Thermal ecology, sexual dimorphism, and diet of Xenosaurus tzacualtipantecus from Hidalgo, Mexico

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THERMAL ECOLOGY, SEXUAL DIMORPHISM, AND DIET OF
XENOSAURUS TZACUALTIPANTECUS FROM HIDALGO, MEXICO

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ABSTRACT.—Our knowledge of the biology of lizards in the genus Xenosaurus has increased over the past 20 years. Several generalities appear to hold for these lizards; however, some traits appear to vary among populations and species of Xenosaurus. Here we report on the thermal ecology, sexual dimorphism, and diet of a population of the recently described Xenosaurus tzacualtipantecus from Hidalgo, Mexico. The mean body temperature (Tb) of X. tzacualtipantecus in our population (18.1 °C) is the lowest mean Tb yet observed in Xenosaurus. The close relationships between Tp and air temperatures (Tα) suggest that X. tzacualtipantecus is closer to the thermoconformer end of the thermoconformer-thermoregulator continuum. Females of X. tzacualtipantecus had greater snout–vent lengths than males, males had longer femurs than females, and there was no difference in head size between the sexes. Xenosaurus tzacualtipantecus consumes a variety of invertebrates, primarily insects, suggesting that it is an opportunistic or generalist predator. The diets of lizards in the wet season were dominated by caterpillars, whereas in the dry season beetles were more important. Our observations on the ecology and natural history of X. tzacualtipantecus are generally consistent with previous observations on similar traits in other Xenosaurus.

RESUMEN.—Nuestro conocimiento de la biología de las lagartijas del género Xenosaurus ha incrementado en los últimos 20 años. Varias generalidades parecen aplicarse a estas lagartijas; sin embargo, algunas características parecen variar entre poblaciones y especies de Xenosaurus. Aquí reportamos la ecología térmica, dimorfismo sexual, y dieta de una población de la especie de lagartija recientemente descrita Xenosaurus tzacualtipantecus de Hidalgo, México. El promedio de temperatura corporal (Tb) de nuestra población de X. tzacualtipantecus (18.1 °C) es el más bajo que se ha observado en Xenosaurus. La relación cercana entre la temperatura corporal y la temperatura ambiental (Tα) sugiere que X. tzacualtipantecus está más cerca del extremo termoconformista del continuo termoconformista-termoregulador. Las hembras de X. tzacualtipantecus tuvieron LHC mayores que los machos, los machos tuvieron fémures más largos que las hembras, y no hubo diferencias en el tamaño de la cabeza entre sexos. Xenosaurus tzacualtipantecus consume una variedad de invertebrados, principalmente insectos, sugiriendo que estas lagartijas son depredadores oportunistas o generalistas. La dieta de estas lagartijas en la época de lluvias estuvo dominada por orugas; mientras que en la época seca los escarabajos fueron más importantes. En general, nuestras observaciones sobre la ecología e historia natural de X. tzacualtipantecus son consistentes con observaciones previas sobre características similares en otros Xenosaurus.

Our knowledge of the biology of lizards in the genus Xenosaurus has dramatically increased in the past 20 years. In addition to the description of 5 new species of Xenosaurus since 1993 (Xenosaurus rectocollaris, Smith and Iverson 1993; Xenosaurus penni, Pérez-Ramos et al. 2000; Xenosaurus phalaroanthereon, Nieto-Montes de Oca et al. 2001; Xenosaurus tzacualtipantecus, Woolrich-Piña and Smith 2012; Xenosaurus mendozai, Nieto-Montes de Oca et al. 2013), several studies on populations of Xenosaurus have contributed to a greater understanding of the ecology and natural history of the genus (see Ballinger et al. 2000, Lemos-Espinal et al. 2012 for reviews). Several generalities appear to hold for these lizards. Xenosaurus species are crevice- or hole-dwellers, viviparous, and opportunistic foragers. However, some traits appear to be more variable among populations and species of Xenosaurus. For example, reproductive characteristics, sexual dimorphism, and thermal ecology can differ among (and within) populations and species of Xenosaurus (see Lemos-Espinal et al. 2012 for review). The recent description of several new species of Xenosaurus also hints at greater variation, at least taxonomically, than has been understood.

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in the recent past. The fact that individuals are relatively sedentary (Lemos-Espinal et al. 2003b), with Xenosaurus populations thus tending to be isolated from one another, has probably contributed to speciation and diversification at a taxonomic level (see Woolrich-Piña and Smith 2012, Nieto-Montes de Oca et al. 2013), but it is also likely to have led to ecological differentiation among populations and species.

Here, we report on the thermal ecology, sexual dimorphism, and diet of a population of the recently described Xenosaurus tzacualtipanensis from Hidalgo, Mexico (Woolrich-Piña and Smith 2012). The only information on this species of Xenosaurus appears in the description, and is limited. Unfortunately, the populations of this species appear to be threatened by deforestation and human encroachment; thus, it is critical to obtain a basic understanding of their ecology and natural history. Information on thermal ecology is important because tropical or subtropical lizards, especially those that occur in forested areas, may be particularly prone to the negative impacts of rising temperatures associated with global climate change (Huey et al. 2009, Sinervo et al. 2010, Gunderson and Leal 2012; but see Logan et al. 2013). In addition, body temperature (Tb; measured to nearest 0.2 °C) was taken with a quick-reading cloacal thermometer immediately upon capture. We also measured air temperature (Ta; shaded thermometer 1 cm above substrate where individual was first observed), and substrate temperature (Ts; shaded thermometer touching substrate where individual was first observed). We noted whether the lizard was first observed in a sunny microhabitat or a shaded microhabitat. Given the high correlation between Ta and Ts in this population (n = 69, r = 0.99), we only present the analyses involving Ta (analyses including Ts produced qualitatively identical results). We used linear regression to analyze the relationships between Tb and Ta, SVL, and BM. We compared Tb and Ta between sunny and shaded microhabitats and among sex/age classes using analyses of variance (ANOVAs).

In addition to field observations, we measured various morphological traits of preserved specimens (n = 62) from the herpetological collection of the Laboratorio de Ecología of the Unidad de Biología, Tecnología y Prototipos (LEUBIPRO Series 11427–11483, 14885–14894) to assess sexual dimorphism in these structures. Preserved specimens were from near the same location as the field observations. We measured head width (HW; at the widest point), head length (HL; from anterior edge of ear to tip of snout), and femur length (FL; from knee to middle of pelvic region) to the nearest 0.01 mm using calipers. Sexual dimorphism in HW, HL, and FL was analyzed using analysis of covariance (ANCOVA) with SVL as the covariate (all 3 variables were significantly influenced by SVL). The slopes in the ANCOVAs were homogeneous and interaction
terms were removed from the final model. Given the potential for correlations among the morphological variables we measured, we also used a principal components analysis (PCA) to examine these variables. We ran a PCA and then compared the resultant principal components scores between the sexes with an ANOVA. Means are given with one standard error.

We also dissected preserved lizards \( n = 67 \) from the herpetological collection of the Laboratorio de Ecología of the Unidad de Biología, Tecnología, y Prototipos to obtain information on diets. Diet items were identified to order, and the volume of each prey item was determined using volumetric displacement by placing each prey item into a graduated cylinder containing a known volume of water and recording how much the volume changed. We analyzed diets for the wet (May–October) and dry (November–April) seasons separately. We calculated the importance value for each prey type (pooled by order and life stage for insects) using the proportion of occurrence, total number of items, and total prey volume (Powell et al. 1990). We compared the frequency of empty stomachs between the wet and dry seasons using a chi-square test.

**RESULTS**

**Thermal Ecology**

Mean \( T_b \) was 18.09 °C (SE 0.24, \( n = 69 \), range 14.6–26.8 °C). Body temperature was significantly related to \( T_a \) (Fig. 1; \( n = 69, r^2 = 0.73, P < 0.0001; T_b = 3.91 + 0.81T_a \)).

Lizards observed in sunny microhabitats had significantly higher \( T_b \) values than those in shaded microhabitats (sun: \( \bar{x} = 18.88 \) °C, SE 0.35, \( n = 32 \); shade: \( \bar{x} = 17.42 \) °C, SE 0.30, \( n = 37 \); \( F_{1,67} = 10.20, P = 0.002 \)). Air temperatures were significantly higher in sunny microhabitats compared to shaded microhabitats (sun: \( \bar{x} = 18.40 \) °C, SE 0.40, \( n = 32 \); Shade: \( \bar{x} = 16.82 \) °C, SE 0.28, \( n = 37 \); \( F_{1,67} = 10.58, P = 0.002 \)).

Body size did not affect the \( T_b \) of \( X. tzacualtipantecus \) (SVL: \( n = 69, r^2 = 0.0002, P = 0.90 \); BM: \( n = 69, r^2 = 0.0004, P = 0.87 \)). Body temperature did not differ with sex/age class (Table 1; \( F_{3,65} = 0.026, P = 0.99 \)). Air temperature did not differ among sex/age classes (Table 1; \( F_{3,65} = 0.35, P = 0.79 \)).

**Sexual Dimorphism**

Females were larger than males in SVL (Table 2; \( F_{1,59} = 24.75, P < 0.0001 \)). Males had longer femurs than females (Table 2; \( F_{1,59} = 24.75, P < 0.0001 \)).
Femur length increased with SVL ($F_{1,59} = 244.7, P < 0.0001$). Females and males did not differ in HL (Table 2; $F_{1,59} = 0.29, P = 0.59$). Head length increased with SVL ($F_{1,59} = 223.8, P < 0.0001$). There was also no difference in HW between the sexes (Table 2; $F_{1,59} = 0.20, P = 0.66$). Head width increased with SVL ($F_{1,59} = 182.0, P < 0.0001$).

The PCA resulted in a single significant principal component (eigenvalue = 3.63, percent variation explained = 90.8%). This principal component had strong positive loadings for all the morphological variables measured (SVL: 0.97, FL: 0.94, HL: 0.96, HW: 0.94). Females ($\bar{x} = 1.03, SE 0.33, n = 26$) had significantly higher principal component scores than males ($\bar{x} = −0.74, SE 0.28, n = 36; F_{1,60} = 16.44, P < 0.0001$), suggesting females are larger overall than males.

**Diet**

Eight of 34 stomachs (23.5%) examined in the dry season were empty. Three of 33 stomachs (9.1%) from the wet season were empty. The relative number of empty stomachs did not differ between the dry season and the wet season ($\chi^2_1 = 2.54, P = 0.11$).

Beetles collectively were the most important prey items for *X. tzacualtipantecus* from the dry season, followed by caterpillars and spiders (Fig. 2). Beetles, caterpillars, and spiders were also the 3 most important prey types numerically and volumetrically (Table 3).

During the wet season, the diet of *X. tzacualtipantecus* was dominated by caterpillars in importance value, number, and volume (Fig. 2, Table 4). Caterpillars were followed in importance by beetles collectively and centipedes in importance value; beetles, centipedes, and millipedes in number; and beetles and centipedes in volume (Fig. 2, Table 4).

**DISCUSSION**

**Thermal Ecology**

The mean $T_b$ of *X. tzacualtipantecus* in our population (18.1 °C) is the lowest mean $T_b$ yet observed in *Xenosaurus*. This mean $T_b$ is close to the mean $T_b$ of *X. phalaroanthereon* (20.3 °C, Lemos-Espinal and Smith 2005), *X. platyceps* (19.1 °C, Lemos-Espinal et al. 1997), and *X. mendozai* (20.6 °C, Lemos-Espinal et al. 2004). Other species of *Xenosaurus* have higher mean $T_b$ values, with *Xenosaurus grandis* (22.7 °C, Ballinger et al. 1995), *Xenosaurus neumanorum* (22.9 °C, Lemos-Espinal et al. 1998), and *X. rectocollaris* (22.9–23.2 °C, Lemos-Espinal et al. 1996, Woolrich-Piña et al. 2012) having intermediate mean $T_b$ values; and *X. grandis agrenon* (25.6 °C, Lemos-Espinal et al. 2003a) having the highest mean $T_b$.

The close relationship between $T_b$ and environmental temperatures ($T_a$ and $T_s$) in *X. tzacualtipantecus* suggests that these lizards are closer to the thermoconformer end of the thermoconformer-thermoregulator continuum. This is consistent with previous observations on temperature relationships in *Xenosaurus*. For example, Woolrich-Piña et al. (2012) used operative models to show that *X. rectocollaris*
is a relatively inefficient thermoregulator. Other studies have suggested that *Xenosaurus* species are thermoconformers based on the strong relationship between $T_b$ and $T_a$ and/or $T_s$ (e.g., *X. rectocollaris*, Lemos-Espinal et al. 1996; *X. grandis*, Ballinger et al. 1995; *X. grandis agrenon*, Lemos-Espinal et al. 2003a; *X. newmanorum*, Lemos-Espinal et al. 1998; *X. phalaroanthereon*, Lemos-Espinal and Smith 2005; *X. platyceps*, Lemos-Espinal et al. 1997; *X. mendozai*, Lemos-Espinal et al. 2004). In particular, the inability of *Xenosaurus* to thermoregulate appears to be a function of the limited amount of sunlight that reaches their crevices or holes (Lemos-Espinal et al. 1997). Indeed, the fact that *X. tzacualtipantecus* individuals observed in crevices in the sun had higher $T_b$ values than those in crevices in the shade suggests the importance of sun to these lizards’ thermal ecology, even though we never observed individuals outside their crevices.

We did not find any difference in $T_b$, $T_a$, or $T_s$ among males, females, juveniles, and
neonates. Woolrich-Piña et al. (2012) found that $T_b$ values did not differ greatly among males, nonpregnant females, neonates, and juveniles in *X. rectocollaris*. Male and female *X. mendozai* and *X. grandis agrenon* had similar mean $T_b$ values (Lemos-Espinal et al. 2003a, 2004). Male *X. newmanorum* and *X. rectocollaris* had lower $T_b$s than females (Lemos-Espinal et al. 1996, 1998). Adults of *X. newmanorum* had lower $T_b$ values than neonates (Lemos-Espinal et al. 1998). These results suggest that there is some variability in how $T_b$ varies within populations of *Xenosaurus*. Further studies are needed to examine why body temperatures vary within some populations and species and not in others.

Our observations on the thermal ecology of *X. tzacualtipantecus* suggest that these lizards are thermoconformers, perhaps because of the limited scope of the environment to provide a heterogeneous thermal environment, as well as the crevice-dwelling habit of *Xenosaurus*. Unfortunately, the limited ability of *Xenosaurus* to thermoregulate (this study; see also Lemos-Espinal et al. 1997, Woolrich-Piña et al. 2012) suggests that they may be susceptible to the negative impacts and increased temperatures expected to occur due to global climate change (see Huey et al. 2009, Sinervo et al. 2010, Gunderson and Leal 2012). We encourage additional, more detailed, explorations of the potential for *Xenosaurus* to respond to temperature changes.

### Sexual Dimorphism

Females of *X. tzacualtipantecus* had greater SVLs than males. This result is consistent with all other populations of *Xenosaurus* in which significant sexual dimorphism has been found (e.g., *X. newmanorum*, Smith et al. 1997; *X. phalareoantheron*, Lemos-Espinal and Smith 2005; *X. mendozai*, Lemos-Espinal et al. 2004; *X. platyceps*, Lemos-Espinal et al. 1997; *X. rectocollaris*, Woolrich-Piña et al. 2012). However, there are some *Xenosaurus* species that do not show sexual dimorphism in SVL (e.g., *X. grandis*, Smith et al. 1997, Lemos-Espinal et al. 2003a, Goldberg 2009; *X. rectocollaris*, Lemos-Espinal et al. 1996). It is interesting that there is no difference in growth rate between the sexes in species that show body size dimorphism (e.g., *X. newmanorum*, Lemos-Espinal et al. 2003b; *X. mendozai*, Zamora-Abrego et al. 2012). The same is also true for those species that do not show body size dimorphism (e.g., *X. grandis*, Zúñiga-Vega et al. 2005). These observations suggest that differential growth rates between the sexes are not the likely proximate cause of sexual size dimorphism in *Xenosaurus*.

We found no sexual dimorphism in head size in *X. tzacualtipantecus*. As with SVL, there is variation in the appearance of sexual dimorphism in head size among *Xenosaurus* species. Although most species have males with larger heads compared to females (e.g., *X. grandis*, Smith et al. 1997, Lemos-Espinal et al. 2003a; *X. mendozai*, Lemos-Espinal et al. 2003b; *X. phalareoantheron*, Lemos-Espinal et al. 2005; *X. rectocollaris*, Woolrich-Piña et al. 2012), there are cases where there is no sexual dimorphism (e.g., *X. grandis*, Smith et al. 1997, Lemos-Espinal et al. 2003a, Goldberg 2009; *X. rectocollaris*, Lemos-Espinal et al. 1996). It is interesting that there is no difference in growth rate between the sexes in species that show body size dimorphism (e.g., *X. newmanorum*, Lemos-Espinal et al. 2003b; *X. mendozai*, Zamora-Abrego et al. 2012). The same is also true for those species that do not show body size dimorphism (e.g., *X. grandis*, Zúñiga-Vega et al. 2005). These observations suggest that differential growth rates between the sexes are not the likely proximate cause of sexual size dimorphism in *Xenosaurus*.

### Table 4. Wet season (May–October) diet of *Xenosaurus tzacualtipantecus* from Hidalgo, Mexico.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Number of stomachs</th>
<th>Number of items</th>
<th>Total volume (mm$^3$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coleoptera Larvae</td>
<td>3 (10.0%)</td>
<td>9 (11.8%)</td>
<td>0.60 (5.6%)</td>
</tr>
<tr>
<td>Carabidae</td>
<td>1 (3.3%)</td>
<td>1 (1.3%)</td>
<td>0.16 (1.5%)</td>
</tr>
<tr>
<td>Meloidae</td>
<td>1 (3.3%)</td>
<td>6 (7.9%)</td>
<td>0.61 (5.7%)</td>
</tr>
<tr>
<td>Diptera Larvae</td>
<td>1 (3.3%)</td>
<td>1 (1.3%)</td>
<td>0.05 (0.5%)</td>
</tr>
<tr>
<td>Lepidoptera Larvae</td>
<td>12 (40.0%)</td>
<td>34 (44.7%)</td>
<td>7.75 (72.7%)</td>
</tr>
<tr>
<td>Orthoptera Acridiida</td>
<td>1 (3.3%)</td>
<td>1 (1.3%)</td>
<td>0.23 (2.2%)</td>
</tr>
<tr>
<td>Thysanura</td>
<td>1 (3.3%)</td>
<td>1 (1.3%)</td>
<td>0.11 (1.0%)</td>
</tr>
<tr>
<td>Aracnae</td>
<td>2 (6.7%)</td>
<td>1 (1.3%)</td>
<td>0.31 (2.9%)</td>
</tr>
<tr>
<td>Thysanura</td>
<td>5 (16.7%)</td>
<td>13 (17.1%)</td>
<td>0.61 (5.7%)</td>
</tr>
<tr>
<td>Diplopoda</td>
<td>2 (6.7%)</td>
<td>10 (13.2%)</td>
<td>0.18 (1.7%)</td>
</tr>
<tr>
<td>Gastropoda</td>
<td>1 (3.3%)</td>
<td>1 (1.3%)</td>
<td>0.05 (0.5%)</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>30</td>
<td>76</td>
<td>10.66</td>
</tr>
</tbody>
</table>
al. 2004; X. newmanorum, Smith et al. 1997; X. platyceps, Lemos-Espinal et al. 1997), others have no significant sexual dimorphism in head size (e.g., X. rectocollaris, Lemos-Espinal et al. 1996; Woolrich-Piña et al. 2012).

It is interesting that when sexual dimorphism in SVL is observed in Xenosaurus it is female biased whereas when sexual dimorphism in head size is observed it is male biased. Such a result suggests that body size selection may be for larger females to allow for increased litter size or neonate size (Cox et al. 2003). For head size, selection may be for males with larger heads to be successful in intrasexual interactions associated with mating success. Indeed, some evidence suggests that male-biased head size dimorphism is related to intrasexual conflict (Ballinger et al. 1995, Smith et al. 1997) and difference in head shape is related to bite force, resulting in males generating greater bite force than females (Herrel et al. 2001).

In our univariate analyses, we found that males have relatively longer femurs than females, but the multivariate (PCA) analysis suggests that, overall, females are larger than males. Our univariate result is similar to several other studies that have found that male Xenosaurus species have longer femurs than females (e.g., X. grandis agrenon, Lemos-Espinal et al. 2003a; X. mendozai, Lemos-Espinal et al. 2004; X. newmanorum, Smith et al. 1997; X. platyceps, Lemos-Espinal et al. 1997). However, no sexual dimorphism in femur length was found in X. grandis (Smith et al. 1997) and X. rectocollaris (Lemos-Espinal et al. 1996, Woolrich-Piña et al. 2012). Femur length can be related to habitat or microhabitat use (e.g., Losos 1990, Herrel et al. 2002). However, given no apparent differences between the sexes in their use of microhabitats in other Xenosaurus species (Ballinger et al. 1995, Lemos-Espinal et al. 1996, 1997, 1998, 2003a, 2004, Lemos-Espinal and Smith 2005) and the sedentary nature of Xenosaurus (Lemos-Espinal et al. 2003b), we find it hard to explain the observed sexual dimorphism in femur length by invoking differential microhabitat or habitat use. However, males do move more than females, at least in X. newmanorum, the only species for which such data are available (Lemos-Espinal et al. 2003b). Possibly, the observed sexual dimorphism in femur length is related to the greater propensity for males to move greater distances. Future studies looking at the role of femur length in the performance and behavior of Xenosaurus may help explain why there is sexual dimorphism in this trait.

**Diet**

Our results suggest that X. tzacualtipantecus consumes a variety of invertebrates, primarily insects, perhaps indicating that it is an opportunistic or generalist predator. The diets we observed in X. tzacualtipantecus are consistent with previous studies suggesting that Xenosaurus species are opportunistic foragers. Xenosaurus primarily consume insects and other invertebrates (Ballinger et al. 1995, Lemos-Espinal et al. 2003c, 2004) but have been shown to eat vertebrates, including mammals and lizards (Presch 1981, Ballinger et al. 1995, Lemos-Espinal et al. 2003c, García-Vázquez et al. 2009), and vegetation (Lemos-Espinal et al. 2003c). The opportunistic and relatively broad diets consumed by Xenosaurus species suggest that Xenosaurus may be able to cope with changes in their prey base that may accompany changes in their environment, including those associated with increased human encroachment and impact to their environments (see Briggs et al. 2013, Nichols et al. 2013, and Ruiz-Guerra et al. 2013 for examples of how human alteration of the environment negatively impacts insect populations).

Of particular interest is the fact that diets of X. tzacualtipantecus from the wet and dry seasons were different. Diets of lizards in the wet season were dominated by caterpillars, whereas in the dry season beetles were more important. Caterpillars were also an important diet item in X. newmanorum individuals collected during the wet season (Ballinger et al. 1995). This seasonal shift may reflect a shift in the availability of specific prey items between the seasons. For example, caterpillars tend to be more abundant in the wet season than in the dry season (e.g., Williams-Linera and Herrera 2003, Pessoa-Queiroz et al. 2008). The differences we observed in the composition of the diet between the wet and dry seasons may be consistent with previous studies that have found individual growth rates in the wet season to be higher than those in the dry season (X. grandis, Zúñiga-Vega et al. 2005; X. mendozai, Molina-Zuluaga et al. 2005; X. rectocollaris, Zúñiga-Vega et al. 2005; X. newmanorum, Smith et al. 1997).
2013; *X. newmanorum*, Lemos-Espinal et al. 2003b; but see Zamora-Abrego et al. 2012 for *X. mendozai* that shows no difference in growth between wet and dry seasons), and suggests food availability, either in quantity or quality, may be limiting during the dry season, at least in some populations of *Xenosaurus*. Seasonal difference in growth may also be related to seasonal differences in temperature. Indeed, Zúñiga-Vega et al. (2005) found that growth rate in *X. grandis* was significantly affected by the interaction of body size, prey availability, and environmental temperatures. Additional study is needed to partition the relative roles of temperature and food availability on the seasonal growth patterns of *Xenosaurus*.

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**LITERATURE CITED**


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