Phrynosoma cornutum (Harlan, 1825). The Texas Horned Lizard is a common species with a widespread distribution that extends throughout the eastern portion of the southwestern United States and eastern Mexico, south to the states of Durango and San Luis Potosí. The prominent cephalic spines of this lizard provide obvious protection from predation, but the following report details a strategy of decapitation of adults of this lizard by Swainson's Hawks (*Buteo swainsoni*), which feed the prey to their young. Pictured here is an individual found at Mina, Nuevo León, Mexico, on the Carretera Mina-El Espinazo to El Espinazo, in an area of microphyllous scrubland. 📷 © Michael S. Price

Texas Horned Lizards (*Phrynosoma cornutum*) as prey in Swainson's Hawk (*Buteo swainsoni*) nest sites at La Reserva de la Biosfera de Janos, Chihuahua, Mexico

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Abstract: We recovered 33 severed heads of *Phrynosoma cornutum* found in 19 *Buteo swainsoni* nests at La Reserva de la Biosfera de Janos, Chihuahua, Mexico. We estimated the snout–vent lengths of these lizards by inserting their head lengths into a scaling model relating head length to body length for *P. cornutum*, derived from an ontogenetic series of complete specimens, and by adding the calculated body lengths to the corresponding head lengths. The estimated snout–vent lengths for the prey sample occupied the upper part of the size-range of *P. cornutum*. *Buteo swainsoni* evidently avoided consuming the heads of captured *P. cornutum*, thus circumventing the cephalic defensive armament present in this species.

Key Words: Diet, horned lizard, predation, protected area, raptors

Resumen: Recuperamos 33 cabezas cercenadas de *Phrynosoma cornutum* encontradas en 19 nidos de *Buteo swainsoni* en La Reserva de la Biosfera Janos, Chihuahua, México. Estimamos las longitudes de hocico–cloaca de estas lagartijas insertando las longitudes de sus cabezas en un modelo de escala que relaciona la longitud de la cabeza con la longitud del cuerpo de *P. cornutum,* derivada de una serie ontogenética de especímenes completos, y agregando las longitudes calculadas del cuerpo a las longitudes de las cabezas correspondientes. La longitud hocico–cloaca estimada para la muestra de la presa ocupa la parte superior del rango de tamaño de *P. cornutum*. *Buteo swainsoni* evidentemente evita consumir las cabezas de *P. cornutum* capturdos, eludiendo así el armamento defensivo cefálico presente en esta especie.

Palabras Claves: Área protegida, aves rapaces, depredación, dieta, lagartija cornuda

INTRODUCTION

The Texas Horned Lizard, *Phrynosoma cornutum*, is widely distributed in the United States and Mexico, ranging from Kansas southwestward to southeastern Arizona, southward throughout the northeastern portion of the Sierra Madre Occidental in Chihuahua as far south as Durango, and eastward throughout the states of Coahuila, Nuevo León, and Tamaulipas (Knowlton and Stanford, 1942; Miller, 1948; Price, 1990; Baur and Montanucci, 1998; Sherbrooke, 2003; Lemos-Espinal and Smith, 2007). In Mexico, the conservation status of this species has been listed in the category of special protection (Pr = Protección especial; SEMARNAT, 2010), and globally the IUCN has assessed this species as Least Concern (Hammerson, 2007).

Phrynosoma cornutum has been recorded in the diet of a variety of predators that consume small prey. Among its reptilian predators are Coachwhips (*Masticophis flagellum*) and Sonoran Whipsnakes (*M. bilineatus*) (Tyler, 1977; Sherbrooke, 2008); rattlesnakes (*Crotalus* spp.) (Milne and Milne, 1950; Klauber, 1972; Sherbrooke, 2013); and Leopard Lizards (*Gambelia wislizenii*) (Sherbrooke, 2013). Mammalian predators of *P. cornutum* include Coyotes (*Canis latrans*), Gray Foxes (*Urocyon cinereoargenteus*) (Munger, 1986; Sherbrooke and Mason, 2005), Kit Foxes (*Vulpes macrotis*) (Middendorf and Sherbrooke, 1992; Sherbrooke and Middendorf, 2004), Bobcats (*Lynx rufus*) (Sherbrooke et al., 2012), and Grasshopper Mice (*Onychomys torridus*) (Munger, 1986; Sherbrooke, 1991; Endriss et al., 2007). Avian predators of *P. cornutum* include Loggerhead Shrikes (*Lanius ludovicianus*) (Montgomery and Mackessy, 2003), owls (genus and species unknown) (Anderson and Ogilvie, 1957), Greater Roadrunners (*Geococcyx californianus*) (Sutton, 1922; Milne and Milne, 1950; Sherbrooke, 1990; 2013; Holte and Houck, 2000), Chihuahuan Ravens (*Corvus cryptoleucus*) (Sherbrooke, 2003), Swainson's Hawks (*Buteo swainsoni*) (Milne and Milne, 1950; Thiollay, 1981; Bednarz, 1988; Montgomery and Mackessy, 2003), Harris' Hawks (*Parabuteo unicinctus*) (Bednarz, 1988), and Red-tailed Hawks (*Buteo jamaicensis*) (Thiollay, 1981).

Swainson's Hawk (*Buteo swainsoni*) is widely distributed throughout much of North America, from Alaska and western Canada to northwestern Mexico (Bent, 1937; Peterson and Chalif, 2000). This species, however, migrates to South America, where it overwinters primarily in Argentina (Bent, 1937; England et al., 1997). This bird is a relatively large raptor with the body masses of males and females ranging from 693 to 936 g and 937 and 1,367 g, respectively; the body lengths of males and females range from 51 to 56 cm and 44 to 48 cm, respectively (Palmer, 1988). Historically, this hawk probably foraged in upland and seasonally flooded perennial grasslands (Woodbridge, 1998). In Mexico, *B. swainsoni* is listed in the Pr category (SEMARNAT, 2010), and the IUCN has evaluated this species as Least Concern (BirdLife International, 2016).

Buteo swainsoni is known to feed mainly on small to medium sized mammals, such as pocket gophers (*Cratogeomys castanops*, *Geomys bursarius*, and *Thomomys talpoides*), kangaroo rats (*Dipodomys ordii* and *D. merriami*), deer mice (*Peromyscus maniculatus* and *P. fasciatus*), Cotton Rats (*Sigmodon hispidus*), ground squirrels (*Ictidomys tridecemlineatus*, *Spermophilus beecheyi*, *Urocitellus columbianus*, *U. richardsonii*, *U. townsendii*, and *Xerospermophilus spilosoma*), prairie dogs (*Cynomys leucurus* and *C. ludovicianus*), Hares (*Lepus californicus*), and Desert Cottontails (*Sylvilagus audubonii*) (Munro, 1929; Bent, 1937; Dunkle, 1977; Bechard, 1983; Bednarz, 1988; Andersen, 1995; Gerstell and Bednarz, 1999; Rodriguez-Estrella, 2000). Other vertebrates consumed include many species of birds (Cameron, 1913; Dunkle, 1977; Bechard, 1983; Gilmer and Stewart, 1984; Andersen, 1995; List et al., 2010). Santos-Barrera et al., (2008) reported the presence of four families, five genera, and 13 species of amphibians and 26 families, 19 genera, and 257 species of reptiles in the diet of *B. swainsoni*. Among the reptiles are *P. cornutum*, the Gophersnake (*Pituophis catenifer*), and the Eastern Fence Lizard (*Sceloporus undulatus*) (Bechard, 1983; Bednarz, 1988; Andersen, 1995). Insects, such as grasshoppers, crickets, and dragonflies,

occasionally form a large part of its diet (Cameron, 1913; Munro, 1929; Bent, 1937; Johnson et al., 1987; Jaramillo, 1993; Woodbridge et al., 1995; Serrachin-Araujo and Tirnanti, 1996; Canavelli et al., 2012). Collectively, these data demonstrate that the diet of *B. swainsoni* is diverse, and thus this bird likely is opportunistic and versatile in its feeding habits.

Thiollay (1981) investigated the diets of *B. swainsoni* and the Red-tailed Hawk (*B. jamaicensis*) at La Reserva de Mapimi in Chihuahua, by dissecting pellets found around the nests and examining prey remains within them, and by observing hunting hawks. In general, lizards were twice as common in the diet of *B. swainsoni* as in that of *B. jamaicensis*; *P. cornutum*, which was more abundant at the study site than *P. modestum*, was found more frequently in the diet of *B. swainsoni* (Thiollay, 1981). The frequency of captures of *P. cornutum* by *B. swainsoni* generally matched the diel activity pattern of the lizard, with capture frequencies peaking early in the morning and late in the afternoon (Thiollay, 1981), when these lizards forage in the open (Burrow et al., 2001; Montgomery and Mackessy, 2003; Eifler et al., 2012). Of the relatively small sample of adult *P. cornutum* taken by *B. swainsoni* that Thiollay (1981) examined, approximately one half were gravid females. Between them, *B. jamaicensis* and *B. swainsoni* were estimated to take from 5 to 20% of the adult *P. cornutum* population in the study area, a much greater percentage than found for other lizard species. As expected, most of these lizards were taken by *B. swainsoni*, and thus this species was considered to be a major predator of *P. cornutum* in northern Mexico (Thiollay, 1981). In contrast, however, Bednarz (1988) noted that *P. cornutum* made up only 6.2% of the dietary biomass of *B. swainsoni* in southeastern New Mexico.

Here we present data on a sample of severed *P. cornutum* heads recovered from *B. swainsoni* nests in northwestern Mexico, and reconstruct the range in body sizes of this sample. Our data allowed us to characterize *B. swainsoni* as a predator of *P. cornutum*, and to hypothesize about the usefulness of defensive strategies used by *P. cornutum* against large hawks. The variety of antipredator defenses used by *P. cornutum* have been described by Winton (1916), Sutton (1922), Milne and Milne (1950), Lambert and Ferguson (1985), Middendorf and Sherbrooke (1992), Montgomery and Mackessy (2003), Cooper and Sherbrooke (2010), Sherbrooke et al., (2012), and Sherbrooke (1987, 1990, 1991, 2002, 2008, 2013).

MATERIALS AND METHODS

Study Site

The study site is part of a large protected area known as La Reserva de la Biosfera de Janos, which encompasses 526,482.8 ha (Fig. 1). The reserve consists of grassland and scrubland southeast of the Sierra Madre Occidental, in Janos-Nueva Casas Grandes, Chihuahua, Mexico, and the following coordinates represent the extremes of the study site: (R12 713796°E, -3467593°N; R12 764548°E, -3469637°N; R12 769160°E, 3364399°N; R12 740438°E, 3341460°N). The reserve occupies an area of 99,090 ha, with elevations between 1,000 and 3,000 m. The northern boundary lies approximately 75 km south of the border with the United States, and extends to the northwest of the Chihuahuan Desert scrubland and to the southeast of the slopes of the Sierra Madre Occidental. The climate is arid, with hot summers (average 30.7°C) and cold winters (average 0°C), with an annual average of 17°C (CONAGUA, 2017). This area receives an average annual precipitation of 307 mm, which falls mostly in July and August, with periodic precipitation occurring during the winter (Manzano-Fisher et al., 2000).

The grassland comprising the study area is dominated by the following species: *Bouteloua gracilis*, *B. hirsuta*, and *Fouqueria splendens*, with isolated patches of cholla (*Opuntia* spp.), yucca (*Yucca* spp.), and Ephedra (*Ephedra trifurca*), and scattered mesquites (*Prosopis* spp.). Sporadic patches of aquatic and riparian vegetation also are present, as well as ecotones of coniferous and oak-grassland forest at the higher elevations (Manzano-Fisher et al., 2000). We conducted our study in open desert scrub dominated by Honey Mesquite (*Prosopis glandulosa*), Viscid Acacia (*Acacia neovernicosa*), Whitehorn Acacia (*A. constricta*), and Catclaw Mimosa (*Mimosa biunicifera*).

Data Collection

We collected our samples three days per week from 15 June to 15 August 2006, and from 17 July to 17 August 2014. We gathered the samples prior to research being conducted on the reproductive biology of *Buteo swainsoni*. We collected regurgitated pellets and the remains of undigested portions of prey from 19 nests containing young,

located in *Prosopis glandulosa* trees. The 40 collected pellets contained the remains of various prey items that we dissociated using a Carl Zeiss stereomicroscope; this procedure allowed us to segregate the remains into invertebrate and vertebrate aliquots. The invertebrate contents consisted mostly of insect parts. With regard to vertebrate remains, we retrieved mammalian hair, teeth and maxillae, avian bones and feathers, and reptile scales and teeth. The vertebrate material from the pellets generally was degraded. We found 33 complete and four incomplete heads of *Phrynosoma cornutum* lying loosely within the nests (average 1 or 2 per nest).

We measured the length (HLp) of each of the complete *P. cornutum* heads (to the nearest 0.01 mm) using calipers (Electronic Digital Caliper Control Company 0–200 mm), as the dorsal straight-line distance from the anteromedial point of the rostral scale to the anteromedial edge of the medial parietal horn (P_1; see Fig. 2).
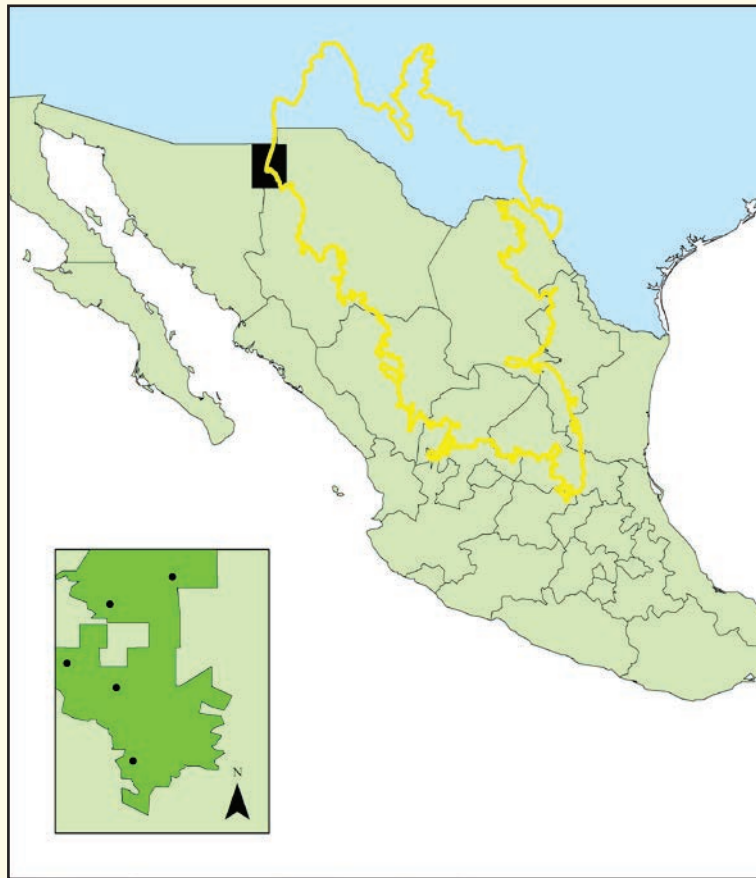

Fig. 1. Map of Mexico and the adjacent United States indicating the boundary of the Chihuahuan Desert (outlined in yellow) and the location of the study area (black rectangle). The inset indicates the study area (pale green) with the limits of the Reserva de la Biosfera de Janos in Chihuahua, Mexico (bright green) and the black dots representing the spatial distribution of the *Buteo swainsoni* nests sampled during the study.
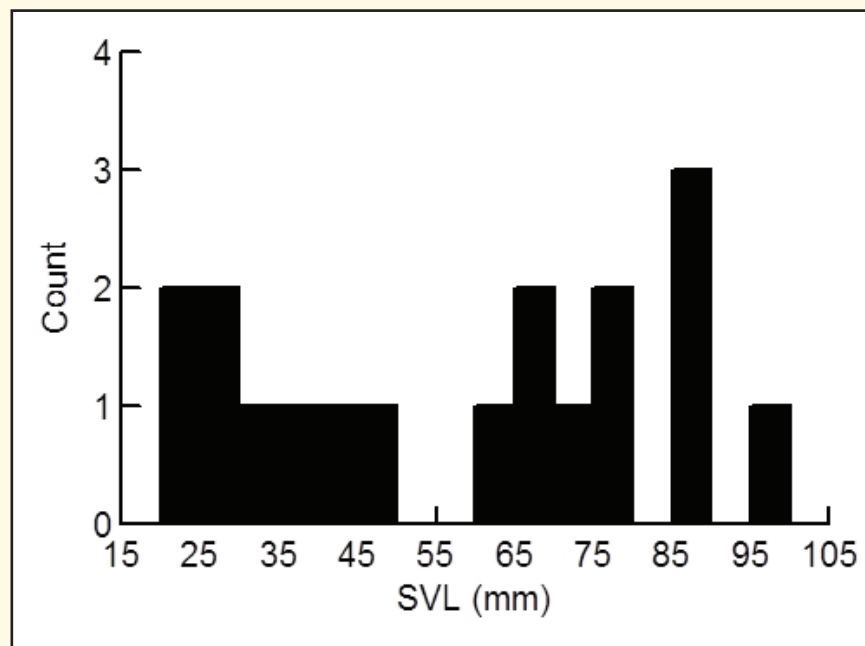
Reference Series

In order to reconstruct the snout–vent length (SVL) distribution of the lizards taken as prey, we estimated the parameters of the allometric relationship between measurements of the head length and body length of an independent ontogenetic series of 19 *Phrynosoma cornutum*. These specimens, preserved in 75% ethanol, were borrowed from museum collections (see Appendix 1), and hereafter are referred to as the reference series.

We measured the SVL (to the nearest mm) from the anterior median tip of the rostral scale to the mid-point of the anterior lip of the cloaca, once for each specimen in the reference series, by placing a stainless steel ruler against the venter of the extended specimen. We measured the head length of each specimen with dial calipers

(Mitutoyo model 505-633-50, Mitutoyo Canada Inc., Mississauga, Ontario, Canada), as described above. The reference series spanned the greater part of the ontogenetic size range of the species (Smith, 1946; Reeve, 1952; Baur and Montanucci, 1998; Price, 1990; Sherbrooke, 2003; Fig. 3), and where possible was divided evenly between the sexes (*P. cornutum* cannot be sexed by external characters before reaching sexual maturity [Baur and Montanucci, 1998; Sherbrooke 2003]).
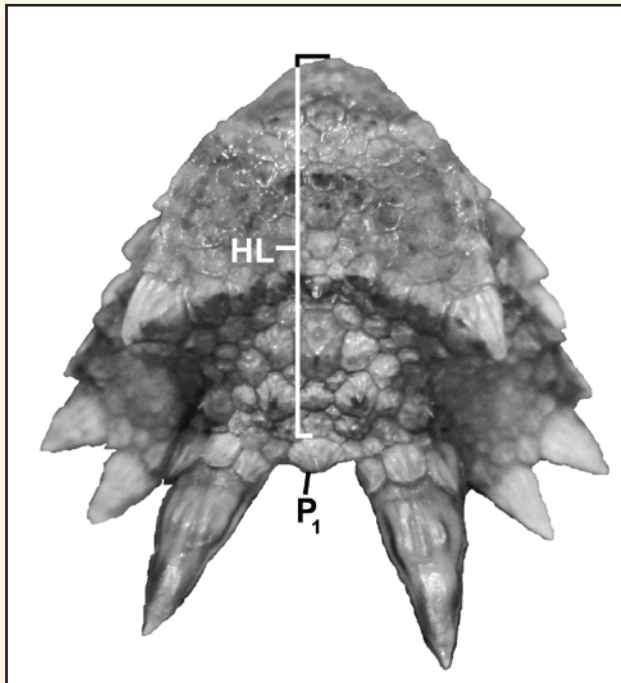
Fig. 2. Dorsal view of the head of an adult *Phrynosoma cornutum* (TWC 15129) from the reference series (SVL = 65 mm) indicating how the head length was measured (the dorsal straight-line distance from the anteromedial point of the rostral scale to the anteromedial edge of the medial parietal horn [P$_1$]).

Fig. 3. Snout–vent distribution of the reference series of *Phrynosoma cornutum* used in the RMA regression to estimate the parameters of allometric relationship between the head length and body length.

 Analysis

We log$_{10}$-transformed all of the body-length (BL) and head-length (HL) measurements in the reference series. Although there are drawbacks to using log-transformed mensural data in estimating allometric parameters (Packard and Birchard 2008; Packard, 2009; Packard and Boardman 2008, 2009 a, b; and Packard et al., 2011), a broad survey of allometric studies undertaken by Xiao et al. (2011) demonstrated that the use of logarithmically transformed data generally yields better fits of allometric models to data than alternative methods.

 We modeled the relationship of HL to BL for specimens in the reference series by means of a reduced major axis (RMA) regression (Imbrie, 1956; Gould, 1966; Seim and Saether, 1983; Ricker, 1984; Jones, 1988) of log$_{10}$(BL) on log$_{10}$(HL). We tested the distributions of the errors of the estimated log$_{10}$(BL)s and log$_{10}$(HL)s derived from the RMA regression of the reference series data for normality of distribution by using Shapiro-Wilk W statistics, and calculated their means. We conducted all of the analyses in PAST v. 2.17b (Hammer et al., 2001).

 The reduced major axis method does not assume that the predictive variable is measured without error (Ricker, 1984; Jones, 1988), and so a predicted log$_{10}$(BL) can be calculated from an observed log$_{10}$(HL). Thus, we inserted the log$_{10}$(HLp) values into the allometric equation derived from the reference series to estimate log$_{10}$(BL)s of the prey items. As most body size estimates of lizards in the literature are given as SVLs, we reconstructed the SVLs of the prey items as back-transformed estimated log$_{10}$(BL) values added to corresponding untransformed HLp values. Such back-transformation yields the geometric, rather than the arithmetic, mean of any predicted *y* on a given *x* (Gould, 1966; Baskerville, 1972; Smith, 1993; Packard and Birchard, 2008; Packard, 2009; Packard et al., 2011; Glaizier, 2013; Niklas and Hammond, 2014), but this difference will be minimal if the variance of the dependent variable is small relative to its arithmetic mean (Kerkhoff and Enquist, 2009), as in our reconstructed body lengths for the prey sample (mean log$_{10}$(BL) = 1.85; variance = 0.0029).

 Our specimens in the reference series (maintained in 75% EtOH) were partially hydrated, whereas the heads recovered from hawk nests were desiccated to varying degrees. These latter specimens, however, retained their soft tissue coverings, which are closely attached to the skull in *Phrynosoma*, and thus the degree of shrinkage likely was minimal. Because of this factor, our reconstructed SVLs will not differ greatly from the original SVLs of the prey lizards, but they could slightly underestimate the SVLs of the lizards in life.

RESULTS

The parameter estimates for the allometric equation derived from the reference series are as follows: slope (with SE) = 1,492 (0.044746); intercept (with SE) = 0.010491 (0.0023568); R^2 = 0.98471; and t(p) = 33.088 (7.0932E-17). The distributions of the errors of log$_{10}$(HL)s and log$_{10}$(BL)s resulted in means close to zero and were not significantly different from normality (estimated log$_{10}$(HL) error: mean = -2.632E-08, Shapiro-Wilk W = 0.9385, P = 0.248; estimated log$_{10}$(BL) error: mean = -7.900E-08, Shapiro-Wilk W = 0.9385, P = 0.248). The allometric parameters estimated by this equation, therefore, are acceptable for further analysis.

 The distributions of the HLps and HLs differ; the HLs cover the majority of the ontogenetic size range of *Phrynosoma cornutum*, whereas the HLps are concentrated in the upper portion of the species' ontogenetic size range and exceed the upper limit of the HL distribution, although the two series of measurements overlap to a considerable degree (Fig. 4; Smith, 1946; Reeve, 1952; Price, 1990; Baur and Montanucci, 1998; Sherbrooke, 2003).

 The reconstructed SVLs of the 33 prey items range from 66.54 mm to 116.04 mm (median value = 86.48), with both extremes being outliers relative to the reference sample. The bulk of the reconstructions, however, were between 75 mm and 105 mm (Fig. 5). The mean reconstructed SVL is 87.68 mm (SD = ± 10.14 mm) (Table 3). The upper limit of the reconstructed SVLs (Fig. 5) is greater than that for the SVLs of the reference series (Figs. 3, 5).

DISCUSSION

Limitations of Our Reconstruction Method

The size range of our HLps exceeds that of our HLs (Fig. 3), upon which we based the reduced-major axis regression used in reconstructing the SVLs of our prey sample. Regression parameters generally should not be used for

estimating values beyond the limits of the data used in their derivation, although we used them here. We have no reason to believe, however, that the allometric relationship established for HL and BL of our reference series data changes beyond its upper size limit; there is no sign of greater variation of the observations above the regression line at its upper end than at smaller BLs in this series (Fig. 6). We consider it reasonable, therefore, to assume that the allometric parameters estimated from the data over the size range of the reference series can be extended for some small distance.
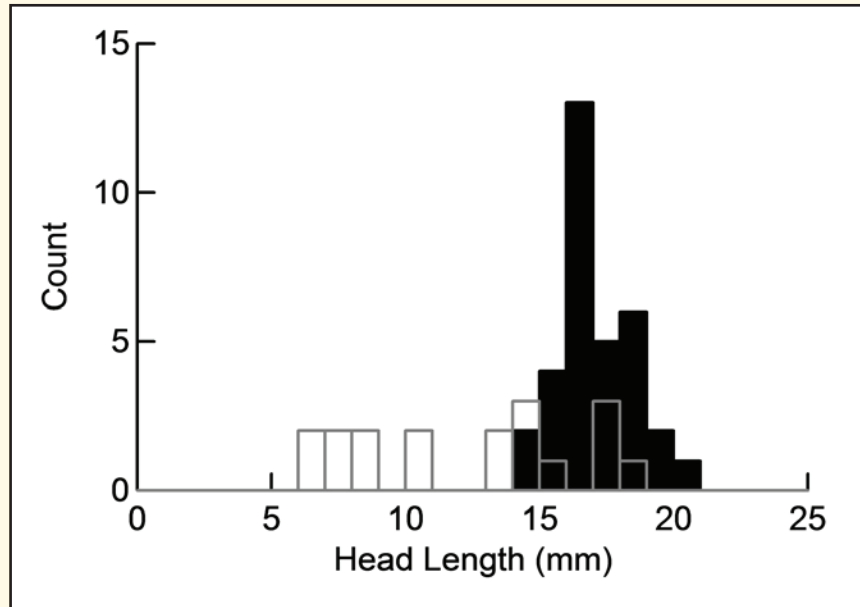

Fig. 4. Distributions of *Phrynosoma cornutum* head lengths collected from *Buteo swainsoni* nests at La Reserva de la Biosfera de Janos, Chihuahua, Mexico, from 15 June to 15 August 2006, and from 17 July to 17 August 2014 (HLp = black bars) and head lengths of the reference series of *P. cornutum* (HL = unfilled bars). The gray-outlined black bars indicate the area of range overlap.
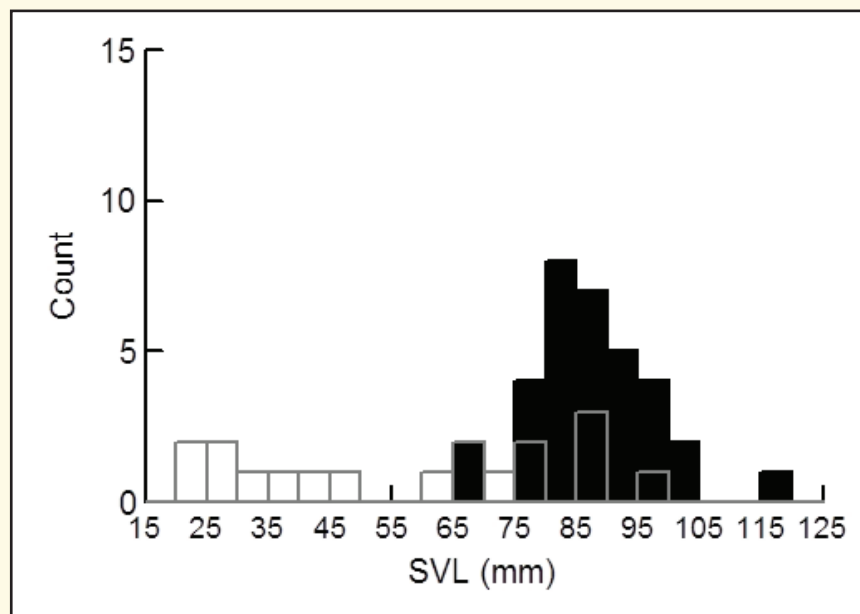
Fig. 5. Distribution of SVLs of *Phrynosoma cornutum* estimated by fitting HLps to RMA regression of HL on BL. See text for details of the SVL estimation process. The unfilled gray bars represent the SVLs of the reference series, and the gray-outlined black bars indicate the area of range overlap.
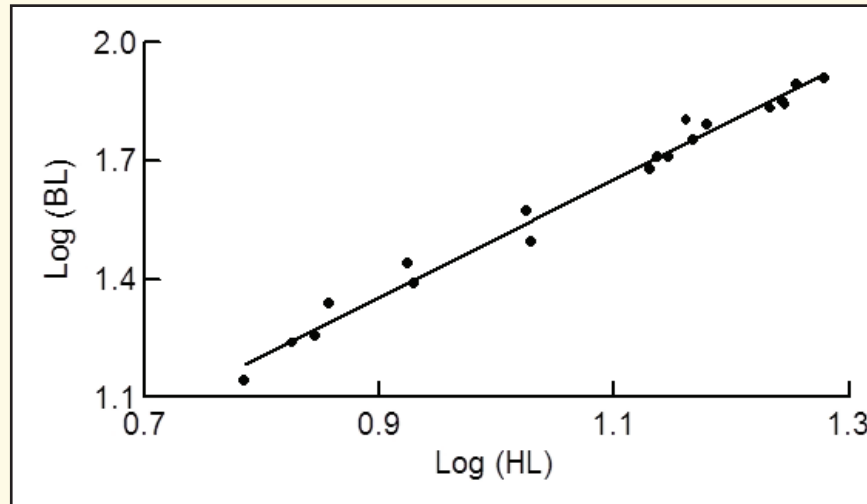
Fig. 6. RMA regression of $\log_{10}$(BL = body length) on $\log_{10}$(HL = head length) derived from the reference series. The filled circles indicate the specimens in the reference series.

We did not include sex as a source of variance in our regression analysis. *Phrynosoma cornutum* exhibits sexual size dimorphism (Smith, 1946; Price, 1990; Baur and Montanucci, 1998; Sherbrooke, 2003), but there is no evidence of sexual dimorphism in relative head size or in relative horn length in this species. Likewise, we did not include possible geographic variation as a source of variance in our regression analysis. No geographic variation in size or relative horn length has been documented for this species (Smith, 1946; Reeve, 1952; Price, 1990; Baur and Montanucci, 1998; Sherbrooke, 2003), and thus we did not expect that the lizards in the prey sample would exhibit a difference in the allometric relationship of HL to BL different than that derived from the specimens in the reference series.

Size Distribution of Prey Lizards

The reconstructed SVLs of the prey sample (Fig. 5) fall within the size range of adult *Phrynosoma cornutum* (60–120 mm SVL; Smith, 1946; Reeve, 1952; Price, 1990; Baur and Montanucci, 1998; Sherbrooke, 2003). The absence of heads of juveniles and subadults of *P. cornutum* in the prey sample suggests that smaller individuals are being fed to the young of *Buteo swainsoni* without being decapitated, and thus their skulls might have been digested, or that their skulls might have been disarticulated by the prey-handling techniques used by adult birds; although unlikely, another possibility is that smaller individuals of *P. cornutum* were not taken as prey.

Defensive Responses of *Phrynosoma* and the Prevalence of *P. cornutum* in the Diet of *Buteo swainsoni*

The long cephalic horns exhibited by most species of *Phrynosoma* commonly have been considered as a deterrent to predation (Pianka and Parker, 1975), particularly by gape-limited predators, and there is abundant direct and in-direct evidence for the use of these horns in defense (Dumas, 1964; Munger, 1986; Sherbrooke, 1987; 1990; 1991; 2003; 2008; 2013; Holte and Houck, 2000; Young et al., 2004). Within any species of *Phrynosoma*, the effective-ness of the horn array in defense likely will be greater in larger individuals than in smaller ones (Pianka and Parker, 1975; Sherbrooke 2003, 2013; Bergmann and Berk, 2012). Nevertheless, our results indicate that *Buteo swainsoni* preys upon individuals of *P. cornutum* from the upper end of this species' body size range (Figs. 4, 5), in which the cephalic horn array is most formidable as a deterrent to gape-limited predators. Recovered heads were intact, and evidently had not been ingested by the hawks that captured these lizards, which suggests that *B. swainsoni* either specifically decapitated the larger *P. cornutum* captured before consuming the rest of the body, or that the heads were left as remnants as part of the hawks' general dismemberment of the lizards. Dismemberment at the nest is part of the prey-handling technique used by raptors when provisioning their young, and the head of the prey item

frequently is left uneaten (Slagsvold and Sonerud, 2007; Slagsvold et al., 2010). Conceivably, the heads found in this study were unconsumed prey remnants, rather than indicating that the heads were removed before ingestion as part of some special prey-handling technique used by *B. swainsoni* to circumvent the cephalic armament of *P. cornutum*. Fatalities of hawks that have swallowed entire specimens of long-horned *Phrynosoma* species (Miller, 1948; Sherbrooke, 2003) demonstrate the utility of rejecting the head while consuming the remainder of the body.

Phrynosoma cornutum relies upon an array of postural and behavioral defensive strategies, and deploys different ones against different predators (Sutton, 1922; Milne and Milne, 1950; Klauber, 1972; Sherbrooke, 1990, 1991, 2003, 2013; Middendorf and Sherbrooke, 1992; Holte and Houck, 2000; Sherbrooke and Middendorf, 2004; Sherbrooke and Mason, 2005; Cooper and Sherbrooke, 2010; Sherbrooke et al., 2012). Additionally, this species is well protected against predators reliant upon vision. Lizards of the genus *Phrynosoma* rely heavily upon camouflage and are difficult to locate visually, even in open situations (Sherbrooke, 2002, 2003, 2013). *Phrynosoma cornutum* exhibits dorsal polychromatism and tends to match its background (Lowe, 1947). This effect is augmented by a white middorsal stripe, which can further render the lizard difficult to see when sheltering under clumped vegetation (Sherbrooke, 2002). The double row of lateral fringing scales (Smith 1946; Sherbrooke, 2003) are thought to aid in breaking up the shadow cast by a lizard resting on the substrate in sunlight (Sherbrooke, 2013).

Sherbrooke (2013) simulated hawk attacks upon *P. cornutum* by "flying" a stuffed *B. jamaicensis* on monofilament toward adult lizards in an enclosure. He varied the hawk model's approach between descending directly toward the lizard and descending 0.5 to 1 m to its side. Lizards approached directly by the hawk model showed a strong preference for escaping, but those not directly on the line of flight almost invariably remained immobile (Sherbrooke, 2013). None of the lizards tested in this fashion exhibited any of the behaviors deployed by *P. cornutum* to deter other predators (Sherbrooke, 2013), but instead apparently relied upon camouflage. Sherbrooke (2013) concluded that none of the post-capture defensive strategies of *P. cornutum* were useful against raptors, although hawk fatalities resulting from swallowing long-horned *Phrynosoma* heads, in which the horns punctured the internal organs have been observed (Miller, 1948; Sherbrooke 2003).

Phrynosoma cornutum often is found in areas with reduced cover (Whiting et al., 1993; Fair and Henke, 1997; Montgomery and Mackessy, 2003), and its use of open areas apparently is associated with feeding and thermoregulation. Feeding takes place in the open (Eifler et al., 2012), and corresponds with the timing of harvester ant activity, early and late in the day (Burrow et al., 2001; Montgomery and Mackessy, 2003). This species also uses areas with denser vegetation (Stark et al., 2005), particularly as thermal refugia during the hotter parts of the day (Burrow et al., 2001). Population densities generally appear to be low (3 individuals/ha [Whiting et al., 1993]; 5/ha [Endriss et al., 2007]). Home ranges are large and non-overlapping (Fair and Henke, 1999), and individuals scatter widely and seldom are encountered.

Phrynosoma cornutum, therefore, is a cryptic species that is well defended against predators that rely upon vision, only is active in the open during portions of the day, and is relatively uncommon and scattered in its distribution throughout its habitat. Thus, it appears unlikely that most predators would hunt preferentially for such prey, as it also bears an array of large cephalic horns that has been shown to be effective in deterring predators. Nonetheless, we present evidence that *B. swainsoni* takes *P. cornutum* in some numbers, and prefers to prey upon better-defended, large individuals (Figs. 4, 5). Thiollay (1981) noted that *P. cornutum* was an important prey item of *B. swainsoni* in northern Mexico, accounting for 31% of predatory strikes and 24.5% of consumed prey biomass, and that this lizard was found more frequently as a prey item than in the environment. This finding does not appear to be the result of opportunistic capture on the part of *B. swainsoni*, as Thiollay (1981) recorded a much lower incidence of *P. cornutum* in the diet of the syntopic *B. jamaicensis*, which is similar in size and habits to *B. swainsoni* and might be expected to show comparable predatory habits. Similarly, fewer *P. cornutum* were found in the diet of *Parabuteo unicinctus*, which is syntopic with *B. swainsoni* (Bednarz, 1988). Evidently, *B. swainsoni* is an important predator upon adult *P. cornutum* in northern Mexico, and might have considerable effects on populations of this lizard in this part of its geographic distribution.

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Appendix 1. The sample of *Phrynosoma cornutum* used to estimate allometric relationships between head length and body length. The collections are as follows: RRM = private collection of Richard R. Montanucci; TCWC = Texas Cooperative Wildlife Collection; and UCMZ = University of Calgary Museum of Zoology.

Catalogue Numbers: RRM 2560, RRM 2560i; TCWC 14855, TCWC 15039, TCWC 15040, TCWC 15129, TCWC 15131; TCWC 15133, TCWC 15140, TCWC 15141, TCWC 20300, TCWC 29232, TCWC 29365, TCWC 30989, TCWC 30993, TCWC 30994, TCWC 47638; and UCMZ 1975.239.

David Lazcano is a herpetologist who earned a Bachelor's degree in Chemical Science in 1980, a Bachelor's degree in Biology in 1982, a Master's degree in Wildlife Management in 1999, and a Ph.D. in biological sciences with a specialty in Wildlife Management in 2005, all at the Facultad de Ciencias Biológicas, Universidad Autónoma de Nuevo León (UANL). Currently, he is a full-time professor at UANL, where he has taught courses in Biology, Soil Sciences, Animal Ethology, Biogeography, Biology of Chordates, and Wildlife Management. Since 1993 he also has been in charge of the Laboratorio de Herpetología, and also the Coordinator of Academic Interchange in the Faculty of Biological Sciences. Since 1979, he has been teaching and assisting in both undergraduate and graduate programs. To date, David has authored or co-authored over 216 articles and notes on the herpetology of northeastern Mexico. His research interests include studying the herpetofaunal diversity of northeastern Mexico, as well as the ecology, biogeography, and captive maintenance techniques of montane herpetofauna. Over the years David has received national and international awards for his studies in herpetology, and recently he received an award from AICAR (Associacion para la Investigacion y Conservacion de los Anfibios y Reptiles de Mexico) in recognition of his lifelong dedication to studying the herpetofauna of Mexico.

Erika Sofia Bailón-Cuellar is a biology student in her eighth semester in the Facultad de Ciencias Biologicas, who has worked in the Herpetological Laboratory since her third semester. Her research interests include studying the herpetofaunal diversity of northeastern Mexico, as well as the ecology, biogeography, and captive maintenance techniques of montane herpetofauna. Currently, she is preparing her Bachelor's degree thesis on the biology of rattlesnakes in captivity, as well as several articles in association with the research group of herpetologists at FCB/UANL.

Gabriel Ruiz-Ayma is an ornithologist who earned his Bachelor's degree in Biology in 2001, a Master's degree in Wildlife Management in 2009, and a Ph.D. in Biological Sciences with a specialty in Wildlife Management in 2014, all at the Facultad de Ciencias Biológicas de la Universidad Autónoma de Nuevo León. Currently, he is an investigator and professor at this institution, where he teaches courses in Biology, Evolution and Systematics, Ethics, Profession and Society, and Physiography and Climates. He also is involved with the Conservation Biology and Sustainable Development Laboratory, Facultad de Ciencias Biológicas, at UANL. Gabriel's research interests include studying the diversity of vulnerable species of northeastern Mexico, as well as ecology, biogeography, and wildlife management.

Roberto Mercado-Hernández was born in Mexico, D.F, in 1946. He earned a Bachelor's degree in Mathematical Physics and a Master's degree specializing in Human Genetics at the Universidad Autónoma de Nuevo León (UANL), and a Ph.D. in sciences, specializing in Medical Entomology, through a scholarship granted by CONACYT. His teaching career at UANL began in 1968, and since 1974 he has been a full time professor of biophysics, radiobiology, and statistics, including graduate courses in Civil Engineering, Mechanical Engineering, Sport Sciences, and Dental Sciences. He was in charge of the Department of Exact Sciences (1986–1996), Assistant Director of Research (1989–1991), and Assistant Director and Acting Director of Academics (1991–1994). Additionally, he served the university on various academic committees, including in the updating of curricula and academic programs, as well as the Information Director (2001–2004). Roberto has authored or co-authored over 25 research articles at the national and international

levels, and four of his projects have received national awards. He has overseen more than 20 dissertations in the area of life sciences, and has been an advisor for over 380 theses at the undergraduate and graduate levels in various faculties at UANL and the Instituto Tecnológico de Estudios Superiores de Monterrey. Over the years he participated as a speaker at numerous national and international conferences, received awards for academic dedication, and collaborated in the publication of three books and authored two more in the area of life sciences. Lastly, Roberto is a member of the Consolidated Academic Body of Entomology and Acarology, a permanent advisor of the Graduate School of Orthodontics, and currently is the President of the Academy of Biostatistics.

Bryan Navarro-Velázquez received a Bachelor's degree in Biology in 2017 at the Universidad de Guadalajara, in Jalisco, Mexico. His interests include studying the herpetofauna of Jalisco, and toward this end, he has been involved with different workshops, conferences, and herpetofaunal surveys in Sierra de Quila, a protected area located in the municipalities of Tecolotlán, Tenamaxtlán, Ameca, and San Martín Hidalgo, and also in Jalisco has conducted surveys at La Primavera, a protected area near the city of Guadalajara, in the municipalities of Zapopan, Tala, and Tlajomulco de Zúñiga. Bryan currently is working on his Master's degree at the Faculty of Biomedical Sciences at the University of Guadalajara. To date, he has been involved with several articles with a research group of herpetologists in the biological sciences department at the Universidad Autonoma de Nuevo León.

Larry David Wilson is a herpetologist with lengthy experience in Mesoamerica. He has authored or co-authored 390 peer-reviewed papers and books on herpetology, including two papers published in 2013 entitled "A conservation reassessment of the amphibians of Mexico based on the EVS measure" and "A conservation reassessment of the reptiles of Mexico based on the EVS measure," one in 2014 entitled "Snakes of the genus *Tantilla* (Squamata: Colubridae) in Mexico: taxonomy, distribution, and conservation," four in 2015 entitled "A conservation reassessment of the Central American herpetofauna based on the EVS measure," "The herpetofauna of Oaxaca, Mexico: composition, physiographic distribution, and conservation status," "The herpetofauna of Chiapas, Mexico: composition, distribution, and conservation," and "A checklist and key to the snakes of the *Tantilla* clade (Squamata: Colubridae), with comments on taxonomy, distribution, and conservation," and three in 2016 entitled "The herpetofauna of Tamaulipas: composition, distribution, and conservation," "The herpetofauna of Nayarit: composition, distribution, and conservation status," and "The herpetofauna of Nuevo León: composition, distribution, and conservation." He is also a co-author of a 2017 paper entitled "The herpetofauna of Jalisco, Mexico: composition, distribution, and conservation status." Larry is the senior editor of *Conservation of Mesoamerican Amphibians and Reptiles* and the co-author of seven of its chapters. His other books include *The Snakes of Honduras*, *Middle American Herpetology*, *The Amphibians of Honduras*, *Amphibians & Reptiles of the Bay Islands and Cayos Cochinos, Honduras*, *The Amphibians and Reptiles of the Honduran Mosquitia*, and *Guide to the Amphibians & Reptiles of Cusuco National Park, Honduras*. To date, he has authored or co- authored the descriptions of 71 currently recognized herpetofaunal species, and seven species have been named in his honor, including the anuran *Craugastor lauraster*, the lizard *Norops wilsoni*, and the snakes *Oxybelis wilsoni*, *Myriopholis wilsoni*, and *Cerrophidion wilsoni*. Currently, Larry is an Associate Editor and Co-chair of the Taxonomic Board for the journal *Mesoamerican Herpetology*.

G. Lawrence Powell has worked as a field biologist and researcher on a variety of projects, largely involving amphibian and reptile ecology, conservation, and morphology. His publications include studies on the ecology of Short-horned Lizards (*Phrynosoma brevirostris*), Long-toed Salamanders (*Ambystoma macrodactylum*) and Prairie Rattlesnakes (*Crotalus viridis*) in Alberta, Canada, and he also has collaborated on a number of morphometric studies of reptiles, mammals, and dinosaurs. Currently, he is investigating the evolutionary morphology of the head in lizards of the genus *Phrynosoma*. He received his doctorate from the University of Calgary, in Canada.

Anthony Patrick Russell was born in London, United Kingdom, in 1947. He completed his Bachelor's degree at the University of Exeter (First Class Honours) and his Ph.D. at the University of London. Soon after completing his doctorate degree, he undertook a short teaching appointment at the University of Botswana, Lesotho and Swaziland, before becoming an Instructor at the University of Calgary in August 1973, where since then he ascended to the level of Full Professor. Anthony has authored over 300 peer-reviewed scientific articles, 19 book chapters, and three books, and during his career has supervised and mentored 40 graduate students. In recognition of his contributions he has received several awards, including the National Sciences and Engineering Research Council of Canada for 25 Years of Excellence Award, the Alberta Foundation for Environmental Excellence Award, and the University of Calgary Distinguished Faculty Award, and also has been inducted as a member of the Order of the University of Calgary, and as an Alberta Science and Technology Honoree. His fieldwork has taken him to Australia, New Zealand, many islands in the Eastern Caribbean, Namibia, and, most recently, Trinidad and Tobago. For six years, he served as head of the Department of Biological Sciences, and six years as Associate Dean (Students), Faculty of Science. Outside of the University, he has served as President of the Canadian Society of Zoologists, and President of the International Society of Vertebrate Morphologists.