard); (D) *L. inagoi* (Tierra Colorada Tropical Night Lizard); (E) *L. pajapanense* (Pajapan Tropical Night Lizard); (F) *Phyllodactylus delcampoi* (Del Campo's Leaf-toed Gecko); (G) *Sceloporus stejnegeri* (Stejneger's Blackcollar Spiny Lizard); (H) *Xenosarus newmanorum* (Newman's Knob-scaled Lizard). (Photographed by Adán Bautista-del Moral).

We estimated rates of water loss using a flowing-air desiccation system (Krakauer et al. 1968; Gans et al. 1968). The system consisted of an Active Aqua™ aquarium air pump (model AAPA15L; 120/60Hz; about 15.98 kPa; Hydrofarm Horticultural Products, Petaluma, California, USA) by which air was conducted at 15 L/min through a series of hygroscopic compounds: first to a container of calcium chloride (CaCl_2), then to a desiccation tube containing calcium sulfate (CaSO_4 ; Indicating Drierite™, W.A. Hammond Drierite Co. Ltd., Xenia, Ohio, USA) and, finally, to another container of CaCl_2 . The air then passed through a 7.9 mm (5/16

in) copper pipe spiral and then to a Kitasato-type flask, which acted as a drying chamber for the unrestrained specimens (one lizard at the time). To maintain a standard temperature throughout the experiments (26°C), we placed a thermal plate beneath the desiccation system and monitored the temperature using a Fluke 51-II digital read-out thermometer ($\pm 0.1^\circ\text{C}$; Fluke Corporation, Everett, Washington, USA).

We made the experiments from 1700–0100. Immediately prior to the tests, we gently palpated the abdomen of the lizards to induce urination (Neilson 2002), dried the excess of water from their skin with

absorbent paper towels, and weighed them on a semi-analytical balance (U.S. Solid™ USS-DBS3-3, ± 0.001 g; U.S. Solid Store, Cleveland, Ohio, USA). To reduce activity/agitation of lizards during the tests, which can increase respiratory water loss, we protected them from direct light by enclosing the flask with a tubular wall of cardboard that did not interfere with the temperature treatment (Gans et al. 1968; Heatwole and Veron 1977). Whereas some authors limit the activity of organisms during the desiccation period through the application of anesthesia (Neilson 2002), the estimation of EWL rates in unrestrained or unanesthetized individuals is widely applied in studies of EWL (e.g., Mautz 1980; Osojnik et al. 2013; Parker 2014). For our study, we assumed that induced darkness conditions during the tests resembled those experienced by organisms in their shelters, where they are inactive (Beck and Jennings 2003). In the case of the supposedly nocturnal taxa (*Lepidophyma*, *Phyllodactylus*), delimitation of activity/inactivity phases seems complicated, as previous studies have found that when environmental temperature matches the selected temperature range, some species can be active during daytime (Lara-Reséndiz et al. 2013; Arenas-Moreno et al. 2018). In fact, we noticed indications of both diurnal and nocturnal activity in *L. inagoi* and *P. delcampoi* during fieldwork, as evidenced by exposure in cave entrances, diurnal movements, and in the case of *P. delcampoi*, foraging behavior.

After collecting data, we weighed individuals again on the same scale on which they were initially weighed. We also registered the body (cloacal) temperature of the individuals at the end of each test to ensure the organisms were at the desired temperature (26.1° C, SD = 0.9). We limited exposure to dry air to exactly one hour to avoid excessive stress (Nava 2004), and calculated water loss as the difference between the initial and final masses in terms of mg H₂O g⁻¹ h⁻¹. Once the study was finished, we provided the individuals with water to allow them to rehydrate. We discarded data from lizards that urinated or defecated during the tests. We processed animals according to the standards for treatment of amphibians and reptiles in research (Beaupre et al. 2004. Guidelines for use of live amphibians and reptiles in field and laboratory research. Available from <https://www.asih.org/sites/default/files/documents/resources/guidelinesherpsresearch2004.pdf> [Accessed 20 January 2018]), and at the end of the procedure we returned all individuals to their respective collecting sites.

Statistical analyses.—Prior to the analyses, we log transformed the data set (Blamires and Christian 1999; Neilson 2002). This transformation is appropriate to investigate the allometric relationship of EWL and body mass, as it simplifies the calculations and, in some cases, homogenizes the variance of the sample

data (Sprugel 1983; Williams 1996). To compare water loss rates, we implemented an Analysis of Covariance (ANCOVA) with log EWL as the dependent variable, species as the fixed factor and the initial mass of the organisms as a covariate, and then proceeded with a Bonferroni adjustment for multiple comparisons to identify differences among species ($\alpha_{\text{altered}} = 0.006$; $\alpha_{\text{critical}} = 0.049$; Neilson 2002; Parker 2014).

We additionally performed correlation analyses between the rate of EWL of each species and its corresponding log mean annual precipitation, log mean temperature of the warmest month, and log mean annual temperature of the study sites, obtained from WorldClim Version 2 (Fick and Hijmans 2017. Worldclim 2: New 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology. Available at <http://worldclim.org/version2> [Accessed 11 January 2018] at 2.5 arc minutes (about 5 km²) resolution (Acevedo 2009). We refrained using data from local meteorological stations because most of the localities studied lacked operating stations and some others were distant from these localities. Although climatic data offered by WorldClim 2 has not been rigorously validated at local scales (Bedia et al. 2013), it allowed us to work with more reliable data at a reasonable resolution for all the study sites. Based on these estimated climate normals, we calculated the habitat aridity index (Q) of each locality (Tieleman et al. 2002) as follows:

$$Q = P / ((T_{\text{max}} + T_{\text{min}}) \times (T_{\text{max}} - T_{\text{min}})) \times 1000$$

Where P is the mean annual precipitation, T_{max} is the mean maximum temperature of the warmest month, and T_{min} is the mean minimum temperature of the coldest month. According to this index, lower Q values correspond to more arid environments, whereas higher values are characteristic of more mesic habitats (Tieleman et al. 2002; Oufiero et al. 2011; Wegener et al. 2014). In the same way as with the individual climatic variables, we performed a correlation analysis between log EWL of each species and their respective log habitat aridity index. Finally, to determine the existence of size-related water loss patterns, we performed correlations between log body mass and log EWL (Neilson 2002).

We tested all data for normality (Shapiro-Wilk test) and homoscedasticity (Levene's test) prior to analyses ($\alpha = 0.05$). We tested the normality of the regression residuals through graphical analyses and Shapiro-Wilk normality tests (Kaps and Lamberson 2004). All data we obtained (log EWL, log mass, residuals of regressions, and log transformed climatic variables) were normally distributed ($P > 0.05$). We conducted the analyses using the statistical packages SigmaPlot 11.0 (Systat Software, San Jose, California, USA) and SPSS 15.0.1 (SPSS Inc., Chicago, Illinois, USA) using an $\alpha = 0.05$ (Zar 2010).

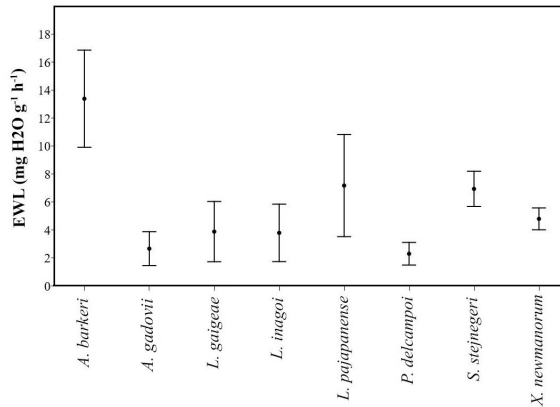


FIGURE 3. Mean evaporative water loss rates (mg H₂O g⁻¹ h⁻¹) of eight habitat specialist lizards from México. Error bars are one standard deviation.

RESULTS

There were interspecific differences in the rates of log EWL after the effect of the initial mass was removed ($F_{7,88} = 30.38, P < 0.001$). In general, there were significant differences among species from the Tropical Rainforest and the Tropical Deciduous and Semideciduous Forest in rates of EWL, except for *S. stejnegeri*, which had surprisingly high rates of EWL (Table 2; Appendix). As expected, the semiaquatic lizard, *A. barkeri*, presented the highest values of EWL, whereas *A. gadovii* and *P. delcampoi*, from Tropical Semideciduous Forest, and *L. gaigeae*, from Tropical Deciduous Forest, had the lowest. In contrast, *X. newmanorum*, a mesophilic temperate forest lizard, differed from the two *Anolis* species and from *P. delcampoi* (Table 2, Fig. 3).

Log EWL rates did not correlate significantly with log mean annual precipitation ($t = 2.327, df = 7, P = 0.059$),

log mean maximum temperature ($t = -1.825, df = 7, P = 0.118$), or log mean annual temperature ($t = -0.617, df = 7, P = 0.560$). We found, however, a significant relationship with the habitat aridity index ($r = 0.710, t = 2.500, df = 7, P = 0.048$), which combines elements of both temperature and moisture. We found significant negative correlations between log transformed mass-specific EWL and log mass in *A. barkeri* ($r = -0.467, t = -2.241, df = 19, P = 0.038$; Fig. 4A) and *L. pajapanense* ($r = -0.763, t = -2.889, df = 7, P = 0.028$; Fig. 4B), and a positive relationship in *S. stejnegeri* ($r = 0.806, t = 3.601, df = 8, P = 0.009$; Fig. 4C).

DISCUSSION

The species studied exhibited relatively high mass-specific water loss rates, even in comparison to some other mesic environment squamates (see Mautz 1982b; Cox and Cox 2015). Moreover, their rates of EWL broadly followed the general pattern of habitat-related water loss, with the rainforest species showing the highest desiccation rates and the deciduous and semideciduous species the lowest. While the relationship of EWL and habitat aridity was not so strong, this might be influenced by the secretive habits of some of the species studied and their high habitat (or even microhabitat) specificity. Nonetheless, the habitat aridity index, which considers thermal variables, proved to be a better predictor of water loss than precipitation alone, which highlights the role of temperature in the water relations of these lizards. Indeed, temperature and humidity conditions have been seen to influence microhabitat and shelter use in other terrestrial ectotherms (Leclair 1978; Seebacher and Alford 2002; Guillon et al. 2013). Based on their differences in microhabitat use and EWL, we suggest

TABLE 2. Sample size (n), body mass, evaporative water loss (EWL) rates (mass-specific and percentage of the initial mass), and habits of eight habitat-restricted lizards endemic to Mexico. Measurements are mean ± standard deviation (minimum value – maximum value).

Species	n	Mass (g)	EWL (mg H ₂ O g ⁻¹ h ⁻¹)	EWL (%/h)	Habits
<i>Anolis barkeri</i> Barker's Anole	20	6.908 ± 3.450 (2.340–12.260)	13.4 ± 3.5 (9.0–20.5)	1.34	Semiaquatic
<i>A. gadovii</i> Gadow's Anole	17	6.321 ± 2.056 (2.816–10.104)	2.7 ± 1.2 (0.5–5.3)	0.27	Saxicolous
<i>Lepidophyma gaigeae</i> Gauge's Tropical Night Lizard	10	2.614 ± 0.505 (1.779–3.398)	3.9 ± 2.2 (1.9–7.7)	0.39	Saxicolous
<i>L. inagoi</i> Tierra Colorada Tropical Night Lizard	11	9.550 ± 7.658 (2.156–23.431)	3.8 ± 2.1 (1.3–7.5)	0.38	Troglophile / Saxicolous
<i>L. pajapanense</i> Pajapan Tropical Night Lizard	8	9.074 ± 1.006 (8.020–10.790)	7.2 ± 3.7 (1.9–11.1)	0.72	Saxicolous / Arboreal
<i>Phyllodactylus delcampoi</i> Del Campo's Leaf-toed Gecko	13	12.560 ± 2.884 (7.580–16.985)	2.3 ± 0.8 (1.5–3.9)	0.23	Saxicolous / Troglophile
<i>Sceloporus stejnegeri</i> Stejneger's Blackcollar Spiny Lizard	9	19.077 ± 5.857 (12.117–27.923)	6.9 ± 1.3 (5.4–9.4)	0.69	Saxicolous
<i>Xenosaurus newmanorum</i> Newman's Knob-scaled Lizard	9	21.723 ± 6.991 (4.235 – 28.633)	4.8 ± 0.8 (3.8–5.9)	0.48	Saxicolous

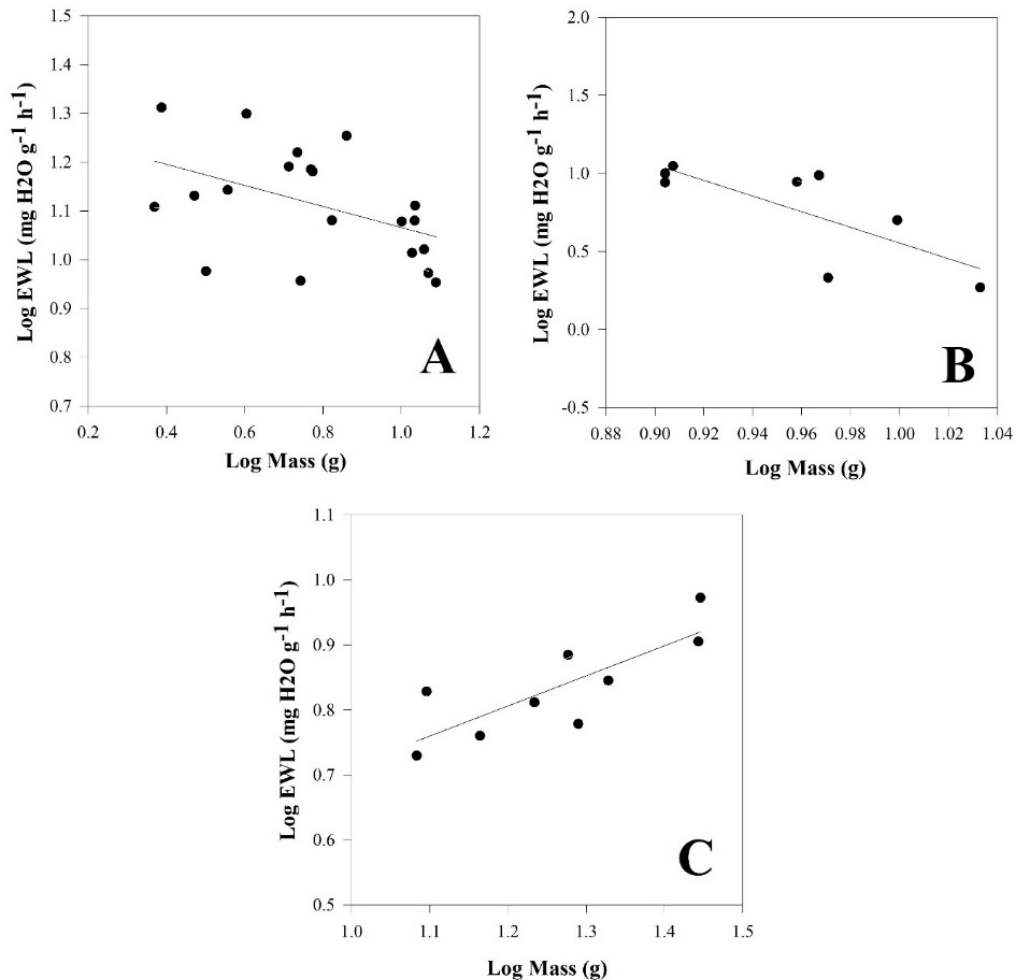


FIGURE 4. Relationships of log transformed evaporative water loss rates (mg H₂O g⁻¹ h⁻¹) and log transformed mass (g) of (A) *Anolis barkeri* (Barker’s Anole), (B) *Lepidophyma pajapanense* (Pajapan Tropical Night Lizard), and (C) *Sceloporus stejnegeri* (Stejneger’s Blackcollar Spiny Lizard).

that microenvironmental conditions are relevant for the water relations of these habitat-restricted lizards.

These results are broadly consistent with previous studies that have found an association between habitat aridity and EWL, even when phylogenetic relationships are considered (Dmi’el 2001; Cox and Cox 2015). The above association is evident when considering that members of the most represented genus in this study, *Lepidophyma*, had contrasting dehydration rates. The same is exemplified by the two *Anolis* species, *A. barkeri* and *A. gadovii*, which were at the highest and lowest EWL extremes, respectively. Although in the case of *A. barkeri*, this phenomenon was predictable given its strong dependence on lotic water bodies. In fact, other studies have documented relatively higher rates of water loss in semiaquatic squamates (Gans et al. 1968; Blamires and Christian 1999; Winne et al. 2001; Moen et al. 2005), and the values of *A. barkeri* are comparable to those of a similar sized individual of Red-tailed

Pipe Snake, (*Cylindrophis ruffus*: Cylindrophiiidae), a semiaquatic, wetland-dwelling snake (Gans et al. 1968).

We found, however, some unexpected results. In particular, the water loss rates of *S. stejnegeri*, a diurnal heliothermic lizard, were higher than those of sympatric crevice- and cavity-dwelling lizards (*L. inagoi* and *P. delcampoi*). The presence of a spectacle (i.e., fused translucent eyelids) in *L. inagoi* and *P. delcampoi* may partially explain this by reducing their potential rates of dehydration, because the moist surfaces of the corneas can account for considerable amounts of water loss in lizards lacking this cover (Mautz 1980, 1982a). Another possibility is that these values reflect different mechanisms of these species to cope with their thermal environment. Whereas *L. inagoi* and *P. delcampoi* remain in crevices and caves where temperatures are cooler, *S. stejnegeri* is often exposed to the warmer temperatures from the outside, basking during short periods and retreating frequently to shaded places

to avoid overheating and, consequently, excessive water loss. Therefore, the high rates of EWL in this species might be acting as a thermal buffer by means of evaporative cooling (Hertz et al. 1979; Tracy et al. 2008). This assumption, however, remains to be tested.

Most species belonging to the *Sceloporus formosus* group inhabit moist temperate forests (Smith and Savitzky 1974; Pérez-Ramos and Saldaña-de la Riva 2008; Acevedo 2009). *Sceloporus stejnegeri* is the only member of this species group dwelling in tropical and relatively dry environments. Acevedo (2009) found a relationship between scale numbers, habitat, and water loss of three species of this group (Adler's Spiny Lizard, *S. adleri*, Graceful Mountain Tree Lizard, *S. druckercolini*, and Striated Emerald Lizard, *S. scitulus*), with populations from moister habitats showing more scales and higher cutaneous water loss rates than populations from less humid environments. Based on this pattern and the overall conditions of its habitat, we would expect *S. stejnegeri* to have low rates of water loss and fewer large scales. This species, however, have a higher number of scales than the species mentioned above (Smith and Savitzky 1974; Pérez-Ramos and Saldaña-de la Riva 2008) and showed high dehydration rates. Therefore, it is likely that EWL rates of *S. stejnegeri* reflect the ancestral condition of the *formosus* group. This would explain the current restriction of this lizard to the relatively moist and thermally stable granite boulders of Tierra Colorada.

Body size is another important determinant of cutaneous water loss, because exposed surface area generally scales negatively with body volume (Gans et al. 1968; Mautz 1982a, b; Willmer et al. 2005; Parker 2014). This was the case for *A. barkeri* and *L. pajapanense*. In *S. stejnegeri*, however, rates of EWL increased with size. As far as we know, a positive relationship between EWL and body size has not been documented before. Although we did not notice any indication of activity of individuals during the desiccation tests that could affect the rates of respiratory water loss, we are unable to ascertain if this was the cause of such relationship in *S. stejnegeri*. In *L. gaigeae*, the small body size and, consequently, high body surface to volume ratio would imply considerably high mass-specific rates of desiccation. This lizard, nevertheless, exhibited the lowest rates of water loss after *A. gadovii*. Whereas habitat humidity undoubtedly plays a role in determining this phenomenon, environmental temperature might also be involved in the EWL of *L. gaigeae*, as in its locality this lizard might experience temperatures up to 40° C (pers. obs.). Furthermore, its smoother skin, compared to congeneric lizards studied (*L. inagoi* and *L. pajapanense*), might account for its reduced dehydration rates, as species with tuberculate skin tend to lose water at higher rates (Dial and

Fitzpatrick 1982). Although our estimations of EWL for *L. gaigeae* are slightly higher than those reported by Mautz (1980, 1982a) for populations from Querétaro and Hidalgo (Pine-oak Forest), it is possible that the higher air flow of our desiccation system is responsible for such discrepancies. Even so, more pronounced EWL rates in *L. inagoi* and *L. pajapanense* are plausible given the environmental conditions of their habitat, whereas most of the species studied by Mautz came from more xeric environments.

This is the first study to document aspects of water balance for a member of the monogeneric family Xenosauridae, so we have no point of comparison for our data for *X. newmanorum*. This temperate forest species, however, seems to have an EWL rate intermediate between the rainforest and the semideciduous forest species. Although its rates of EWL are similar to those of other squamates from mesic habitats (Cox and Cox 2015), it is possible that the presence of osteoderms helps this crevice-dwelling lizard reduce its EWL rate, as co-ossified regions of the integument have been shown to increase cutaneous resistance to water loss (Seibert et al. 1974; Lillywhite 2006).

As for any mesic-adapted species, the relatively high EWL rates exhibited by the species we studied makes them susceptible to even minor environmental changes. For instance, changes in vegetation cover and removal or disturbance of rocks some of these lizards use as shelters might cause shifts in the environmental conditions (temperature and humidity), which could lead to physiological stress, increased mortality, and, eventually, population declines (Schlesinger and Shine 1994; Neilson 2002; Tracy et al. 2006). In addition to the above, climate change could have synergistic detrimental effects, mainly because of the altered precipitation and cloud cover patterns expected to happen with the increase in global temperatures (Hanna 2011; IPCC 2013), which might pose serious threats to these physiologically specialized lizard species (Deutsch et al. 2008). Because these species have small distributional ranges, loss of any populations would have serious conservation impacts. Despite the implications of water balance on susceptibility to climate change, this topic is often disregarded in physiological studies (Kearney and Porter 2004; Guillon et al. 2014). We therefore suggest incorporating information about hydric sensitivity of habitat specialist lizards that have limited distributions to properly assess their ecophysiological vulnerability to changing environmental conditions.

Acknowledgments.—We thank the Posgrado en Ciencias Biológicas of the UNAM and the Consejo Nacional de Ciencia y Tecnología (CONACYT) for the postgraduate scholarships granted to FJMN, DMAM, RSB, FJGA, and DABB (CVU numbers 775920,

412744, 774550, 699259, and 389135, respectively). We are grateful to Luis Alberto Rodríguez Miranda, Cynthia Dinorah Flores Aguirre, Ramón Eduardo Martínez Grimaldo, and Arnulfo Villanueva Castro for their support in the field. We also wish to thank Rosamond Coates, chief of the Estación de Biología Tropical Los Tuxtlas, to Alejandro Galí Boadella and his wife, Dalila Hernández Ochoa, and to the family Santos-Bibiano for the attention given us during our stay at the Los Tuxtlas, Xilitla, and Guerrero study sites, respectively. Also, we thank Larry David Wilson and Philip Clark Rosen for valuable comments and suggestions to improve the manuscript. This research was funded by the Programa de Apoyo a Proyectos de Investigación e Innovación Tecnológica of the UNAM (PAPIIT; IN 210116). Organisms were collected under permit numbers SGPA/DGVS/01629/16 and SGPA/DGVS/01205/17 granted to Fausto R. Méndez de la Cruz by the Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT).

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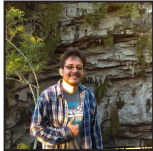
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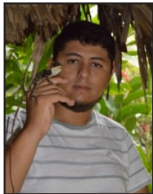
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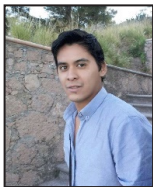
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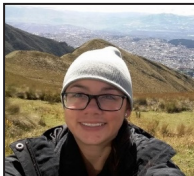
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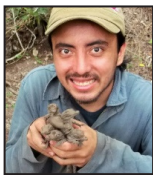
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APPENDIX

CONSERVATION STATUS

Based on our results and on the data available, we suggest reconsidering the conservation status for some of the species studied. For example, according to the IUCN, *Anolis gadovii*, *Lepidophyma pajapanense*, *Phyllodactylus delcampoi*, and *Sceloporus stejnegeri* are in the Least Concern category (Table), this despite their microendemism and high degree of habitat specialization. Justifications for listing these species in this category are their adaptability to changing conditions and the absence of threats to their populations (Calderón Mandujano and Lopez-Luna 2007; Canseco-Márquez et al. 2007a, b, c), which seems not to be the case for these lizards. For example, the region of Los Tuxtlas, where *L. pajapanense* occurs, has been under severe pressure due habitat loss and fragmentation derived from cattle ranching and other agricultural activities (Guevara et al. 1997; Mendoza et al. 2005). On the other hand, seasonally dry tropical forests are strongly dependent on the rainy season, and drought can cause high tree mortality, modify forest structure, and, thereby, habitat and other resources availability (Hanna 2011). Accordingly, the population of *L. gaigeae* from Jalpan de Serra and lizards from the Palo Gordo (Tierra Colorada) study site could be more affected by precipitation regime changes. In the case of *S. stejnegeri*, Wilson et al. (2013) assigned it to the medium vulnerability category (EVS = 13). We recalculated for this species an EVS of 16 (6+7+3), however, placing it in the high vulnerability category. It is probable that discrepancies between the two calculations are due to the inclusion by Wilson et al. (2013) of records from pine-oak forest, which unequivocally would correspond to *S. druckercolini*. Another aspect of concern is the lack of natural protected areas encompassing the distributions of the Tierra Colorada species (CONANP 2016), even despite the high herpetofaunal richness and endemism for the region (Saldaña de la Riva and Pérez Ramos 1987). To properly implement conservation actions for these species, it is imperative to establish a protection status for this area.

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TABLE A1. Conservation status of the species studied according to the Mexican endangered species act (NOM-059; SEMARNAT, 2010), International Union for Conservation of Nature (IUCN, 2017), and Wilson et al.'s (2013) Environmental Vulnerability Score (EVS). Abbreviations are Pr = under special protection; A = threatened; LC = least concern; VU = vulnerable; EN = endangered; NA = not assessed; (M) = medium vulnerability category of EVS; (H) = high vulnerability category of EVS. Scores marked with an asterisk (*) correspond to our calculations. Environmental Vulnerability Scores from Wilson (2013).

Species	NOM-059	IUCN	Geographic Distribution	Ecological Distribution	Degree of Human Persecution	Total Score
<i>A. barkeri</i>	Pr	VU	5	7	3	15 (H)
<i>A. gadovii</i>	A	LC	5	8	3	16 (H)
<i>L. gaigeae</i>	Pr	VU	5	6	2	13 (M)
<i>L. inagoi</i>	NA	NA	6*	8*	2*	17 (H)*
<i>L. pajapanense</i>	Pr	LC	5	7	2	13 (M)
<i>P. delcampoi</i>	A	LC	5	8	3	16 (H)
<i>S. stejnegeri</i>	Pr	LC	6*	7*	3	16 (H)*
<i>X. newmanorum</i>	Pr	EN	5	7	3	15 (H)

TABLE A2. Adjusted *P* values of pairwise comparisons for evaporative water loss (EWL) rates of eight Mexican habitat-restricted lizards. Asterisks (*) indicate statistically significant differences.

Species	<i>A. barkeri</i>	<i>A. gadovii</i>	<i>L. gaigeae</i>	<i>L. inagoi</i>	<i>L. pajapanense</i>	<i>P. delcampoi</i>	<i>S. stejnegeri</i>	<i>X. newmanorum</i>
<i>A. barkeri</i>		<0.001*	<0.001*	<0.001*	0.012*	<0.001*	1.000	0.017*
<i>A. gadovii</i>	<0.001*		1.000	1.000	<0.001*	1.000	<0.001*	0.001*
<i>L. gaigeae</i>	<0.001*	1.000		1.000	0.027*	1.000	0.005*	0.273
<i>L. inagoi</i>	<0.001*	1.000	1.000		0.050	1.000	0.001*	0.263
<i>L. pajapanense</i>	0.012*	<0.001*	0.027*	0.050		<0.001*	1.000	1.000
<i>P. delcampoi</i>	<0.001*	1.000	1.000	1.000	<0.001*		<0.001*	0.001*
<i>S. stejnegeri</i>	1.000	<0.001*	0.005*	0.001*	1.000	<0.001*		1.000
<i>X. newmanorum</i>	0.017*	0.001*	0.273	0.263	1.000	0.001*	1.000	

TABLE A3. Raw data of evaporative water loss of eight habitat-specialist Mexican lizards. Mi = initial mass; Mf = mass after desiccation period; EWL (mg h⁻¹) = absolute rates of water loss; EWL (mg g⁻¹ h⁻¹) = mass-specific rates of water loss; EWL (%/h) = percentage of the initial mass lost due to evaporation.

Species	Sex	SVL (mm)	Mi (g)	Mf (g)	EWL (mg h ⁻¹)	EWL (mg g ⁻¹ h ⁻¹)	EWL (%/h)
<i>Anolis barkeri</i>	M	64.22	5.16	5.08	80	15.50	1.55
<i>Anolis barkeri</i>	F	27.64	7.25	7.12	130	17.93	1.79
<i>Anolis barkeri</i>	F	65.76	5.94	5.85	90	15.15	1.52
<i>Anolis barkeri</i>	M	51.46	2.44	2.39	50	20.49	2.05
<i>Anolis barkeri</i>	M	83.75	10.03	9.91	120	11.96	1.20
<i>Anolis barkeri</i>	F	57.75	3.6	3.55	50	13.89	1.39
<i>Anolis barkeri</i>	M	88.26	11.44	11.32	120	10.49	1.05
<i>Anolis barkeri</i>	M	87.69	10.82	10.69	130	12.01	1.20
<i>Anolis barkeri</i>	F	55.68	2.34	2.31	30	12.82	1.28
<i>Anolis barkeri</i>	M	54.64	2.96	2.92	40	13.51	1.35
<i>Anolis barkeri</i>	M	50.64	3.17	3.14	30	9.46	0.95
<i>Anolis barkeri</i>	F	47.75	5.53	5.48	50	9.04	0.90
<i>Anolis barkeri</i>	F	67.54	5.43	5.34	90	16.57	1.66
<i>Anolis barkeri</i>	M	83.27	10.85	10.71	140	12.90	1.29
<i>Anolis barkeri</i>	F	71.18	6.65	6.57	80	12.03	1.20
<i>Anolis barkeri</i>	M	85.77	12.26	12.15	110	8.97	0.90

Herpetological Conservation and Biology

TABLE A3 (CONTINUED). Raw data of evaporative water loss of eight habitat-specialist Mexican lizards. Mi = initial mass; Mf = mass after desiccation period; EWL (mg h⁻¹) = absolute rates of water loss; EWL (mg g⁻¹ h⁻¹) = mass-specific rates of water loss; EWL (%/h) = percentage of the initial mass lost due to evaporation.

Species	Sex	SVL (mm)	Mi (g)	Mf (g)	EWL (mg h ⁻¹)	EWL (mg g ⁻¹ h ⁻¹)	EWL (%/h)
<i>Anolis barkeri</i>	F	72.77	5.88	5.79	90	15.31	1.53
<i>Anolis barkeri</i>	M	87.57	10.66	10.55	110	10.32	1.03
<i>Anolis barkeri</i>	F	55.46	4.02	3.94	80	19.90	1.99
<i>Anolis barkeri</i>	M	80.51	11.73	11.62	110	9.38	0.94
<i>Anolis gadovii</i>	F	64.46	5.506	5.489	17	3.09	0.31
<i>Anolis gadovii</i>	F	68.4	6.708	6.683	25	3.73	0.37
<i>Anolis gadovii</i>	F	58.02	5.069	5.050	19	3.75	0.37
<i>Anolis gadovii</i>	F	49.98	2.816	2.801	15	5.33	0.53
<i>Anolis gadovii</i>	F	57.69	5.520	5.497	23	4.17	0.42
<i>Anolis gadovii</i>	M	53.11	3.699	3.697	2	0.54	0.05
<i>Anolis gadovii</i>	M	73.17	8.034	8.014	20	2.49	0.25
<i>Anolis gadovii</i>	M	75.75	9.983	9.964	19	1.90	0.19
<i>Anolis gadovii</i>	F	65.32	6.291	6.275	16	2.54	0.25
<i>Anolis gadovii</i>	F	61.3	5.312	5.299	13	2.45	0.24
<i>Anolis gadovii</i>	M	69.68	9.156	9.136	20	2.18	0.22
<i>Anolis gadovii</i>	F	59.89	5.846	5.839	7	1.20	0.12
<i>Anolis gadovii</i>	F	58.96	6.156	6.147	9	1.46	0.15
<i>Anolis gadovii</i>	M	58.6	4.051	4.035	16	3.95	0.39
<i>Anolis gadovii</i>	F	62.76	6.288	6.277	11	1.75	0.17
<i>Anolis gadovii</i>	M	73	10.104	10.080	24	2.38	0.24
<i>Anolis gadovii</i>	F	66.6	6.920	6.904	16	2.31	0.23
<i>Lepidophyma gaigeae</i>	F	55.1	2.389	2.381	8	3.35	0.33
<i>Lepidophyma gaigeae</i>	F	55.8	3.229	3.223	6	1.86	0.19
<i>Lepidophyma gaigeae</i>	F	55.4	3.398	3.375	23	6.77	0.68
<i>Lepidophyma gaigeae</i>	M	48.9	2.903	2.897	6	2.07	0.21
<i>Lepidophyma gaigeae</i>	M	45.8	1.779	1.771	8	4.50	0.45
<i>Lepidophyma gaigeae</i>	M	52.4	2.484	2.476	8	3.22	0.32
<i>Lepidophyma gaigeae</i>	F	53.2	2.923	2.907	16	5.47	0.55
<i>Lepidophyma gaigeae</i>	F	51.3	2.619	2.614	5	1.91	0.19
<i>Lepidophyma gaigeae</i>	F	53	2.331	2.313	18	7.72	0.77
<i>Lepidophyma gaigeae</i>	M	50.6	2.087	2.083	4	1.92	0.19
<i>Lepidophyma inagoi</i>	F	54.9	3.209	3.185	24	7.48	0.75
<i>Lepidophyma inagoi</i>	F	68.5	6.329	6.321	8	1.26	0.13
<i>Lepidophyma inagoi</i>	M	91.5	17.381	17.35	31	1.78	0.18
<i>Lepidophyma inagoi</i>	M	9.67	21.242	21.202	40	1.88	0.19
<i>Lepidophyma inagoi</i>	F	65.2	5.070	5.044	26	5.13	0.51
<i>Lepidophyma inagoi</i>	F	52.8	2.156	2.146	10	4.64	0.46
<i>Lepidophyma inagoi</i>	F	59.4	4.186	4.16	26	6.21	0.62
<i>Lepidophyma inagoi</i>	F	72.2	6.723	6.692	31	4.61	0.46
<i>Lepidophyma inagoi</i>	F	61.4	4.023	4.017	6	1.49	0.15
<i>Lepidophyma inagoi</i>	F	101.1	23.431	23.354	77	3.29	0.33
<i>Lepidophyma inagoi</i>	F	81.2	11.297	11.253	44	3.89	0.39

TABLE A3 (CONTINUED). Raw data of evaporative water loss of eight habitat-specialist Mexican lizards. Mi = initial mass; Mf = mass after desiccation period; EWL (mg h⁻¹) = absolute rates of water loss; EWL (mg g⁻¹ h⁻¹) = mass-specific rates of water loss; EWL (%/h) = percentage of the initial mass lost due to evaporation.

Species	Sex	SVL (mm)	Mi (g)	Mf (g)	EWL (mg h ⁻¹)	EWL (mg g ⁻¹ h ⁻¹)	EWL (%/h)
<i>Lepidophyma pajapanense</i>	F	76.45	9.27	9.18	90	9.71	0.97
<i>Lepidophyma pajapanense</i>	M	74.34	9.98	9.93	50	5.01	0.50
<i>Lepidophyma pajapanense</i>	M	70.12	8.02	7.95	70	8.73	0.87
<i>Lepidophyma pajapanense</i>	M	69.64	8.08	7.99	90	11.14	1.11
<i>Lepidophyma pajapanense</i>	F	72.36	8.02	7.94	80	9.98	1.00
<i>Lepidophyma pajapanense</i>	F	69.68	9.08	9	80	8.81	0.88
<i>Lepidophyma pajapanense</i>	F	74.5	9.35	9.33	20	2.14	0.21
<i>Lepidophyma pajapanense</i>	M	83.66	10.79	10.77	20	1.85	0.19
<i>Phyllodactylus delcampoi</i>	M	84.5	14.324	14.289	35	2.44	0.24
<i>Phyllodactylus delcampoi</i>	F	83.3	12.404	12.386	18	1.45	0.15
<i>Phyllodactylus delcampoi</i>	M	88.1	9.412	9.381	31	3.29	0.33
<i>Phyllodactylus delcampoi</i>	F	73.6	7.580	7.569	11	1.45	0.15
<i>Phyllodactylus delcampoi</i>	F	76.9	8.544	8.514	30	3.51	0.35
<i>Phyllodactylus delcampoi</i>	F	81.9	11.504	11.480	24	2.09	0.21
<i>Phyllodactylus delcampoi</i>	F	87.2	14.096	14.072	24	1.70	0.17
<i>Phyllodactylus delcampoi</i>	M	96.1	16.985	16.956	29	1.71	0.17
<i>Phyllodactylus delcampoi</i>	F	89.5	15.791	15.765	26	1.65	0.16
<i>Phyllodactylus delcampoi</i>	M	86.4	14.718	14.684	34	2.31	0.23
<i>Phyllodactylus delcampoi</i>	F	79.7	10.393	10.352	41	3.94	0.39
<i>Phyllodactylus delcampoi</i>	F	89.3	13.545	13.517	28	2.07	0.21
<i>Phyllodactylus delcampoi</i>	F	88.3	13.985	13.954	31	2.22	0.22
<i>Sceloporus stejnegeri</i>	M	79.9	21.289	21.140	149	7.00	0.70
<i>Sceloporus stejnegeri</i>	F	75.7	14.598	14.514	84	5.75	0.58
<i>Sceloporus stejnegeri</i>	F	77	19.492	19.375	117	6.00	0.60
<i>Sceloporus stejnegeri</i>	F	70.2	12.473	12.389	84	6.73	0.67
<i>Sceloporus stejnegeri</i>	M	80	17.134	17.023	111	6.48	0.65
<i>Sceloporus stejnegeri</i>	F	90.5	18.916	18.771	145	7.67	0.77
<i>Sceloporus stejnegeri</i>	M	89.5	27.750	27.527	223	8.04	0.80
<i>Sceloporus stejnegeri</i>	M	98	27.923	27.661	262	9.38	0.94
<i>Sceloporus stejnegeri</i>	F	68.4	12.117	12.052	65	5.36	0.54
<i>Xenosaurus newmanorum</i>	M	62.9	4.235	4.217	18	4.25	0.43
<i>Xenosaurus newmanorum</i>	F	100.8	21.018	20.929	89	4.23	0.42
<i>Xenosaurus newmanorum</i>	M	100.8	23.24	23.14	100	4.30	0.43
<i>Xenosaurus newmanorum</i>	F	108.7	23.702	23.563	139	5.86	0.59
<i>Xenosaurus newmanorum</i>	M	100.7	26.639	26.499	140	5.26	0.53
<i>Xenosaurus newmanorum</i>	F	103.3	23.918	23.793	125	5.23	0.52
<i>Xenosaurus newmanorum</i>	F	102.3	22.933	22.846	87	3.79	0.38
<i>Xenosaurus newmanorum</i>	F	107	21.186	21.061	125	5.90	0.59
<i>Xenosaurus newmanorum</i>	F	110.6	28.633	28.51	123	4.30	0.43