



Comparative ecomorphology of the sandstone night lizard (*Xantusia gracilis*) and the granite night lizard (*Xantusia henshawi*)

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Abstract

It is hypothesized that shape differences between the closely related sandstone night lizard (*Xantusia gracilis*) and the granite night lizard (*X. henshawi*) may be correlated with structural differences in their respective microhabitats. Multivariate and univariate analyses of 22 morphometric characters taken from the head, body, and limbs of both saxicolus specialists recovered statistically significant differences between them with *X. gracilis* having a wider head, longer snout, larger eyes, wider sternum, higher and wider pelvis, thinner limbs, longer forearms and thighs, and longer hind limbs. Many of these same proportional differences have been reported among very closely related saxicolus species in other lizard families (i.e. Eublepharidae, Gekkonidae, Phrynosomatidae) that also live on different rocky substrates. This supports the inference that morphometric differences between *X. gracilis* and *X. henshawi* are ecomorphological adaptations for navigating the substantially different substrates of their respective microhabitats. *Xantusia gracilis* is restricted to a loose, heterogeneous, sandstone microhabitat composed of large boulders, small rocks, and cliff faces where cracks, crevices, holes, and exfoliations are used as retreats versus the compact, more homogeneous, granite boulder microhabitat of *X. henshawi* where narrow spaces beneath exfoliations and cap-rocks are the preferred retreats.

Key words

Anza-Borrego, ecomorph, microhabitat, scansorial, saxicolus, Xantusiidae

Introduction

The concept that an animal's form has evolved in response to the way it navigates its habitat underpins the study of ecomorphology—the intersection of organismal morphology, life history, and adaptation (Van der Klaauw 1948; Wainwright and Reilly 1994). Many studies have shown that locomotor performance is linked to morphology and strongly associated with structural features of the environment (i.e. ecomorphological specialization; Losos 1990, 2009, Luxbacher and Knouft 2009, Kaliontzopoulou et al. 2010a). Within diurnal lizards, ecomorphology has been

well-studied in a number of ecologically diverse lineages of skinks, anoles, tropidurines, and wall lizards (Melville and Swain 2000; Bergmann and Irschick 2010; Kaliontzopoulou et al. 2010a; Losos 2010; Lee et al. 2013; Pincheira-Donoso and Meiri 2013; Pincheira-Donoso et al. 2015; Grismer et al. 2018; Toyama 2017) but comparatively little has been done on nocturnal lizards—and most of those involved only a single gekkonid genus (Grismer et al. 2015; 2017; 2020; Grismer and Grismer 2017; Nielson and Oliver 2017; Nguyen et al. 2021; Kaatz et al. 2021).

The Night Lizard family Xantusiidae is a New World lineage composed of three genera and 35 generally nocturnal species that collectively range from Southwestern North America to southern Central America (Noonan et al. 2013; Uetz et al. 2021). The family is dominated by highly cryptic, reclusive species with low vagility (Zweifel and Lowe 1966; Fellers and Drost, 1991; Mautz 1993) where high degrees of microhabitat specialization drive their differing ecomorphologies (Bezy 1989a, 1989b; Noonan et al. 2013). Within southern California, the Xantusiidae is represented by four, possibly five species of *Xantusia* bearing three trenchantly different ecomorphs and four different microhabitat preferences (Fig. 1): *X. riversiana*, an insular habitat generalist (Mautz 1993; Fellers and Drost 1991; Fellers et al. 1998); species of the *X. vigilis* complex (sec. Leavitt et al. 2007), vegetative specialists (Zweifel and Lowe, 1966); and *X. gracilis* and *X. henshawi*, “rock-crevice-dwelling” (sec. Leavitt et al. 2007) specialists (Grismer and Galvin 1986; Lee 1975, respectively). Nonetheless, there have been only limited discussions extolling the ecomorphological differences between rock-crevice species and vegetation specialists within the genera *Lepidophyma* and *Xantusia* (Bezy 1967; Ramírez-Bautista et al. 2008; Adams et al. 2018) and only limited data have been generated to quantitatively evince the degree of morphological differences between the rock-crevice species *X. henshawi*—a granite exfoliation specialists (Lee 1975) and *X. gracilis*—a more generalized sandstone inhabitant (Grismer and Galvin 1986). Using a limited number of metrics, Grismer and Galvan (1986) noted differences in head proportions and the growth trajectories of body width and limb length, suggesting these were correlated with the more “terrestrial” life-style of *X. gracilis*. In the analyses herein, multivariate and univariate tests are used to quantify morphometric differences between *X. gracilis* and *X. henshawi* using an expanded data set comprised of 22 characters that have proven useful as ecomorphological indicators across a wide taxonomic range of lizard groups (Losos 1990, 2009, 2010; Melville and Swain 2000; Luxbacher and Knouft 2009, Bergmann and Irschick 2010; Kaliontzopoulou et al. 2010a; Lee et al. 2013; Pincheira-Donoso and Meiri 2013; Pincheira-Donoso et al. 2015; Grismer et al. 2015, 2018, 2020; Grismer and Grismer 2017; Nielson and Oliver 2017; Toyama 2017; Kaatz et al. 2021). These data are compared to similar data generated from distantly related lizard groups as leverage to generate preliminary hypotheses as to the adaptive significance of how the different ecomorphologies between *X. gracilis* and *X. henshawi* may correlate with their structurally different microhabitats.

Materials and methods

Microhabitat

***Xantusia gracilis*.** Grismer and Galvin (1986) found *X. gracilis* to be restricted to a small (11.7 km²), circumscribed region known as the Truckhaven Rocks that fringe

the eastern flanks of the Santa Rosa Mountains in the Anza-Borrego Desert State Park, San Diego County, California. The area is composed of crumbling sandstone and siltstone sediments that have undergone tremendous erosion, resulting in a number of slot canyons and massive, heavily weathered, titled outcroppings that form a complex microhabitat of boulders, rocks, and cliff faces bearing cracks, crevices, holes, and exfoliations (Fig. 2)—all of which are utilized by *X. gracilis*. This species is not found in the adjacent granitic habitat of the Santa Rosa Mountains that abut the Truckhaven Rocks (Grismer and Galvin 1986). As such, *X. gracilis* is considered a sandstone specialist.

***Xantusia henshawi*.** Lee (1975) indicated that the distribution and density of *X. henshawi* is closely tied to suitable rock crevices and exfoliations of granitic boulders throughout coastal and ecotonal regions in Riverside, San Diego, and Imperial counties, California and northern Baja California. Granite boulders lacking such features are uninhabitable, and thus the distribution of this species is fragmented in places (Lee 1975). For example, some hilly areas on the border of Riverside and San Diego counties bear extensive granitic outcroppings that lack exfoliations and cracks and do not harbor *X. henshawi*. Nor do areas where the granite boulders are extremely weathered and eroding, producing a coarse crumbling substrate, and crevices filled with decomposed granite. *Xantusia henshawi* is far more common in areas where the more compact, granitic surface of the boulders is relatively smooth and subject to cracking and exfoliating (Fig. 2). Specimens used in this analysis are listed in Table 1.

Mensural data

The following 22 measurements were taken from the left side of the body when possible to the nearest 0.1 mm using Mitutoyo dial calipers under a Nikon SMZ 1500 dissecting microscope:

SVL (snout-vent length) – measured from the tip of the snout to the cloacal opening.

HL (head length) – measured from the tip of the snout to the posterior margin of the retroarticular process of the mandible.

HW (head width) – measured across the widest portion of the head, posterior to the eyes.

HD (head depth) – measured from top of the head above the center of the orbit to the ventral surface of the mandibles.

SL (snout length) – measured from the anterior margin of the bony orbit to the tip of the snout.

SW (sternal width) – measured from the articulation point of the humeri and the glenoid fossae across the sternum from one side to the other.

ED (eyeball diameter) – measured in a horizontal plane from the posterior to the anterior margins of the eyeball.

FLW (forelimb width) – measured from the anterior and posterior insertion points of the forelimb on the body.



Figure 1. A. The Island Night Lizard, *Xantusia riversiana*, from Santa Barbara Island, Santa Barbara County, California—a habitat generalist. Photo by Gary Nafis. B. Heterogeneous habitat of *X. riversiana* on Santa Barbara Island. Photo by Gary Nafis. C. The Yucca Night Lizard, *X. cf. vigilis*, from Anza-Borrego, San Diego County, California—a vegetative specialist. D. *Yucca* habitat of *X. cf. vigilis* at Blair Valley, San Diego County. E. The granite night lizard, *X. henshawi*, from Deep Creek, Riverside County, California—a granite exfoliation specialist. F. Granite boulder habitat of *X. henshawi* at Lost Valley, San Diego County. G. The sandstone night lizard, *X. gracilis*, from the Truckhaven Rocks, San Diego County—a sandstone specialist. H. Sandstone habitat of *X. gracilis* at the Truckhaven Rocks, San Diego County.

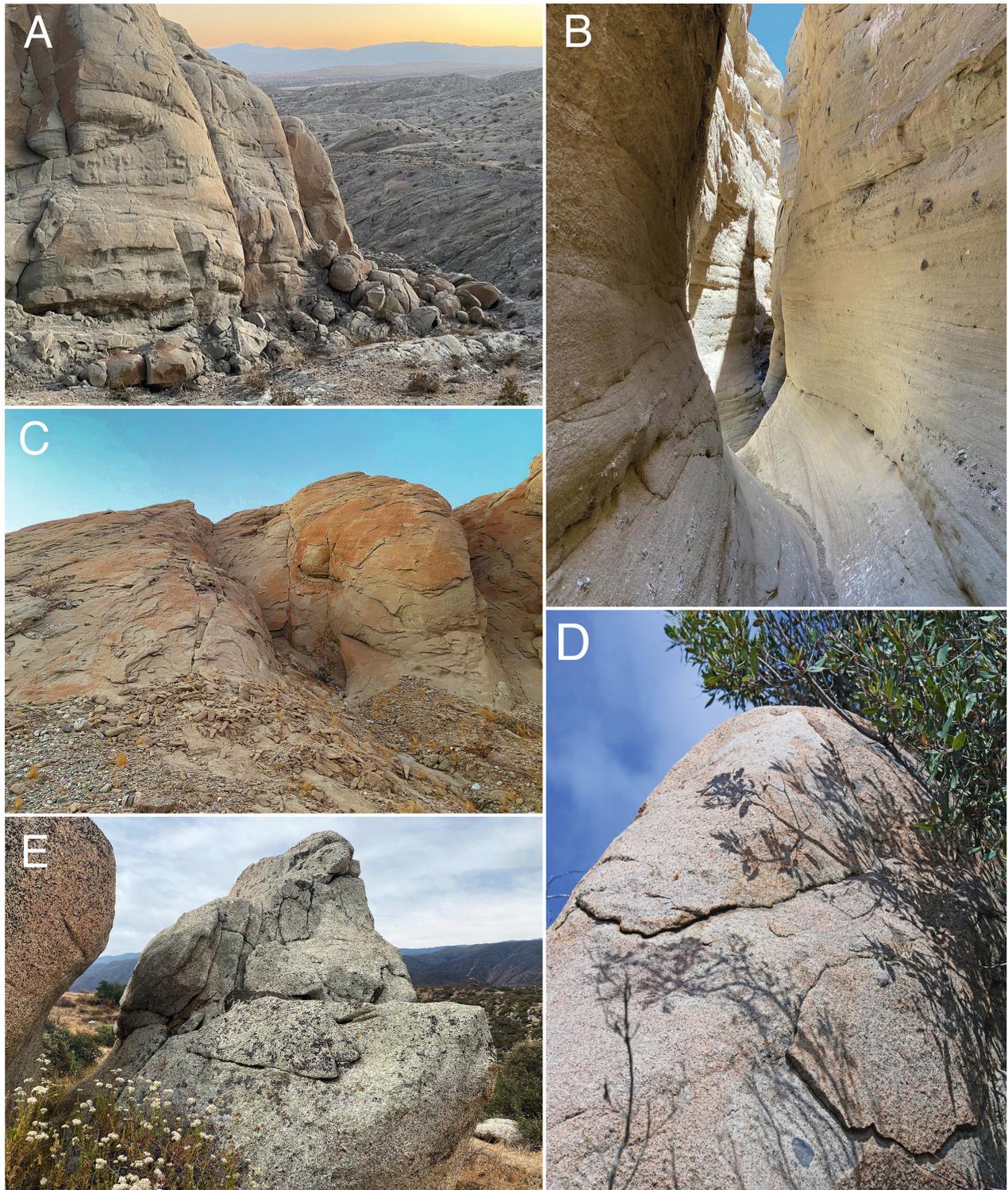


Figure 2. A. The sandstone boulder and cliff face habitat of *Xantusia gracilis*, Truckhaven Rocks, San Diego County, California. B. Slot canyon microhabitat of *X. gracilis*, Truckhaven Rocks. C. Crumbling, exfoliation-like microhabitat of *X. gracilis*, Truckhaven Rocks. D. Relatively smooth, compact granite boulder microhabitat of *X. henshawi* showing a cap-rock (at top) and an exfoliation (in lower right), Mountain Meadows, San Diego County, California. E. Granite boulder outcrop habitat of *X. henshawi*, Aguanga, Riverside, County, California.

FL1 (brachial length) – measured from the articulation point of the humerus and the glenoid fossa to the distal margin of the elbow joint while flexed 90° .

FL2 (forearm length) – measured from the proximal margin of the elbow joint while flexed 90° to the distal margin of the ulna while the wrist joint is extended.

FL3 (manus length) – measured from the distal margin of the ulna to the base of the 4th finger.

FL4 (fourth finger length) – measured from the base of the fourth finger to the tip of the claw.

Table 1. Locality of specimens of *Xantusia henshawi* used in this analysis. Based on distribution, all are presumed to belong to haplotype A of Lovich (2001) along with *X. gracilis*.

Catalog number	County	Locality
LSUHC 1530	Riverside	Aguanga
LSUHC 1531	Riverside	Aguanga
LSUHC 1998	San Diego	Intersection of Deer Springs Road and Interstate 15
LSUHC 1999	San Diego	Intersection of Deer Springs Road and Interstate 15
LSUHC 2000	San Diego	Intersection of Deer Springs Road and Interstate 15
LSUHC 2001	San Diego	Intersection of Deer Springs Road and Interstate 15
LSUHC 2002	San Diego	Intersection of Deer Springs Road and Interstate 15
LSUHC 2004	San Diego	Intersection of Deer Springs Road and Interstate 15
LSUHC 2005	San Diego	Intersection of Deer Springs Road and Interstate 15
LSUHC 2006	San Diego	Intersection of Deer Springs Road and Interstate 15
LSUHC 2007	San Diego	Intersection of Deer Springs Road and Interstate 15
LSUHC 2009	San Diego	Intersection of Deer Springs Road and Interstate 15
LSUHC 2010	San Diego	Ranchita
LSUHC 2011	San Diego	Ranchita
LSUHC 2013	San Diego	Ranchita
LSUHC 2015	San Diego	Ranchita
LSUHC 2016	San Diego	Ranchita
LSUHC 2017	Riverside	Hemet
LSUHC 2018	Riverside	Hemet
LSUHC 2019	Riverside	Hemet
LSUHC 2020	Riverside	Aguanga
LSUHC 2021	Riverside	Aguanga

FLL (forelimb length) – the sum of FL1–FL4. These data were used in separate analyses so as not to overleverage the analysis with forelimb dimensions.

AG (axilla-groin length) – measured from the posterior margin of the forelimb at its insertion point on the body to the anterior margin of the hind limb at its insertion point on the body.

PW (pelvic width) – measured from the lateral margins of the ilia across of the body.

PH (pelvic height) – measured from top of the ilium to the ventral surface of the pubic bone.

HLW (hind limb width) – measured from the anterior and posterior insertion points of the thigh on the body.

HL1 (thigh length) – measured from the articulation point of the femur and the acetabulum to the distal margin of the knee joint while flexed 90°.

HL2 (tibia length) – measured from the proximal margin of the knee joint while flexed 90° to the distal margin of the tibia while the ankle joint is extended.

HL3 (pes length) – measured from the distal margin of the tibia to the base of the 4th toe.

HL4 (fourth toe length) – measured from the base of the fourth toe to the tip of the claw.

HLL (hind limb length) – the sum of HL1–HL4. These data were used in separate analyses so as not to overleverage the analysis with hind limb dimensions.

Data analysis

To ensure that allometric biases in the raw data were appropriately removed prior to analysis, hatchlings were

omitted from the data set and the raw data were adjusted using the following equation: $X_{adj} = \log(X) - \beta[\log(SVL) - \log(SVL_{mean})]$, where X_{adj} = adjusted value; X = measured value; β = unstandardized regression coefficient for each population; and SVL_{mean} = overall average SVL of all populations (Thorpe 1975, 1983; Turan 1999; Lleonart et al. 2000)—accessible in the R package *GroupStruct* (available at <https://github.com/chankinonn/GroupStruct>). The morphometrics of each species were adjusted separately and then concatenated so as not to conflate intra- with interspecific variation (Reist 1985; McCoy et al. 2006). Small sample sizes for *X. gracilis* (females $n=5$, males $n=6$) recovered no sexual dimorphism in data that were non-parametric (Welch's t -test; $p>0.05$). Lee (1975) also, noted no sexual dimorphism in *X. henshawi* for head and body dimensions. Although this may change with larger sample sizes bearing normally distributed data (Grismer in prep), data from both sexes were combined herein for each species. The raw and adjusted data are presented in Tables S1 and S2.

A principal component analysis (PCA) of the adjusted data was employed to visualize and assess the degree of difference in morphospacial clustering among *Xantusia gracilis* and *X. henshawi*. Principal component analysis is an unsupervised analysis that does not group individuals *a priori* according to species. All adjusted data were scaled to their standard deviation to ensure they were analyzed on the basis of correlation and not covariance. A subsequent supervised analysis, discriminant analysis of principal components (DAPC) from the ADEGENET package in R (Jombart and Collins 2015), that does group individuals *a priori* according to species, was also per-

Table 2. Summary statistics and principal component analysis scores for the adjusted morphometric characters of *Xantusia gracilis* and *C. X. henshawii*. Abbreviations are listed in the Materials and methods.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11	PC12	PC13	PC14	PC15	PC16	PC17	PC18	PC19
Standard deviation	2.2054	1.7470	1.4168	1.2978	1.1505	1.0746	0.9953	0.9130	0.8209	0.8062	0.7670	0.7392	0.6512	0.5647	0.5257	0.4700	0.3956	0.3585	0.2336
Proportion of variance	0.2432	0.1526	0.1004	0.0842	0.0662	0.0577	0.0495	0.0417	0.0337	0.0325	0.0294	0.0273	0.0212	0.0159	0.0138	0.0111	0.0078	0.0064	0.0027
Cumulative proportion	0.2432	0.3958	0.4962	0.5804	0.6466	0.7043	0.7538	0.7955	0.8292	0.8617	0.8911	0.9184	0.9396	0.9556	0.9694	0.9804	0.9883	0.9947	0.9974
Eigenvalue	4.8639	3.0519	2.0074	1.6842	1.3237	1.1547	0.9907	0.8337	0.6739	0.6500	0.5883	0.5464	0.4241	0.3189	0.2763	0.2209	0.1565	0.1285	0.0546
SVL	-0.0460	0.0228	-0.0248	-0.0261	0.0684	-0.1519	0.9766	-0.0130	0.0754	-0.0590	0.0090	-0.0255	0.0430	-0.0102	0.0425	-0.0083	0.0136	0.0200	-0.0063
SW	-0.2892	-0.1317	-0.1023	0.0910	0.2057	0.4154	0.0675	-0.1512	-0.3248	-0.0858	-0.1846	-0.1978	-0.4010	0.0830	-0.0303	0.2506	0.2321	0.3123	0.2526
PW	-0.2512	-0.0802	-0.1529	0.3721	0.1465	-0.0176	-0.0677	-0.3703	0.0745	-0.0421	0.1929	-0.4709	0.3354	-0.3291	0.1055	-0.0410	-0.2292	0.1113	-0.2007
PH	-0.1867	-0.3630	-0.1312	-0.1903	-0.1488	0.0572	0.0208	0.4195	-0.0990	-0.0684	0.0696	0.1754	0.2863	-0.2852	-0.2235	0.3139	-0.3085	0.2742	0.1269
AG	-0.1108	0.2409	0.3821	0.0879	-0.3953	0.0238	0.0179	0.1533	-0.1344	-0.0526	0.3443	-0.3094	0.2248	0.4206	0.1415	0.0975	-0.0471	0.1767	0.2479
HL	-0.2116	0.0075	-0.4318	-0.0909	0.3720	0.0187	-0.0681	0.1262	0.1352	-0.2869	0.0702	0.0078	0.2013	0.5023	0.0509	0.1113	-0.1491	-0.3707	0.1272
HW	-0.3053	-0.1526	0.0302	-0.1844	-0.1926	0.2856	0.0578	-0.1830	-0.3340	0.1723	-0.0038	0.1887	0.4262	-0.0951	0.0999	-0.1738	0.3573	-0.3721	-0.0292
HD	0.0081	-0.2928	-0.3123	-0.0469	-0.3221	-0.1252	0.0199	0.2661	0.0584	0.3856	-0.2227	-0.5662	-0.1361	0.1123	0.0306	-0.0414	0.0891	-0.2157	-0.0212
SL	-0.2577	-0.1572	-0.2075	-0.0470	-0.0632	-0.5067	-0.0868	0.1029	-0.3064	-0.1576	0.1161	0.1626	-0.2036	0.0379	0.3259	-0.3725	0.0382	0.2865	-0.0889
ED	-0.2577	-0.0667	0.2509	-0.2691	0.1566	0.2469	-0.0406	0.1892	0.4907	0.1218	-0.1264	0.0079	-0.0145	-0.0273	0.5796	0.0034	0.0185	0.1936	-0.1562
HLW	0.3574	0.0377	-0.2416	-0.2525	0.0224	0.1556	0.0336	-0.0038	-0.0648	0.2479	0.2246	-0.0562	0.0488	0.0310	-0.0119	0.2396	-0.0296	0.2114	-0.3282
HL1	-0.3529	0.1922	-0.0454	-0.0006	-0.0421	-0.0825	-0.0040	-0.0578	0.2445	0.4127	0.2082	0.1154	-0.2648	-0.2445	-0.1273	-0.0254	-0.2040	-0.1569	0.4699
HL2	-0.1740	0.3774	-0.1458	-0.1107	0.1231	0.3465	0.0597	0.2172	-0.1894	0.1996	0.1832	-0.0433	-0.1015	0.0880	-0.2176	-0.4541	-0.1989	0.1086	-0.2820
HL3	-0.2522	0.1909	0.0408	0.2413	0.1977	-0.3155	-0.0467	0.0682	-0.0081	0.4223	-0.3749	0.1487	0.3156	0.2341	-0.2189	0.1763	0.1736	0.2612	-0.1430
HL4	0.0042	0.3999	-0.3671	-0.0151	-0.2082	-0.0619	-0.0041	-0.1709	-0.1529	0.1224	0.0656	0.1736	-0.0619	-0.0824	0.4443	0.4465	-0.0003	-0.0407	-0.0312
FLW	0.3487	0.0654	-0.1820	-0.2334	0.2797	-0.0473	-0.0435	-0.0528	-0.0168	0.1550	0.0096	-0.1226	0.3234	-0.0815	0.1305	-0.2782	0.1859	0.2877	0.5633
FL1	-0.0687	0.3241	0.1363	-0.4109	-0.0156	-0.1196	-0.0281	-0.0762	-0.2560	-0.1797	-0.5469	-0.2552	0.0564	-0.1626	0.0184	0.0051	-0.3853	-0.0866	0.0239
FL2	-0.2166	0.1027	0.1193	-0.4759	0.1490	-0.2987	-0.0930	-0.0532	0.0827	-0.1257	0.3310	-0.2550	-0.0767	-0.1240	-0.2801	0.2112	0.4371	-0.0345	-0.1439
FL3	-0.1165	0.1300	-0.3238	-0.1213	-0.4945	0.1219	-0.0175	-0.2852	0.4354	-0.2624	-0.1847	0.0797	0.0758	0.1193	-0.2311	-0.1652	0.1268	0.3024	-0.0040
FL4	0.0129	0.3657	-0.1499	0.3011	-0.0147	0.0993	-0.0150	0.5446	0.0443	-0.2714	-0.0791	-0.0847	0.0657	-0.3969	0.0477	-0.0165	0.3661	-0.0863	0.0181

formed. A DAPC relies on data calculated from its own PCA as a prior step to ensure that variables analyzed are not correlated and number fewer than the sample size. Dimension reduction of the DAPC prior to plotting is accomplished by retaining the first set of principal components that account for 90–95% of the variation as determined from a scree plot generated as part of the analysis.

To search for and quantify significant morphological differences between *Xantusia gracilis* (n=11) and *X. henshawii* (n=22), all data were first tested for normality with an *F*-test. Those with homogeneous variances ($p < 0.05$) were subjected to a Student's *t*-test and those with unequal variances ($p > 0.05$) were subjected to a Welch's *t*-test. Both tests search for statistically significant different mean values ($p < 0.05$) in all the characters between both species. Violin plots, embedded with boxplots, were generated for the characters bearing statistically different means in order to visualize their range and frequency of variation, mean, 50% quartile, and the degree of difference between the species. All data analyses were performed in R [v3.4.3] (R Core Team 2018).

Results

The PCA demonstrates that *Xantusia gracilis* and *X. henshawii* occupy non-overlapping positions in morphospace among the collective ordination of the first two principal components (Fig. 3A). Principal component 1 accounts for 24.3% of the variation and loads most heavily for limb width (FLW and HLW), thigh length (HL1), head width (HW) and snout width (SW) (Fig. 3C; Table 2). Principal component 2 accounts for an additional 15.3% of the variation and loads most heavily for head depth (HD), brachial length (FL1), fourth finger length (FL4), axilla-groin length (AG), pelvic height (PH),

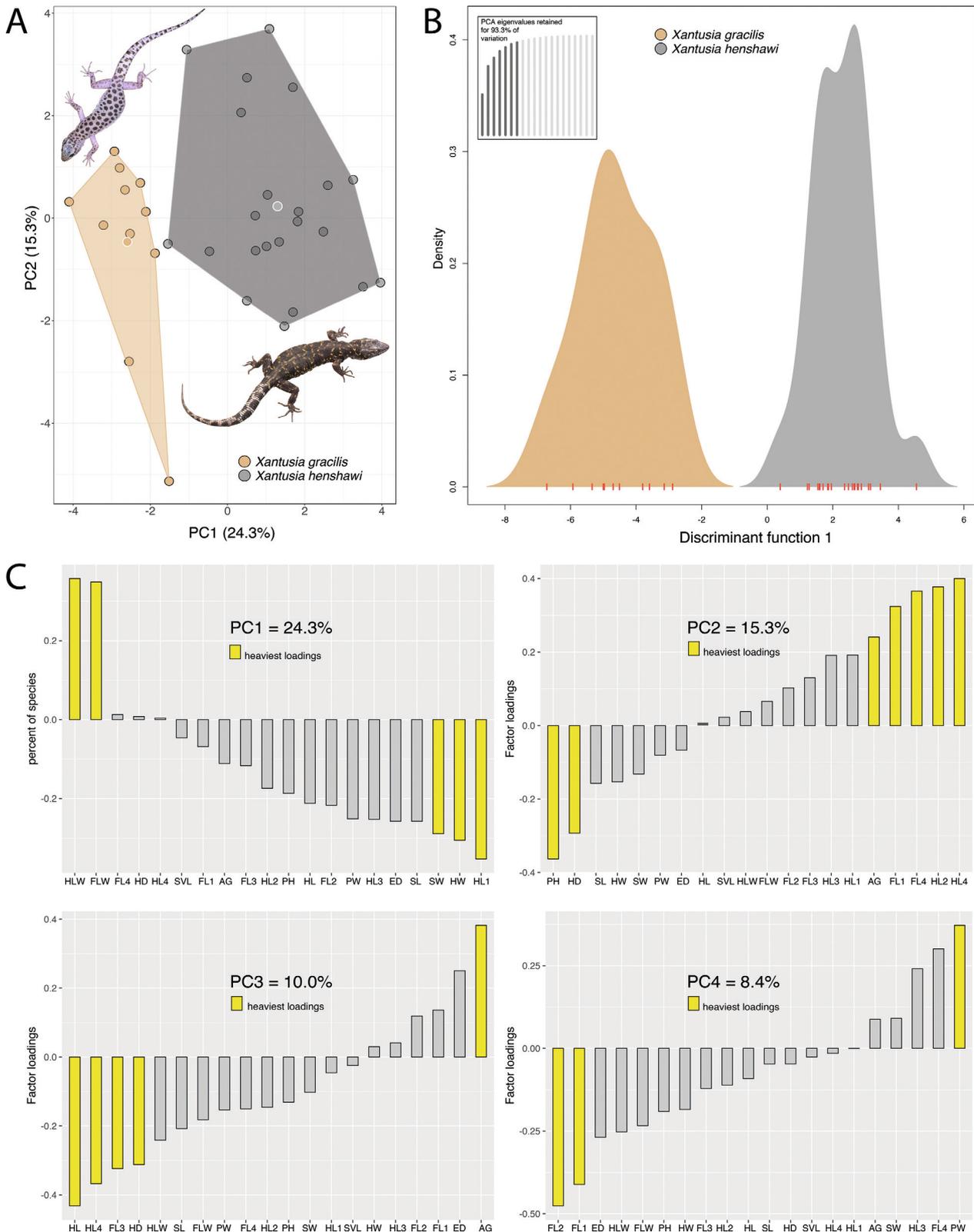


Figure 3. A. PCA and B. DAPC of *Xantusia gracilis* and *X. henshawi*. C. Bar plots of PCA loading scores of PC1–PC4.

tibia length (HL2) and fourth toe length (HL4). Principal components 3 and 4 account for an additional 10.0% and 8.4%, of the variation, respectively (Fig. 3C; Table 2). Retention of the first seven eigenvalues of the DAPC, accounting for 93.3% of the variation, further recovered complete separation of *X. gracilis* and *X. henshawi* along the first discriminant function (Fig. 3B).

Although *Xantusia gracilis* and *X. henshawi* do not differ significantly in SVL, they do differ in a number of other proportions. The Student’s and Welch’s *t*-tests of the adjusted data recovered 11 characters bearing statistically significant mean differences between them (Fig. 4; Table 3), illustrating that *X. gracilis* has a significantly wider head (HW), longer snout (SL), larger

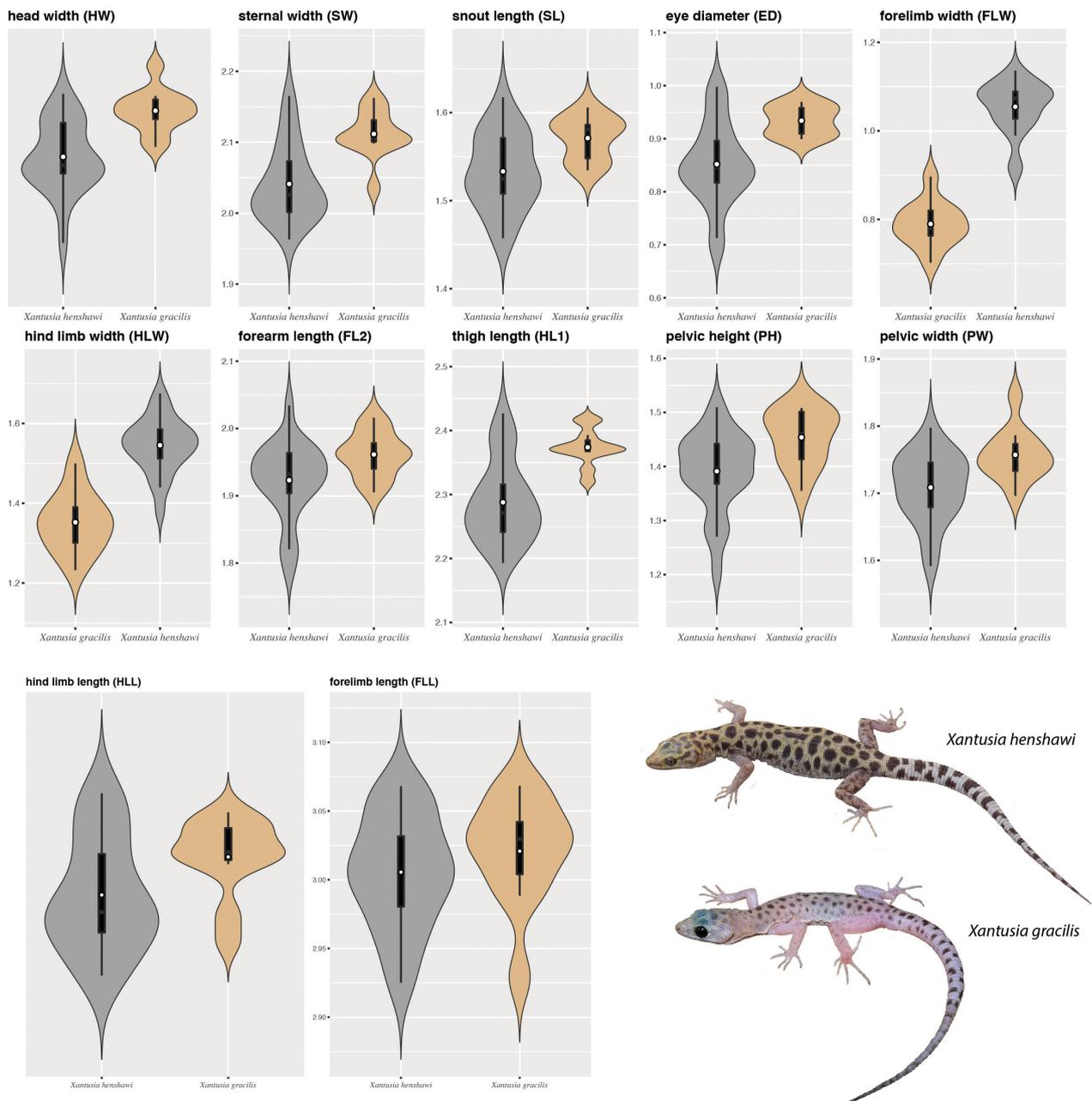


Figure 4. Violin plots overlain with box plots of *Xantusia gracilis* and *X. henshawi* showing the range, frequency, mean (white dot), and 50% quartile (black rectangle) of the significantly different size-adjusted morphometric characters. The means of FLL are not significantly different.

eyes (ED), wider sternum (SW), thinner limbs (FLW and HLW, i.e. reduced limb mass), longer forearms (FL2), longer thighs (HL1), and a wider and higher pelvis (PW and PH, respectively). Welch's *t*-test also demonstrated that *X. gracilis* has significantly longer hind limbs (HLL) than *X. henshawi* but not significantly longer forelimbs (FLL). Grismer and Galvin (1986) also noted that *X. gracilis* had a thinner body (inter-forelimb and inter-hind limb distances) than *X. henshawi*. Although *X. gracilis* has a longer snout, it does not have a significantly longer head and similarly, it has a significantly longer forearm, but does not have a significantly longer foreleg. These metrics indicate that not all components of the head and forelimb scale isometrically (i.e. they do not grow at the same rate).

Discussion

The quantification of ecomorphological differences among species is important to many downstream analyses based on body size and shape. These types of data are not just necessary for comparative methods that combine phylogenies with phenotypic data to understand evolutionary processes such as the mode and tempo of trait evolution (Mahler et al. 2010). They also apply to a multitude of ecological principles where phenotypic differences within and among populations can influence the rate and direction of evolution, population dynamics, and the outcome of several other community interactions (Bolker et al. 2003; Werner and Peacor 2003; Krohne 2018).

Table 3. Summary statistics of Student and Welch's *t*-tests. Shaded cells are those characters bearing significantly different means between *Xantusia gracilis* and *X. henshawi*. Character abbreviations are in the Materials and methods.

character	<i>t</i> -test	<i>t</i> value	<i>p</i> value
HL	Welch's	0.7763	0.4453
HW	Welch's	4.6329	6.828e-05
HD	Student's	0.3646	0.7170
SL	Welch's	3.1815	0.0033
SW	Welch's	4.6399	6.938e-05
ED	Student's	3.3674	0.002
FLW	Welch's	-13.362	3.48e-12
FL1	Welch's	-0.1597	0.0742
FL2	Welch's	2.3969	0.023
FL3	Welch's	1.4885	0.1551
FL4	Welch's	-0.5856	0.5674
FLL	Welch's	1.0322	0.3137
AG	Welch's	1.7186	0.1078
PW	Welch's	0.0271	0.0056
PH	Welch's	2.8392	0.0083
HLW	Welch's	-7.1422	9.989e-07
HL1	Student's	4.2352	0.0002
HL2	Welch's	0.3227	0.7504
HL3	Welch's	1.9674	0.0646
HL4	Welch's	-0.9722	0.3424
HLL	Welch's	2.2286	0.0341

These data clearly demonstrate that *Xantusia gracilis* and *X. henshawi* are proportioned differently and do not scale equally across various components of their bodies. Overall, *X. gracilis* is more slender and less robust than *X. henshawi* (Fig. 5) as was first reported by Grismer and Galvin (1986) using a limited data set. They inaccurately suggested these differences correlated with a more “terrestrial” life style. Using an expanded, more highly partitioned data set, however, reveals precisely where such differences occur and aptly justifies functional ecomorphological comparisons and inferences across a wide range of distantly related lizard groups bearing the same traits. It is logical to posit that the morphological differences between *X. gracilis* and *X. henshawi* are somehow related to their abilities to navigate their respective microhabitats. It has been well-established in a number of small clades of very closely related lizard species, that longer and thinner limb components increase climbing performance and are ecomorphological adaptations for a scansorial life style, as opposed to shorter, more robust limbs that occur in their less scansorial or strictly terrestrial (non-climbing) close relatives (Grismer and Grismer 2017; Neilson and Oliver 2017; Grismer et al. 2021; Kaatz et al. 2021). We hypothesize here, that these same adaptations in *X. gracilis* help it to navigate a more complex heterogeneous and less firm, topographically complex sandstone substrate (i.e. sandstone is not necessarily a flat, smooth, hardened surface; Fig. 2C) as compared to a more homogeneous, relatively flat, hardened granite boulder substrate (Fig. 2D). The smaller eye diameter (and obligatorily flatter head) and shorter pelvic height of *X. henshawi* would be more adaptive for taking refuge within narrow, restrictive retreats beneath granitic exfo-

liations and cap rocks (Fig. 2D). Although both species share adaptations for a scansorial, saxicolous life style—trenchantly different from that of strictly terrestrial species (e.g. *X. riversiana*)—differences in the complexity of their associated microhabitats are likely the driver of their ecomorphological differences.

What little work has been done looking at morphological adaptations related to climbing and clinging ability among closely related species living on different rock substrates is illustrative. In the eublepharid gecko genus *Goniurosaurus*, Grismer et al. (2021) demonstrated that the highly scansorial *G. catbaensis*, *G. huiliensis*, and *G. luii*, which are adapted to topographically complex karstic substrates, have significantly longer limbs, wider heads, longer snouts, and larger eyes than does the less scansorial *G. lichtenfelderi* that is adapted to a less complex granite substrate. Similarly, Cobos et al. (submitted), has shown experimentally, that reduced limb mass (i.e. thinner limbs), longer limbs, smaller hands and feet, and shorter digits, underpin the superior clinging ability of karst-adapted gekkonid species in the *Cyrtodactylus pulchellus* group as opposed to their closely related granite-adapted species. The point is, that very closely related saxicolous species navigating different rocky substrates are proportioned differently and that there may be a general convergence in relative limb and head proportions shared among those species that lead a more scansorial life style on topographically complex substrates.

The above research opens up several avenues of inquiry as to the locomotor performance between *Xantusia gracilis* and *X. henshawi* on their respective substrates as compared to that on one another's substrate. Exper-



Figure 5. A. Adult male *Xantusia gracilis*, Truckhaven Rocks, San Diego County, California. B. Adult female *X. gracilis*, Truckhaven Rocks. C. Juvenile *X. gracilis*, Truckhaven Rocks. D. Adult male *X. henshawi*, Deep Canyon, Riverside County, California. E. Adult female *X. henshawi*, Ramona, San Diego County, California. F. Adult female *X. henshawi*, Deep Canyon.

imental trials such as those done by Cobos et al. (submitted) where climbing and clinging ability are measured on different substrates among different ecomorphs, could be used to test the morphology-based inference here that a complex sandstone habitat and a more homogenous granitic substrate require different ecomorphologies. Additionally, similar experiments can be designed to test the effects of unequal scaling in the various components (e.g. different limb and head dimensions) within functional systems (e.g. the limbs and skull) in order to ascertain what adaptive value different allometric trajectories may have during the course of ontogeny. Kaliontzopoulou et al. (2010a, 2010b) have shown that plasticity in limb trait variation in the saxicolous *Podacris bocagei* (Lacertidae) is under the influence of total body size. Whereas habitat-related differentiation is amplified for other limb

characters when size effects are removed, and for others, it is completely eliminated or even reversed. Studying the ontogeny of limb traits in *X. gracilis* and *X. henshawi* (Grismer in prep.) may help to understand the putatively adaptive mechanisms underlying their ecomorphological differences.

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Supplementary material 1

File 1

Authors: Grismer LL (2021)

Data type: .pdf

Explanation note: Table S1. Raw mensural data from *Xantusia gracilis* from the Truckhaven Rocks, San Diego County, California and *X. henshawi* from throughout its range in San Diego County. SDNHM = San Diego Natural History Museum; LSUHC = La Sierra University Herpetological Collection, Riverside County, California. Abbreviations are in the Materials and methods..

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Link: <https://doi.org/10.3897/vz.71.e69214.suppl1>

Supplementary material 2

File 2

Authors: Grismer LL (2021)

Data type: .pdf

Explanation note: Table S2. Size-adjusted morphometric data. Order of specimens follows that in Table S1. Abbreviations are in the Materials and methods.

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