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Utility of Skeletal Mass as a Measure of Body Size in Lizards

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ABSTRACT.—Appropriate and relevant measures of body size are essential to understand scaling relationships or to compare morphometric data from specimens or taxa of different sizes. Traditionally, body mass and snout–vent length have been used as measures of body size in lizards. Here, we report on the relevance of an alternative measure of size, skeletal mass, which is highly correlated with traditional body size measures and may have more practical value when using skeletal measurements based on museum collections.

Body size has a strong influence on the biology of organisms (McMahon and Bonner, 1983; Schmidt-Nielsen, 1984; Swartz and Biewener, 1992). Different measurements such as standard length, snout–vent length (SVL), or body mass are used as indicators of overall body size depending on the taxon studied. One of the most important uses of body size measurements is their utility as a scaling factor for morphological studies of species and groups that exhibit size variation. For lizards, SVL is typically used as an indicator of body size, rather than body mass, although usually there is a highly significant correlation between body mass and SVL (for a review of regression formulas in lizards, see Blob, 2000). However, although body mass in lizards can vary greatly based on metabolic, nutritional, or reproductive factors (Smith et al., 1995; Wikelski et al., 1997; de

Souza et al., 2004; Zúñiga-Vega et al., 2005), SVL is typically less affected by ecological factors (although see Wikelski et al., 1997) and is, thus, generally preferred as an indicator of overall size.

One problem encountered when conducting studies based on skeletal materials is that body mass and SVL are frequently not available in museum records. Although SVL can potentially be reconstructed from measurements of the vertebral column (Blob, 1998), understanding of the contribution of the intervertebral disc to overall SVL is still limited. Additionally, measurements of individual vertebrae, or lining up the vertebral elements for measurement of the vertebral column length can be difficult and time consuming. For these reasons, the utility of an alternative measure of body size, skeletal mass, is discussed and evaluated in this study.

Skeletal mass has been used as a variable in studies of numerous other vertebrate groups, including fishes (Berrios-Lopez et al., 1996), rattlesnakes (Prange and

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TABLE 1. Taxonomic Composition of Sample.

Family	Number of genera	Number of species	Number of specimens
Agamidae	2	2	2
Anguidae	1	1	1
Chamaeleonidae	2	5	9
Cordylidae	2	4	9
Corytophanidae	2	5	10
Gekkonidae	5	5-6	17
Iguanidae	6	8	15
Lacertidae	2	2	6
Leiocephalidae	1	2	3
Leiolopidae	2	5	8
Liolaemidae	1	1	1
Phrynosomatidae	3	4-5	13
Polychrotidae	1	2	5
Scincidae	1	1	2
Teiidae	4	5	19
Tropiduridae	1	1	2
Varanidae	1	8-9	15
Xantusiidae	1	1	1
Xenosauridae	1	1	2
Total	39	63-66	140

Christman, 1976), birds (Prange et al., 1979; Cubo and Casinos, 1994), and mammals (Prange et al., 1979; Christiansen 1999, 2002). However, the goal of these studies has typically been to evaluate the allometric relationship between skeletal mass and body mass. To our knowledge, no studies have quantified skeletal mass in lizards, and no studies have evaluated the utility of this variable as a measure of body size.

MATERIALS AND METHODS

One hundred forty skeletal specimens, representing 19 families of lizards were measured (Table 1; Appendix 1). Limbless species were not included in the present analysis. Specimens were located at a number of institutions, including the American Museum of Natural History (AMNH), National Museum of Natural History (USNM), Field Museum of Natural History (FMNH), Harvard University Museum of Comparative Zoology (MCZ), Northern

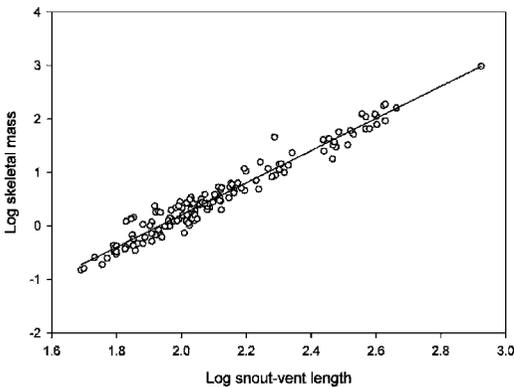


FIG. 1. Regression for Log_{10} skeletal mass on Log_{10} SVL for 140 lizards.

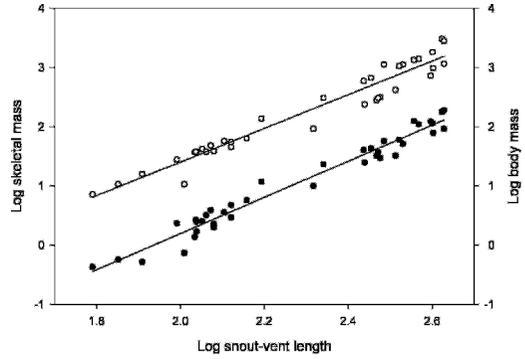


FIG. 2. Regressions for Log_{10} skeletal mass on Log_{10} SVL (open circles) and Log_{10} body mass on log SVL (filled circles) for 40 lizards.

Arizona University Vertebrate Museum (NAUVM), as well as one private collection (A. Herrel, AH). Variation in skeletal preparation method may have introduced some error into this analysis. The skeletonization method used was not listed in museum records. However, collection managers of all institutions indicated that dermestid beetle consumption of soft tissue was the standard skeletal preparation technique. This was confirmed in most cases by the observation that specimens were largely articulated, as is the result when dermestids are used. Some older specimens, particularly those located in the AMNH collection, were completely disarticulated, indicating that they may have been prepared through maceration in water.

All specimens included in this study had SVLs listed in the associated museum record. Prior to measuring skeletal mass, specimens were inventoried to confirm that all skeletal elements were present. Inclusion of specimens in our study was determined by the availability of SVLs in the museum records. Thus, our sample did not consider many species attributes, such as sexual dimorphism or presence of osteoderms. Specimens were thoroughly inventoried and included only if they were judged to be complete. It is possible that some small elements may have been missing (e.g., hyoid components, tail tip vertebrae), but these would make a minimal contribution to total skeletal mass. Skeletal mass was measured using an electronic scale (Ohaus, Model Scout201) to the nearest 0.01 g. Both variables were log_{10} -transformed before statistical analysis. Among all specimens, SVL varied from 49–840 mm (mean = 155 mm), and skeletal mass varied from 0.15–972.75 g (mean = 20.86 g). To assess the relative utility of skeletal mass and body mass as indicators of body size, a subset of specimens that had measures of body mass recorded by collectors prior to preservation, skeletal mass, and SVL present were examined in a second analysis. This subset included 40 specimens.

The relationship between skeletal mass and SVL was examined using reduced major-axis (RMA) regression analysis. Statistical analyses were conducted using Systat 9.0 (Systat Software). Model II regression techniques, such as RMA regression, are considered to be more biologically relevant than Model I methods (e.g., least-squares regression), as

they take into account error in both the dependent and the independent variable (McArdle, 1988; LaBarbera, 1989; Harvey and Pagel, 1991).

RESULTS

There was a highly significant relationship between skeletal mass and SVL (Fig. 1; $r^2 = 0.94$, $P < 0.0001$). The slope of the RMA regression line was 3.07, 95% CI = 2.95–3.21. This confidence interval includes the slope of 3, indicative of an isometric scaling between length and mass. The equation of the RMA regression line was $\text{Log}_{10}[\text{skeletal mass (g)}] = -5.61 + 2.87 \text{Log}_{10}[\text{SVL(millimeters)}]$.

For the second analysis, comparing regressions of body mass and skeletal mass on SVL for a subset of data, the correlation coefficients were very similar between the two analyses for the skeletal mass and SVL regressions (Fig. 2). Body mass and SVL were highly correlated ($r^2 = 0.95$, $P < 0.0001$), and the slope of the RMA regression was not different from the slope predicted for isometry (slope = 2.87, 95% CI = 2.60–3.22). Similarly, skeletal mass and SVL were highly correlated ($r^2 = 0.96$, $P < 0.0001$), and again the slope of the RMA regression was not significantly different from the prediction for isometry (slope = 3.03, 95% CI = 2.76–3.36). Finally, an RMA regression of skeletal mass on body mass was conducted for comparison to studies in other vertebrates. Skeletal mass scaled with negative allometry against body mass for this small subset (slope = 0.716, expectation of isometry = 1.00, 95% CI = 0.53–0.91).

DISCUSSION

The results of this study indicate that for lizards skeletal mass is indeed an appropriate measure of body size that can be used as a proxy for body size when analyzing morphometric data from taxa and individuals of different size (for a modified version of this technique, see Metzger and Herrel, 2005). Skeletal mass is relatively easy to measure and is an accurate and precise measurement if an appropriate scale is used. The primary caveat on this technique is that the skeletal specimen must be inventoried for completeness of skeletal elements. Additionally, variation in skeletal preparation technique may introduce undesirable skeletal mass variation and should be considered.

The allometric relationship between skeletal mass and body size is also of interest because of the impact that increases in body size have on the ability of the skeleton to provide structural support to an animal (Anderson et al., 1979; Schmidt-Nielsen, 1984). Previous studies of birds and mammals (Prange et al., 1979) and rattlesnakes (Prange and Christman, 1976) reported that skeletal mass scales with positive allometry against body mass and length, respectively. In contrast, the results of the present study indicate that, in lizards, skeletal mass scales isometrically with SVL and negatively allometrically with body mass. There is no a priori reason to expect this negative scaling relationship relative to body mass, and indeed, the opposite scaling relationship (positive allometry) is expected considering the types of locomotor and postural forces that lizard skeletons are likely exposed to (Biewener, 2005). A study of birds found allometric variation in the relationship between skeletal mass

and body mass for different skeletal elements (Cubo and Casinos, 1994), and further exploration of this issue in lizards may shed light on the allometric findings of this study.

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- 141789, MCZ R-141790, MCZ R-141792, MCZ R-141793), *Perochirus scutellatus* (USNM 518815, USNM 518816, USNM 518817, USNM 518828), *Thecadactylus rapicauda* (MCZ R-15714, MCZ R-145322).
- IGUANIDAE: *Ctenosaura hemilopha* (AMNH 147852, AMNH 147854, AMNH 147857, MCZ R-79774), *Ctenosaura similis* (AMNH 141157), *Cyclura cornuta* (AMNH 147865, AMNH 147866), *Dipsosaurus dorsalis* (AMNH 69891, AMNH 73238, AMNH 75603), *Iguana iguana* (AMNH 74629, AMNH 74736), *Petrosaurus thalassinus* (FMNH 216154), *Sauromalus ater* (MCZ R-85533), *Sauromalus hispidus* (MCZ R-79777).
- LACERTIDAE: *Lacerta lepida* (MCZ R-15733, MCZ R-15738), *Takydromus septentrionalis* (MCZ R-28884, MCZ R-28893, MCZ R-28894, MCZ R-28901).
- LEIOCEPHALIDAE: *Leiocephalus carinatus* (MCZ R-141246, MCZ R-141248), *Leiocephalus inaguae* (MCZ R-154263).
- LEIOLEPIDIDAE: *Pogona vitticeps* (AMNH 140834), *Uromastix acanthinura* (NAUVM uncat.), *Uromastix aegyptia* (AMNH 73358, AMNH 74816, AMNH 140817), *Uromastix hardwickii* (AMNH 141116, NAUVM), *Uromastix ocellata* (AMNH 140818).
- LIOLAEMIDAE: *Liolaemus signifer* (AMNH 80139).
- PHRYNOSOMATIDAE: *Callisaurus draconoides* (AMNH 141088), *Phrynosoma douglassii* (AH, NAUVM uncat. × 2), *Phrynosoma platyrhinos* (AH SEM3, AH SEM4, AH SEM5, NAUVM uncat. × 3), *Sceloporus* sp. (NAUVM KN006, NAUVM KN008), *Sceloporus magister* (FMNH 216159).
- POLYCHROTIDAE: *Anolis evermanni* (MCZ R-132035, MCZ R-132036, MCZ R-132039, MCZ R-132042), *Anolis equestris* (AMNH 72634).
- SCINCIDAE: *Corucia zebrata* (NAUVM uncat. × 2).
- TEIIDAE: *Ameiva ameiva* (MCZ M60564, MCZ M60573, MCZ M145875, USNM 292417, USNM 292418, USNM 292420, USNM 292421, USNM 292422, USNM 292425, USNM 292427, USNM 292434), *Cnemidophorus tigris* (NAUVM KN005), *Teius teyou* (FMNH 170853), *Tupinambis merianae* (USNM 345075), *Tupinambis teguixin* (AMNH 29931, AMNH 62535, AMNH 75281, AMNH 81879, AMNH 97337).
- TROPIDURIDAE: *Microlophus peruvianus* (AMNH 7275, AMNH 43800).
- VARANIDAE: *Varanus* sp. (USNM 536545), *Varanus beccarii* (AMNH 141072), *Varanus bengalensis* (AMNH 118715, USNM 149140), *Varanus exanthematicus* (AMNH 137237, AMNH 137238), *Varanus indicus* (USNM 323717), *Varanus niloticus* (AMNH 10499, AMNH 137116), *Varanus prasinus* (NAUVM uncat.), *Varanus rudicollis* (AMNH 141071), *Varanus salvator* (AMNH 141148, USNM 287413, USNM 305884, USNM 498916).
- XANTUSIIDAE: *Xantusia henshawi* (AMNH 141092).
- XENOSAURIDAE: *Xenosaurus grandis* (MCZ R-54309, MCZ R-54313).

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APPENDIX 1

Specimens examined (alphabetically by family, then species). Uncatalogued specimens are indicated by "uncat.," followed by the number of specimens if more than one.

AGAMIDAE: *Acanthosaura crucigera* (FMNH 222259), *Calotes nigrilabris* (MCZ R-7208).

ANGUIDAE: *Elgaria multicarinata* (NAUVM KN007).

CHAMAELEONIDAE: *Chamaeleo calypttratus* (NAUVM uncat. × 2), *Chamaeleo chamaeleon* (AMNH 73356), *Chamaeleo dilepis* (NAUVM uncat. × 3), *Chamaeleo namaquensis* (USNM 161275), *Furcifer oustaleti* (USNM 336409, USNM 336410).

CORDYLIDAE: *Cordylus cordylus* (MCZ R-52508, MCZ R-52513, MCZ R-52514), *Platysaurus guttatus* (MCZ R-44415, MCZ R-44416, MCZ R-44545, MCZ R-44547), *Platysaurus imperator* (MCZ R-67619), *Platysaurus mitchelli* (MCZ R-87257).

CORYTOPHANIDAE: *Basiliscus basiliscus* (MCZ R-6565, MCZ R-101409), *Basiliscus galeritus* (MCZ R-165713), *Basiliscus plumifrons* (MCZ R-19490), *Basiliscus vittatus* (USNM 319253, USNM 319258, USNM 319259, USNM 496736, USNM 509526), *Corytophanes hernandesi* (AMNH 147880).

GEKKONIDAE: *Gekko* sp. (NAUVM uncat. × 2), *Gekko gecko* (AMNH 114120, USNM 161276, USNM 287349), *Hemitheconyx caudacinctus* (MCZ R-145876, NAUVM uncat.), *Hoplodactylus pacificus* (MCZ R-