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Morphological Divergence among Populations of *Xantusia riversiana*, a Night Lizard Endemic to the Channel Islands of California

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Morphological variation between closely related island endemics offers a unique system to study ecological and evolutionary processes. The Island Night Lizard, *Xantusia riversiana* (Cope, 1883), is endemic to three of the Southern Channel Islands off the coast of Southern California: Santa Barbara, San Clemente, and San Nicolas. Some authors treat the species as polytypic with the night lizards on San Nicolas (*X. r. riversiana*) distinct from those on Santa Barbara and San Clemente (*X. r. reticulata*). Previous studies failed to find strong morphological divergence, but it remains uncertain if those studies were hampered by a combination of small sample size, small number of characters, and/or the lack of modern morphometric techniques. Here we examined 172 Island Night Lizards from the three islands for nine morphometric and five meristic characters, increasing the number and types of morphological characters examined over previous studies, and applying modern morphometric techniques to test for divergence associated with island and sex. We found significant differences in both body measurements and meristic characters among the nominal subspecies as well as among the three islands. We also detected significant sexual dimorphism in body and scale characteristics for both subspecies. However, assigning individuals to an island based on morphology is difficult because all three islands harbor morphologically overlapping individuals. Our study clarifies Island Night Lizard systematics, as well as informs conservation efforts for an island endemic that was until recently listed as threatened under the U.S. Endangered Species Act.

Island lineages are often morphologically distinct from their mainland progenitor, and colonizers of multiple islands in an archipelago often diverge phenotypically in response to island-specific selective pressures. Differences in climate, substrate, and/or resource availability can promote variation in color, shape, and size of insular populations, and may even promote speciation. The eight Channel Islands off the coast of Southern California are home to many endemic taxa, including the Island Spotted Skunk (*Spilogale gracilis amphiala*; Floyd et al., 2011), the Island Scrub Jay (*Aphelocoma insularis*; Johnson, 1972), and the now extinct Pygmy Mammoth (*Mammuthus exilis*; Agenbroad, 2009), all of which show phenotypic differences from their closest mainland relatives. Several endemic species such as the Island Loggerhead Shrike (*Lanius ludovicianus*; Eggert et al., 2004), the Channel Island Fox (*Urocyon littoralis*; Wayne et al., 1991; Funk et al., 2016), and the Channel Island Deer Mouse (*Peromyscus maniculatus*; Pergams and Ashley, 1999; Pergams et al., 2000) show morphologic and genetic divergence among islands within the archipelago and have proven to be excellent systems for studying speciation.

The Island Night Lizard, *Xantusia riversiana* (Cope, 1883), is only found on the Southern Channel Islands of San Nicolas, San Clemente, and Santa Barbara, as well as Sutil Islet, which is ca. 650 m offshore from Santa Barbara Island (Fig. 1). Island Night Lizards are much larger than other members of the genus, leading some to claim that they are an example of island gigantism (Carlquist, 1965; Schoenherr et al., 1999; Holmes et al., 2016). Their distinctive morphology and life history also led Savage (1957) to place this species in its own genus, *Klauberina*, though most authors follow Bezy (1972) in retaining Island Night Lizards in *Xantusia*.

Regardless of generic assignment, all authors have recognized the distinctiveness of this island endemic and the potential for a long history of isolation on the Southern Channel Islands.

Multiple studies have suggested that *X. riversiana* last shared a common ancestor with its mainland relatives in the Miocene. Bezy et al. (1980), based on allozyme analyses, suggested that *X. riversiana* diverged from its mainland congeners approximately 10–15 mya, and subsequent DNA sequencing studies found similar estimates of 13.7 mya and 16 mya (Leavitt et al., 2007; and Noonan et al., 2013, respectively).

The unique morphology, island endemism, and lengthy divergence from mainland relatives have motivated multiple researchers to examine variation among the various island populations. Nevertheless, a consensus has not emerged regarding the distinctiveness of the different island populations. Early work summarized morphological variation using the concept of subspecies, which here we take to imply some amount of divergence and island-specific evolutionary processes. Based on morphological differences between one specimen from San Clemente Island and three from San Nicolas Island, Smith (1946) proposed recognizing two distinct groups, *X. r. riversiana* on San Nicolas Island and *X. r. reticulata* on San Clemente Island. With a much larger sample, Savage (1951) argued that all three islands overlap considerably in morphological characters and should not be considered as separate taxa. Later, this same author recognized two subspecies based on subtle morphological differences and placed Santa Barbara and San Clemente Island lizards together as *X. r. reticulata* (Savage 1955). Subsequent studies examining morphology, allozymes, and/or clutch size have only referred to night lizards as a monotypic species, even though among-island differences were recovered for multiple types of characters (Goldberg and Bezy, 1974; Bezy et al., 1980). Standard reference works also treated the species as monotypic (Collins et al., 1978, 1982; Collins, 1990; Stebbins, 1985). In their review of the ecology of *X. riversiana*, Fellers and Drost (1991) listed two subspecies. The SSAR Names List then started to include these two subspecies (Collins, 1997) and continues to do so today (de Queiroz et al., 2017), although other standard references continue to list the species as monotypic (Stebbins, 2003).

We suspected that some of the inconsistent results of previous studies might be due to small sample size, small number of morphological characters, and/or the lack of modern morphometric approaches. Understanding the distinctiveness of these island populations is important not just for taxonomic inference, but for understanding divergent ecological and evolutionary processes on the islands and for guiding conservation management aimed at preserving distinct gene pools. Here, we rigorously evaluate morphological divergence among lizards from the three main islands. We include more characters than previous studies increasing our ability to detect novel morphological patterns and possible correlation in traits, and apply modern morphometric techniques. We then use this information to discuss the distinctiveness of the island populations and consider the conservation implications on this island endemic.

MATERIALS AND METHODS

***Sampling*.—** We measured 172 adult *X. riversiana* museum specimens from Santa Barbara Island (n = 40), San Clemente Island (n = 69), and San Nicolas Island (n = 63), which represented the two subspecies *X. r. reticulata* (n = 109) and *X. r. riversiana* (n = 63; Appendix 1). Specimens spanned a range of collection years (1911–2014) and localities within each island (Fig. 1; Appendix 1). Although *X. riversiana* have been reported from Sutil Islet, no museum specimens were available. We defined adults as all individuals larger than the reported minimum size at sexual maturity—females with snout-to-vent length (SVL) > 75 mm and males with SVL > 65 mm (Goldberg and Bezy, 1974). Sex was determined by examination of the gonads. For the two larger islands, San Clemente and San Nicolas, we selected specimens to maximize geographic coverage across each island. Because fewer museum specimens were available for Santa Barbara Island, we examined all available adult specimens.

***Characters examined*.—** We examined nine morphometric characters including (i) snout-to-vent length (SVL), distance from the tip of the snout to the anterior edge of the vent; (ii) head length, measured from the gular fold to the tip of the snout; (iii) head width, measured at the jaw articulation; (iv) head depth, measured immediately posterior to the eyes; (v) snout length, measured from the anterior corner of the eye to the posterior edge of the nostril on the right side; (vi) interorbital distance, measured from the posterior edge of each eye; (vii) forelimb length, measured from the elbow to the tip of the fourth digit on the right side; (viii) hind limb length, measured from the knee to the tip of the fourth digit on the right side; (ix) and pectoral width, measured at the mid-point of the insertion points of the forelimbs. A tenth measurement, tail length, could only be measured on a fraction of the specimens so it was left out of most analyses.

We chose these characters because they are commonly used in studies of lizards and salamanders (e.g. Savage, 1955; Pauly et al., 2007; Davis and Pauly, 2011). Although previous studies of *X. riversiana* examined variation in SVL (Savage, 1955; Bezy et al., 1980), the other nine morphometric characters had not previously been examined. All measurements were taken to the nearest 0.01 mm with a digital caliper. We also calculated repeatability for the nine primary morphometric characters by measuring three to five individuals per island three times; repeatability was quantified as 1 minus the mean coefficient of variation for each character measured. Some specimens were damaged to the point where certain measurements could not be taken; missing body measurements (n = 15) were predicted using a multivariate model with the *predict* function in the R package *stats* (R ver. 3.2.1; R Core Team; page 60 in Claude, 2008).

Additionally, we counted five meristic characters: (i) ventral scales, longitudinal count along the midline from the preanal scales to the gular fold; (ii) gular scales, longitudinal count along the midline from the gular fold to the postmentals; (iii) preanal scales, number of enlarged scales along the midline from vent to ventral scales; (iv) femoral pores, measured on the left side; (v) fourth toe lamellae, measured on the left hind foot. These characters were selected because all were previously examined by Bezy et al. (1980) and three were examined by Savage (1955). We did not examine a sixth meristic character used in Bezy et al. (1980), scales around the midbody, because we found that for many specimens, counts could not be repeated with high confidence. Individuals missing scale count data (n = 10) were excluded from multivariate analyses.

***Data analysis*.—** Univariate and multivariate analyses were conducted to test for morphological differences among the subspecies and among the three island populations. All body measurements were log10-transformed prior to analysis. To assess differences among the islands and to test for sexual dimorphism in the individual characters, we conducted an ANOVA on log10 transformed SVL and additional ANCOVAs were conducted on body measurements and meristic characters with island and sex as factors and log10 transformed SVL as a covariate.

To explicitly test for sexual dimorphism and differences among subspecies and islands, we conducted MANOVAs using the *manova* function in the R package *stats*. The initial MANOVAs included all individuals, but to also examine variation between the two island populations assigned to *X. r. reticulata,* a second set of analyses were conducted that excluded San Nicolas Island specimens. Evidence of sexual dimorphism led us to conduct further analyses, including MANOVAs separately on each sex. We also conducted analyses separately for body measurements and for meristic characters. For the MANOVAs, we first used data that included size and shape information, then we compared differences in shape by removing the effect of body size by dividing each measurement by the *i*th root of the product of all *i* measurements taken from each specimen (Claude, 2008). Additionally, Pillai's Trace (V) was calculated from the MANOVAs to estimate effect size of the factors island, subspecies, and sex.

To visualize separation in multivariate space among all individuals, we conducted a principal component analysis (PCA) on body measurements that first included size and shape then with size excluded to examine shape alone. A PCA of meristic characters was not conducted. The PCA was conducted using the *dudi.pca* function in the R package *ade4* (Chessel et al., 2004) with all variables scaled to have unit variance, and with individuals downweighted by the inverse of their sample size per island. To specifically test our power to assign specimens to islands, we conducted a linear discriminant analysis (LDA) using the *lda* function in the R package *MASS* taking into account both size and shape first, then with size excluded to examine shape alone. Males and females were analyzed separately. For each LDA analysis, we calculated the posterior probability of correctly assigning a specimen to its island of origin, using the *predict.lda* function in R. Then we qualitatively compared these posterior probabilities across islands and sex.

RESULTS

***Island differences and sexual dimorphism in individual traits*.—** Repeatability scores were consistently high for all measurements, and ranged from 98.3% for snout length to 99.7% for SVL. Summary statistics for the morphological characters are listed in Table 1. All characters were significantly different between the two subspecies except for head width and the number of femoral pores; pectoral width was only marginally significant (Table 2). San Nicolas individuals had a larger body size than Santa Barbara and San Clemente individuals (Table 1, 2). For the meristic characters, San Nicolas Island specimens, despite being larger, had fewer ventral scales, gular scales, preanal scales, and fourth toe lamellae (Table 1, 2).

Xantusia riversiana were sexually dimorphic for all morphometric traits except tail length, and in *X. r. reticulata*, hind limb length was marginally significant while pectoral width did not show a significant difference (Table 1, 2). Females had a larger body size, but larger head measurements did not appear to favor one sex (Table 1). However, males on San Nicolas were larger than females for four of the five head measurements. There were no dramatic sexual dimorphisms for the scale characters, except that males had more preanal scales than females (at least for San Nicolas and San Clemente Islands; this could not be assessed for Santa Barbara Island because few male specimens were available (Table 1, 2).

Some differences were also observed between *X. r. reticulata* on Santa Barbara and San Clemente Islands. Head width and pectoral width were larger in lizards from San Clemente, and they had a slightly shorter snout. Santa Barbara Island lizards also had slightly more ventral scales, gular scales, and fourth toe lamellae than lizards from San Clemente Island.

***Island differences in the multivariate analyses*.—** The MANOVA on the complete dataset recovered significant differences among islands ($P < 2.2 \times 10^{-16}$) and between subspecies ($P = 3.19 \times 10^{-16}$) (Table 3). Because many of the morphometric and meristic characters were sexually dimorphic we conducted MANOVAs on males and females separately. When analyzed separately, both the morphometric and meristic datasets revealed significant differences among islands and between subspecies (Table 3). After the effect of size was removed from the morphometric data so that we were only examining shape, significant differences among islands and between subspecies were still recovered (Table 3), indicating that both size (Table 2) and shape differ among islands and subspecies.

Cumulatively, axes I and II of the PCA for log10 body measurements including size and shape explained 89.6% (males) and 87.9% (females) of the variation. Excluding size to examine shape, axes I and II of the PCA for log10 body measurements explained 59.3% (males) and 54.1% (females) of the variation. Despite high statistical significance in the MANOVAs, PCA plots of axis I versus axis II for body measures do not show obvious separation based on islands, even when separated by sex (Fig. 2). For the PCAs including size and shape, all nine body measurements load evenly on the first component axis while head depth, interorbital distance, forelimb length, and hind limb length load more heavily on the second axis than the other traits. With size excluded, body measurements load evenly on the first component axis as well except for head width and pectoral width which load heavier on axis two than the other traits.

MANOVAs revealed significant effects of island and sex, but visual inspection of PCA plots suggested the effects were subtle and largely driven by San Nicolas specimens. Therefore, we repeated the analysis after excluding San Nicolas Island specimens to focus only on differences between Santa Barbara and San Clemente Island lizards, which make up *X. r. reticulata* (sensu Savage, 1955). Using all morphometric and meristic characters, the MANOVA showed a significant difference between the two islands ($P = 8.77 \times 10^{-6}$) and between the two sexes ($P = 9.99 \times 10^{-7}$). When parsed into body measurements and meristic characters separately, MANOVAs showed only females were significantly different between Santa Barbara and San Clemente Islands (Table 3), though these results were impacted by the low number of available male specimens from Santa Barbara Island. After the effect of size was removed, females continued to show significant differences and males were marginally significantly different between the two islands ($P = 7.96 \times 10^{-5}$ and 0.043, respectively). Pillai's Trace (V), a measure of effect size based on the MANOVA, was calculated to be 0.67 ($P < 2.2 \times 10^{-16}$) and 0.43 ($P = 3.2 \times 10^{-16}$) for island and subspecies, respectively, when including samples from San Nicolas. Excluding San Nicolas specimens, V was calculated to be 0.32 ($P = 9.0 \times 10^{-6}$) for the remaining islands. The effect of sex was calculated to be V = 0.38 ($P = 3.9 \times 10^{-13}$) for both islands and subspecies and V = 0.36 ($P = 9.9 \times 10^{-7}$) when San Nicolas specimens were excluded.

Some individuals (n = 15) had missing data due to broken tails or limbs, and all multivariate analyses presented so far had their missing values predicted. We repeated the above analyses without predicting missing values, by simply excluding such specimens, and none of the conclusions changed.

***LDA and assignment probability*.—** The PCAs presented above are blind to island of origin. To further investigate island differences, we performed linear discriminant analyses (LDA) on the body measurements with each sex separately first including size and shape and then for shape alone. These analyses find a shape space that maximally separates specimens based on island of origin. An LDA of the three islands returns two linear discriminant functions. Taken together, these two linear discriminant functions show minimal separation among the three islands (Fig. 2).

Posterior probabilities of correct island assignment were similar whether or not we excluded size, and were similar for the two sexes (Table 4). Lizards from Santa Barbara were generally more difficult to assign to their correct island, with median posterior probabilities falling between 0.50 and 0.62 (Table 4). Assignment success was greater for specimens from San Clemente and San Nicolas Islands for which posterior probabilities of correct assignment fell between 0.76 and 0.88 (Table 4). In all four linear discriminant analyses, the highest posterior probability for every individual was to the correct island, even though in some cases these probabilities were low (Table 4). Thus, specimens were always correctly assigned, but some specimens were difficult to discriminate based on morphometric features.

DISCUSSION

Based on our analyses of nine morphometric and five meristic characters, lizards from the three islands are morphologically different (Table 3). Of particular note is that lizards on San Nicolas Island are larger, have shorter but deeper heads, shorter hind limbs, and also have larger, but fewer scales than the lizards on the other two islands. Specifically, we found that San Nicolas Island lizards had fewer ventral scales, gular scales, preanal scales, and fourth toe lamellae. Bezy et al. (1980) recovered similar results for body size and scale counts, and Savage (1951) found a similar scale count result with lizards from San Nicolas Island having fewer dorsal scale rows, which was the character he used for diagnosing the two subspecies.

***Taxonomy*.—** Given these morphological differences, the obvious question is what classification scheme would best characterize the variation within this Channel Island endemic? Importantly, in addition to the morphological studies, other studies of clutch size, diet, allozymes, and DNA sequences all indicate the uniqueness of the San Nicolas Island lizards. On this island, lizards have a larger clutch size (5.5 young per clutch versus 4.0 for San Clemente and 3.25 for Santa Barbara; Bezy et al., 1980) and consume much less plant matter than lizards from the other islands (20% for San Nicolas Island vs >50% for San Clemente and Santa Barbara Islands; Brattstrom, 1952; Fellers and Drost, 1991). Further, in their allozyme study, Bezy et al. (1980) found that lizards from San Nicolas Island were the most different from the other two islands. Lastly, Noonan et al. (2013) examined sequence data from multiple nuclear and mitochondrial genes. The focus of their study was on relationships among xantusiid species, so the gene and individual sampling was not specifically designed for examining intraspecific variation. Nevertheless, their study provides some insights because it included individuals from all three islands. Consistent with the earlier allozyme results (Bezy et al., 1980), the single individual from San Nicolas Island was the sister lineage to lizards from the remaining two islands, though this was with weak support. These diverse datasets all indicate the uniqueness of lizards from San Nicolas Island, and add further evidence, in addition to that considered by Savage (1955), for treating the San Nicolas Island lizards as a distinct taxon.

Should the lizards from Santa Barbara and San Clemente Islands similarly be recognized as their own distinct taxa? The MANOVAs demonstrate that lizards from these two islands are statistically different morphologically (Table 3), but there is a great deal of overlap. Assigning individuals to an island is challenging (Table 4; Fig. 2, 3). Further, the available allozyme and DNA sequencing studies also demonstrate that lizards from these two islands are quite similar (Bezy et al., 1980; Noonan et al., 2013), and an ongoing genomic study reported that individuals on Santa Barbara and San Clemente Islands are more genetically similar than either is to individuals on San Nicolas Island (Funk and Lovich, unpubl.). Thus, we recommend recognizing the two subspecies as proposed by Savage (1955), with lizards from Santa Barbara and San Clemente Islands treated as *X. r. reticulata* and lizards from San Nicolas as *X. r. riversiana.*

Another option would be to elevate each of these two taxa, *X. r. reticulata* and *X. r. riversiana*, to full species. These two taxa show morphological, genetic, and natural history differences, and being on separate islands with no evidence of ongoing gene flow (Funk and Lovich, unpubl.), they could be considered as having separate evolutionary trajectories, sensu the evolutionary species concept. We take the conservative approach of not elevating to full species at this time; our morphological results, in combination with ongoing genomic studies, will provide a more complete picture for further evaluating the taxonomic status of these endemic Channel Island lineages.

***Sexual dimorphism*.—** Significant sexual dimorphism exists among all island populations across measured morphometric traits (Table 1, 2). Most notably in the current study, *X. riversiana* females have longer SVL than males. This result is consistent with a previous study that identified sexual size dimorphism in *X. riversiana* on Santa Barbara (Fellers and Drost, 1991). One hypothesis for this common occurrence is that female size is linked to reproductive success (Cox et al., 2003), especially in viviparous reptiles such as *X. riversiana* (Qualls and Shine, 1998). A second hypothesis is that females may have a faster growth rate than males (Fellers and Drost, 1991). Additionally, it was suggested that females have a higher survival rate than males perhaps due to male-male combat and achieve larger size over their lifetime (Fellers and Drost, 1991). Within *Xantusia*, *X. vigilis* was also found to have larger females than males (Zweifel and Lowe, 1966), although *X. extorris* was found to have larger males than females (Webb, 1965).

It should be noted that more females than males were examined from all islands, and especially from Santa Barbara (2.3 times more), due to specimen availability. This collection bias may reflect real sex ratio biases or sex differences in activity leading to females being captured more frequently (Fellers and Drost, 1991).

***Morphology, substrate, and diet*.—** San Nicolas Island largely consists of sandstone whereas Santa Barbara and San Clemente Islands are composed mainly of volcanic rocks. These geological differences likely result in numerous habitat differences that could relate to the observed morphological divergence of *X. r. riversiana* and *X. r. reticulata*. One likely difference is in available food sources. Previous studies have found that plant matter is consumed much more frequently by *X. r. reticulata* than by *X. r. riversiana* (Brattstrom, 1952; Fellers and Drost, 1991). This result is consistent with two earlier studies that demonstrated high plant matter consumption for San Clemente Island lizards (Knowlton, 1949; Schwenkmeyer, 1949). Differences in plant communities and/or plant consumption perhaps lead to the significant morphological differences among islands shown in this study. Of particular note is that *X. r. reticulata* have relatively longer heads; consumption of large amounts of plant matter has previously been related to the rapid evolution of a longer and wider head morphology in another island-inhabiting lizard, the Italian Wall Lizard, following introduction to a new island (Herrel et al., 2008). Identifying the causes of morphological divergence between males and females, as well as the differences among islands, await future data detailing life history characteristics, including diet. Unfortunately, the data do not currently exist for rigorous testing of hypotheses of morphological divergence.

Another morphological difference potentially related to habitat differences among the islands is in scale counts. In reptiles, water balance is closely linked to scale number. Evaporative water loss occurs through the skin of reptiles. Larger scales tend to be overlapping and generally reduce the amount of exposed skin. Thus, fewer, but larger, scales tend to be favored in arid conditions (Soulé, 1966; Calsbeek et al., 2006, and references therein). For Island Night Lizards, San Nicolas Island lizards have the fewest but largest scales based on counts of ventral, gular, and preanal scales, and fourth toe lamellae (Table 1, 2). For *X. r. reticulata*, lizards from San Clemente Island have fewer scales than those from Santa Barbara based on counts of ventral scales, gular scales, and fourth toe lamellae (Table 1, 2). Most studies examining relationships between scale counts and aridity of habitat, however, have focused on basking species; Island Night Lizards, although diurnal do not engage in basking activity (Fellers and Drost, 1991). They also spend much of their time in dense vegetation making island-wide measurements of precipitation and aridity less relevant than measurements directly from the microclimates used by the lizards. Thus, future work is needed to understand variation in aridity across the microclimates occupied by Island Night Lizards and whether this is correlated with the observed differences in scale counts.

***Conservation Implications*.—** Inasmuch as subspecies is a concept that implies distinctiveness of populations, we recommend recognizing two subspecies of Island Night Lizards. Further, given that all three island populations of night lizards are morphologically distinctive, they should be managed as separate Evolutionarily Significant Units (ESUs). Our findings add to the growing list of endemic Channel Island species that show significant among-island variation, including having multiple island endemic subspecies as also occurs for the Channel Island Fox (Funk et al., 2016).

Conservation and management strategies that potentially affect *X. riversiana* should recognize the differentiation among these island populations. Although *X. riversiana* was delisted from the US Federal List of Endangered and Threatened Wildlife in 2014 (USFWS, 2014), the species still has a restricted range and confronts modern threats including introduced species, sea level change, and the loss of suitable habitat due to impacts from now-removed, introduced herbivores (Holmes et al., 2016; O'Donnell et al., 2018). Island Night Lizards are especially numerous on San Clemente Island where estimates suggest there may be 21 million individuals (USFWS, 2014; W. Mautz, pers. comm.), but the estimated population size of *X. r. reticulata* on Santa Barbara Island is much smaller at only 17,600 individuals (Fellers and Drost, 1991). Similarly, although a larger island, San Nicolas is home to an estimated 28,500 *X. r. riversiana* (O'Donnell et al., 2018). Thus, conservation management should be especially directed to the ESUs on Santa Barbara and San Nicolas Islands.

One especially worrisome threat is the potential to move *X. riversiana* among the islands, or to move potential competitors or predators to the islands. This could happen with the movement of goods and people to the islands, or among the islands. This threat has already been realized on San Nicolas Island, where the Southern Alligator Lizard, *Elgaria multicarinata*, and Side-blotched Lizard, *Uta stansburiana,* were both introduced in the recent past, likely in the 1960s due to military activities on the island (Banta and Wilson, 1976; Fellers et al., 2008; Bezy et al., 1980). San Nicolas and San Clemente Islands receive heavy US Navy activity making these two islands of greater concern for potential between-island transport of *X. riversiana.* Island biosecurity efforts should recognize the importance of preserving the unique among-island diversity within *X. riversiana*.

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Figure Legends

Fig. 1. — Map of the Southern Channel Islands with location of the Channel Islands shown in the inset map of the United States. Sample collection sites are indicated by square gray markers.

Fig. 2. — Plot of principle component axis 1 versus principle component axis 2 from $\log_{10}$ body measurements PCA for males and females including size (A, B) and corrected for size to examine shape (C, D). Specimens indicated with letters as follows: B = Santa Barbara, C = San Clemente, and N = San Nicolas.

Fig. 3. — Plot of linear discriminant axis 1 versus linear discriminant axis 2 from $\log_{10}$ body measurements LDA for males and females including size (A, B) and corrected for size to examine shape (C, D). Specimens indicated with letters as follows: B = Santa Barbara, C = San Clemente, and N = San Nicolas.

Appendix 1. Sample details for specimens used. Samples were provided by the California Academy of Sciences (CAS), the Natural History Museum of Los Angeles County (LACM), and the San Diego Natural History Museum (SDSNH). Specimens with latitudes and longitudes not reported are indicated with "NR".

Sample	**Specimen**	**Subpecies**	**Island**	**Latitude**	**Longitude**	**Sex**	**Year Collected**
1	LACM 3330	*reticulata*	San Clemente	32.82529	118.39041	F	1939
2	LACM 3368	*reticulata*	San Clemente	32.82529	118.39041	M	1939
3	LACM 3371	*reticulata*	San Clemente	32.82529	118.39041	F	1939
4	LACM 3389	*reticulata*	San Clemente	32.82529	118.39041	M	1939
5	LACM 3390	*reticulata*	San Clemente	32.82529	118.39041	M	1939
6	LACM 3401	*reticulata*	San Clemente	32.82529	118.39041	F	1939
7	LACM 3408	*reticulata*	San Clemente	32.86165	118.47454	F	1941
8	LACM 3415	*reticulata*	San Clemente	32.90913	118.50242	F	1941
9	LACM 3419	*reticulata*	San Clemente	32.87532	118.46787	F	1941
10	LACM 3420	*reticulata*	San Clemente	32.87532	118.46787	M	1941
11	LACM 108511	*reticulata*	San Clemente	33.02304	118.58582	M	1972
12	LACM 108512	*reticulata*	San Clemente	33.02304	118.58582	M	1972
13	LACM 108513	*reticulata*	San Clemente	33.02304	118.58582	M	1972
14	LACM 108514	*reticulata*	San Clemente	33.02304	118.58582	M	1972
15	LACM 108516	*reticulata*	San Clemente	33.02304	118.58582	M	1972
16	LACM 108517	*reticulata*	San Clemente	33.02304	118.58582	M	1972
17	LACM 108518	*reticulata*	San Clemente	33.02304	118.58582	F	1972
18	LACM 108519	*reticulata*	San Clemente	33.02304	118.58582	F	1972
19	LACM 108520	*reticulata*	San Clemente	33.02304	118.58582	F	1972
20	LACM 108521	*reticulata*	San Clemente	33.02304	118.58582	F	1972
21	LACM 108523	*reticulata*	San Clemente	33.02304	118.58582	F	1972

22	LACM 108524	*reticulata*	San Clemente	33.02304	118.58582	F	1972
23	LACM 108532	*reticulata*	San Clemente	33.02304	118.58582	M	1972
24	LACM 108534	*reticulata*	San Clemente	33.02304	118.58582	M	1972
25	LACM 108536	*reticulata*	San Clemente	33.02304	118.58582	F	1972
26	LACM 108537	*reticulata*	San Clemente	33.02304	118.58582	M	1972
27	LACM 108538	*reticulata*	San Clemente	33.02304	118.58582	M	1972
28	LACM 108542	*reticulata*	San Clemente	33.02304	118.58582	M	1972
29	LACM 108544	*reticulata*	San Clemente	33.02304	118.58582	F	1972
30	LACM 108546	*reticulata*	San Clemente	33.02304	118.58582	F	1972
31	LACM 108548	*reticulata*	San Clemente	33.02304	118.58582	F	1972
32	LACM 108551	*reticulata*	San Clemente	33.02304	118.58582	F	1972
33	LACM 108554	*reticulata*	San Clemente	33.02304	118.58582	M	1972
34	LACM 108555	*reticulata*	San Clemente	33.02304	118.58582	M	1972
35	LACM 108557	*reticulata*	San Clemente	33.02304	118.58582	F	1972
36	LACM 108621	*reticulata*	San Clemente	33.01600	118.59685	M	1972
37	LACM 108622	*reticulata*	San Clemente	33.01600	118.59685	M	1972
38	LACM 108623	*reticulata*	San Clemente	33.01600	118.59685	M	1972
39	LACM 108624	*reticulata*	San Clemente	33.01600	118.59685	M	1972
40	LACM 108625	*reticulata*	San Clemente	33.01600	118.59685	M	1972
41	LACM 108628	*reticulata*	San Clemente	33.01600	118.59685	M	1972
42	LACM 108629	*reticulata*	San Clemente	33.01600	118.59685	M	1972
43	LACM 108630	*reticulata*	San Clemente	33.01600	118.59685	F	1972
44	LACM 108631	*reticulata*	San Clemente	33.01600	118.59685	F	1972
45	LACM 108632	*reticulata*	San Clemente	33.01600	118.59685	F	1972
46	LACM 108635	*reticulata*	San Clemente	33.01600	118.59685	F	1972
47	LACM 108637	*reticulata*	San Clemente	33.01600	118.59685	F	1972
48	LACM 108638	*reticulata*	San Clemente	33.01600	118.59685	F	1972

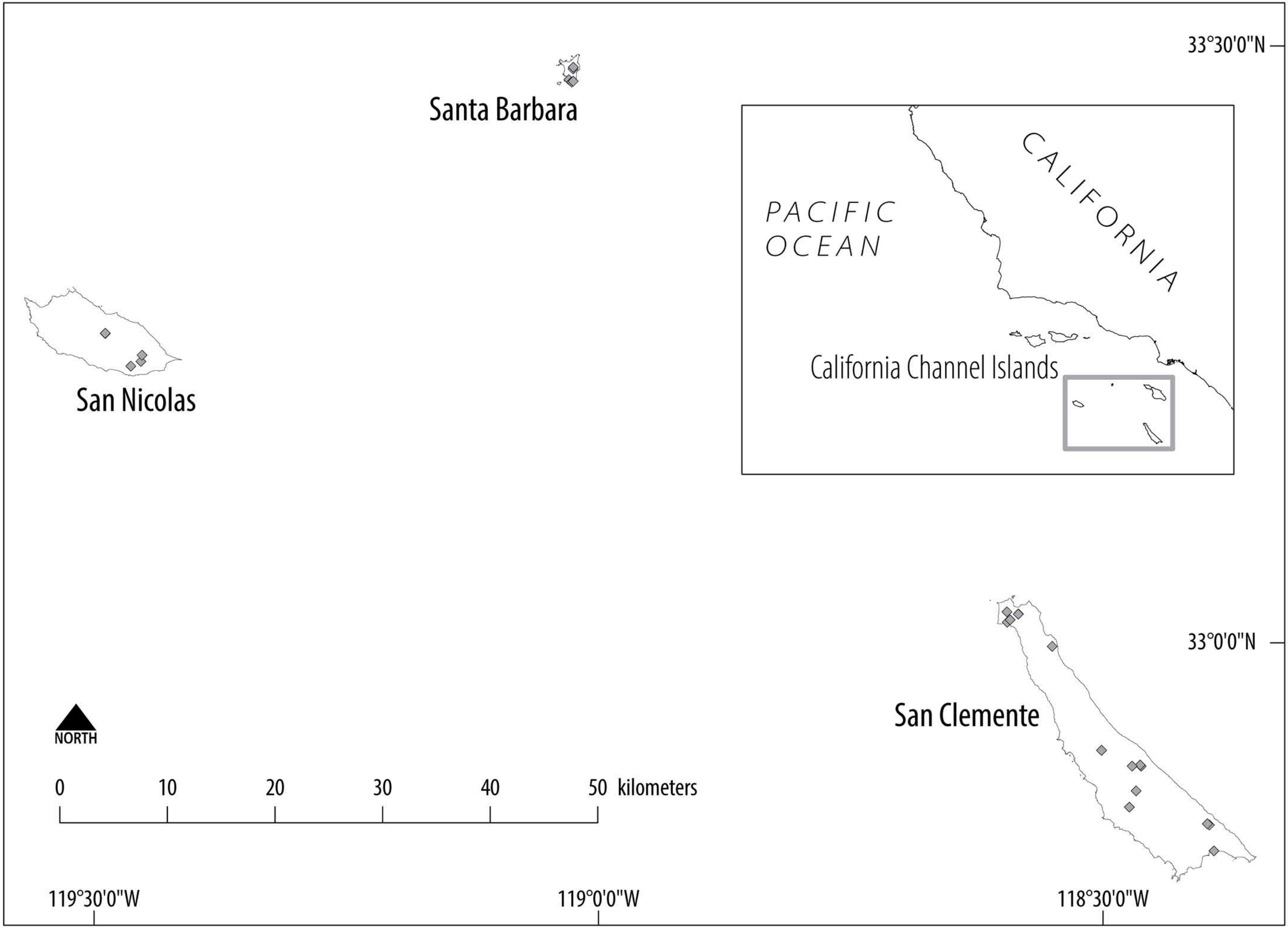
49	LACM 108640	*reticulata*	San Clemente	33.01600	118.59685	F	1972
50	LACM 108641	*reticulata*	San Clemente	33.01600	118.59685	F	1972
51	LACM 108643	*reticulata*	San Clemente	33.01600	118.59685	F	1972
52	LACM 108644	*reticulata*	San Clemente	33.01600	118.59685	F	1972
53	LACM 108645	*reticulata*	San Clemente	33.01600	118.59685	F	1972
54	LACM 108646	*reticulata*	San Clemente	33.01600	118.59685	M	1972
55	LACM 108650	*reticulata*	San Clemente	33.02285	118.58589	M	1972
56	LACM 108651	*reticulata*	San Clemente	33.02285	118.58589	M	1972
57	LACM 108665	*reticulata*	San Clemente	33.02472	118.59718	F	1972
58	LACM 108668	*reticulata*	San Clemente	33.02285	118.58589	F	1972
59	LACM 108671	*reticulata*	San Clemente	33.02285	118.58589	M	1972
60	LACM 108672	*reticulata*	San Clemente	33.02285	118.58589	M	1972
61	LACM 185320	*reticulata*	San Clemente	32.99580	118.55195	F	2014
62	LACM 185322	*reticulata*	San Clemente	32.89626	118.46345	M	2014
63	LACM 185323	*reticulata*	San Clemente	32.89677	118.46358	F	2014
64	LACM 185324	*reticulata*	San Clemente	32.89617	118.47187	F	2014
65	LACM 185325	*reticulata*	San Clemente	33.01844	118.59362	F	2014
66	LACM 185326	*reticulata*	San Clemente	33.01844	118.59362	F	2014
67	LACM 185329	*reticulata*	San Clemente	32.84679	118.39451	F	2014
68	LACM 185330	*reticulata*	San Clemente	32.84810	118.39650	M	2014
69	LACM 185331	*reticulata*	San Clemente	32.84810	118.39650	M	2014
70	CAS-SU 8849	*reticulata*	Santa Barbara	33.47556	119.03528	F	1931
71	CAS-SU 10116	*reticulata*	Santa Barbara	33.47556	119.03528	F	1939
72	CAS 35571	*reticulata*	Santa Barbara	33.47556	119.03528	M	1912
73	CAS 35574	*reticulata*	Santa Barbara	33.47556	119.03528	F	1912
74	CAS 35578	*reticulata*	Santa Barbara	33.47556	119.03528	F	1912
75	CAS 35580	*reticulata*	Santa Barbara	33.47556	119.03528	F	1912

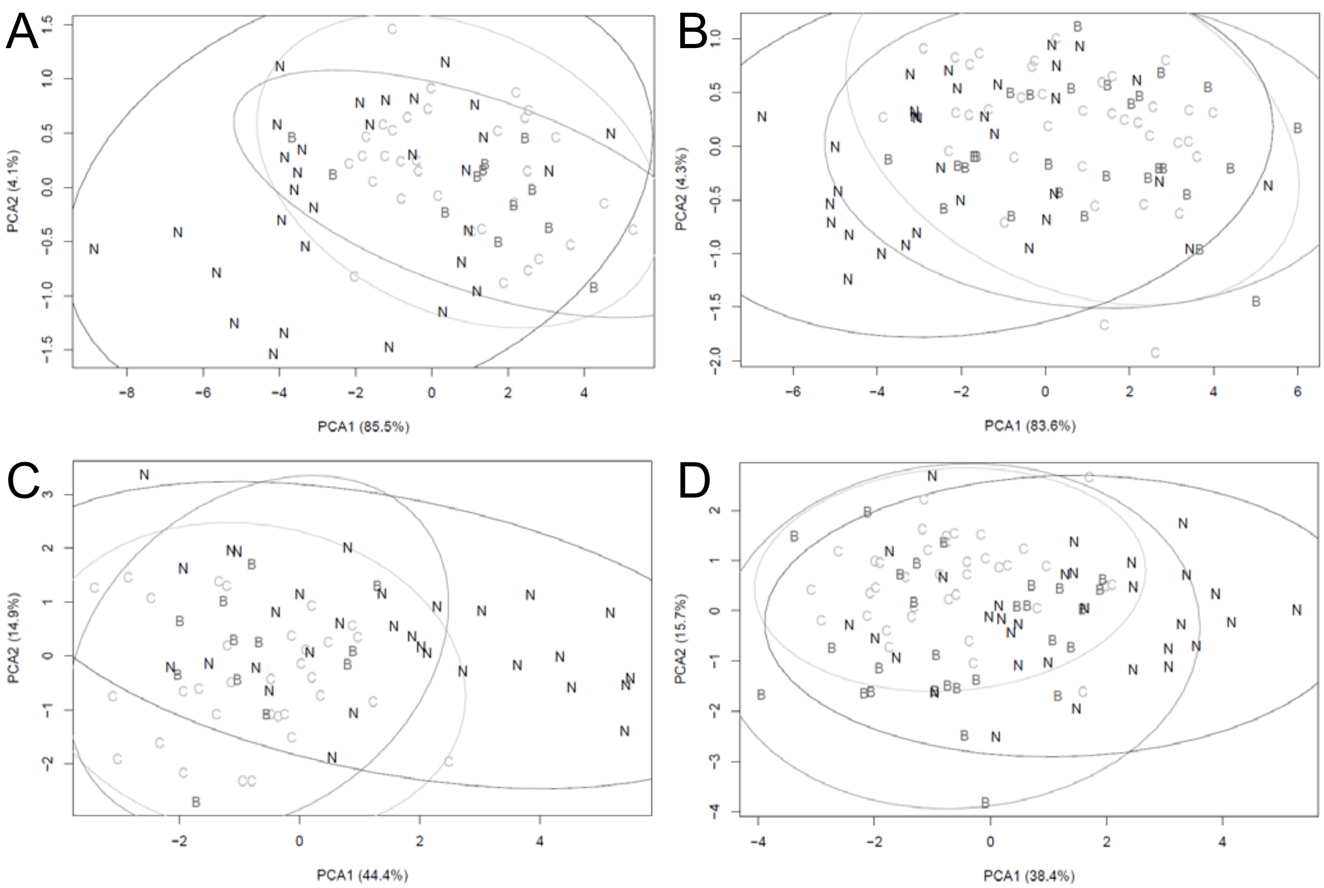
76	CAS 35581	*reticulata*	Santa Barbara	33.47556	119.03528	F	1912
77	CAS 35583	*reticulata*	Santa Barbara	33.47556	119.03528	F	1912
78	CAS 35584	*reticulata*	Santa Barbara	33.47556	119.03528	M	1912
79	CAS 35585	*reticulata*	Santa Barbara	33.47556	119.03528	M	1912
80	CAS 35586	*reticulata*	Santa Barbara	33.47556	119.03528	M	1912
81	CAS 35587	*reticulata*	Santa Barbara	33.47556	119.03528	M	1912
82	LACM 3278	*reticulata*	Santa Barbara	33.47646	119.03430	F	1939
83	LACM 3281	*reticulata*	Santa Barbara	33.47646	119.03430	F	1939
84	LACM 3282	*reticulata*	Santa Barbara	33.47646	119.03430	F	1939
85	LACM 3283	*reticulata*	Santa Barbara	33.47646	119.03430	M	1939
86	LACM 3284	*reticulata*	Santa Barbara	33.47646	119.03430	F	1919
87	LACM 3285	*reticulata*	Santa Barbara	33.47646	119.03430	M	1919
88	LACM 3288	*reticulata*	Santa Barbara	33.47646	119.03430	F	1938
89	LACM 108822	*reticulata*	Santa Barbara	33.46752	119.03827	M	1972
90	LACM 108823	*reticulata*	Santa Barbara	33.46752	119.03827	F	1972
91	LACM 108824	*reticulata*	Santa Barbara	33.46752	119.03827	F	1972
92	LACM 108825	*reticulata*	Santa Barbara	33.46752	119.03827	F	1972
93	LACM 108826	*reticulata*	Santa Barbara	33.46752	119.03827	F	1972
94	LACM 108827	*reticulata*	Santa Barbara	33.46752	119.03827	F	1972
95	LACM 108828	*reticulata*	Santa Barbara	33.46752	119.03827	F	1972
96	LACM 108829	*reticulata*	Santa Barbara	33.46752	119.03827	F	1972
97	LACM 108830	*reticulata*	Santa Barbara	33.46752	119.03827	F	1972
98	LACM 108831	*reticulata*	Santa Barbara	33.46752	119.03827	F	1972
99	LACM 108832	*reticulata*	Santa Barbara	33.46752	119.03827	F	1972
100	LACM 108836	*reticulata*	Santa Barbara	33.46559	119.03552	M	1972
101	LACM 108837	*reticulata*	Santa Barbara	33.46559	119.03552	F	1972
102	LACM 125465	*reticulata*	Santa Barbara	33.46624	119.03400	F	1975

103	LACM 125466	*reticulata*	Santa Barbara	33.46624	119.03400	F	1975
104	LACM 125467	*reticulata*	Santa Barbara	33.46624	119.03400	F	1975
105	LACM 182905	*reticulata*	Santa Barbara	NR	NR	M	1974
106	SDSNH 31983	*reticulata*	Santa Barbara	33.47777	119.03439	M	1939
107	SDSNH 31984	*reticulata*	Santa Barbara	33.47777	119.03439	M	1939
108	SDSNH 31985	*reticulata*	Santa Barbara	33.47777	119.03439	F	1939
109	SDSNH 44469	*reticulata*	Santa Barbara	NR	NR	F	1963
110	CAS 30758	*riversiana*	San Nicolas	33.25000	119.50833	M	1911
111	CAS 30761	*riversiana*	San Nicolas	33.25000	119.50833	M	1911
112	CAS 30764	*riversiana*	San Nicolas	33.25000	119.50833	M	1911
113	CAS 30765	*riversiana*	San Nicolas	33.25000	119.50833	M	1911
114	CAS 30767	*riversiana*	San Nicolas	33.25000	119.50833	M	1911
115	CAS 30768	*riversiana*	San Nicolas	33.25000	119.50833	M	1911
116	CAS 30770	*riversiana*	San Nicolas	33.25000	119.50833	M	1911
117	CAS 30771	*riversiana*	San Nicolas	33.25000	119.50833	M	1911
118	CAS 30779	*riversiana*	San Nicolas	33.25000	119.50833	M	1911
119	CAS 30780	*riversiana*	San Nicolas	33.25000	119.50833	M	1911
120	CAS 30784	*riversiana*	San Nicolas	33.25000	119.50833	M	1911
121	CAS 30831	*riversiana*	San Nicolas	33.25000	119.50833	M	1911
122	CAS 35793	*riversiana*	San Nicolas	NR	NR	M	1912
123	LACM 14487	*riversiana*	San Nicolas	33.2502	119.498	M	1958
124	LACM 108770	*riversiana*	San Nicolas	33.2323	119.461	F	1972
125	LACM 108771	*riversiana*	San Nicolas	33.2323	119.461	F	1972
126	LACM 108772	*riversiana*	San Nicolas	33.2323	119.461	F	1972
127	LACM 108773	*riversiana*	San Nicolas	33.2323	119.461	F	1972
128	LACM 108774	*riversiana*	San Nicolas	33.2323	119.461	M	1972
129	LACM 108777	*riversiana*	San Nicolas	33.2323	119.461	F	1972

130	LACM 108779	*riversiana*	San Nicolas	33.2323	119.461	F	1972
131	LACM 108780	*riversiana*	San Nicolas	33.2323	119.461	F	1972
132	LACM 108782	*riversiana*	San Nicolas	33.2323	119.461	F	1972
133	LACM 108783	*riversiana*	San Nicolas	33.2323	119.461	F	1972
134	LACM 108785	*riversiana*	San Nicolas	33.2323	119.461	F	1972
135	LACM 108786	*riversiana*	San Nicolas	33.2323	119.461	F	1972
136	LACM 108787	*riversiana*	San Nicolas	33.2323	119.461	F	1972
137	LACM 108788	*riversiana*	San Nicolas	33.2323	119.461	F	1972
138	LACM 108791	*riversiana*	San Nicolas	33.2323	119.461	F	1972
139	LACM 108793	*riversiana*	San Nicolas	33.2323	119.461	F	1972
140	LACM 108794	*riversiana*	San Nicolas	33.2323	119.461	F	1972
141	LACM 108795	*riversiana*	San Nicolas	33.2323	119.461	M	1972
142	LACM 108796	*riversiana*	San Nicolas	33.2323	119.461	M	1972
143	LACM 108797	*riversiana*	San Nicolas	33.2323	119.461	M	1972
144	LACM 108798	*riversiana*	San Nicolas	33.2323	119.461	M	1972
145	LACM 108799	*riversiana*	San Nicolas	33.2323	119.461	M	1972
146	LACM 108802	*riversiana*	San Nicolas	33.2323	119.461	M	1972
147	LACM 108805	*riversiana*	San Nicolas	33.2267	119.462	M	1972
148	LACM 108806	*riversiana*	San Nicolas	33.2267	119.462	M	1972
149	LACM 121670	*riversiana*	San Nicolas	33.2502	119.498	M	1975
150	LACM 121671	*riversiana*	San Nicolas	33.2502	119.498	F	1975
151	LACM 122572	*riversiana*	San Nicolas	33.2502	119.498	M	1975
152	LACM 125505	*riversiana*	San Nicolas	33.2502	119.498	M	1975
153	LACM 125511	*riversiana*	San Nicolas	33.2502	119.498	F	1975
154	LACM 125512	*riversiana*	San Nicolas	33.223	119.472	M	1975
155	LACM 125514	*riversiana*	San Nicolas	33.223	119.472	M	1975
156	LACM 125516	*riversiana*	San Nicolas	33.223	119.472	F	1975

157	LACM 126017	*riversiana*	San Nicolas	33.2502	119.498	F	
158	LACM 126232	*riversiana*	San Nicolas	33.223	119.472	F	1975
159	LACM 126996	*riversiana*	San Nicolas	33.223	119.472	M	
160	SDSNH 15487	*riversiana*	San Nicolas	33.2502	119.498	M	1930
161	SDSNH 15488	*riversiana*	San Nicolas	33.2502	119.498	F	1930
162	SDSNH 15489	*riversiana*	San Nicolas	33.2502	119.498	F	1930
163	SDSNH 15490	*riversiana*	San Nicolas	33.2502	119.498	F	1930
164	SDSNH 15491	*riversiana*	San Nicolas	33.2502	119.498	F	1930
165	SDSNH 15492	*riversiana*	San Nicolas	33.2502	119.498	F	1930
166	SDSNH 15494	*riversiana*	San Nicolas	33.2502	119.498	F	1930
167	SDSNH 15495	*riversiana*	San Nicolas	33.2502	119.498	F	1930
168	SDSNH 17213	*riversiana*	San Nicolas	33.2502	119.498	F	1938
169	SDSNH 17215	*riversiana*	San Nicolas	33.2502	119.498	F	1938
170	SDSNH 36334	*riversiana*	San Nicolas	33.2502	119.498	F	1945
171	SDSNH 36671	*riversiana*	San Nicolas	33.2502	119.498	F	1945
172	SDSNH 41615	*riversiana*	San Nicolas	33.2502	119.498	M	1949


33°30'0"N
Santa Barbara
PACIFIC OCEAN
CALIFORNIA
California Channel Islands
San Nicolas
33°0'0"N
San Clemente
NORTH
0 10 20 30 40 50 kilometers
119°30'0"W
119°0'0"W
118°30'0"W


A
B
C
D
PCA1 (85.5%)
PCA2 (4.1%)
PCA1 (83.6%)
PCA2 (4.3%)
PCA1 (44.4%)
PCA2 (14.9%)
PCA1 (38.4%)
PCA2 (15.7%)

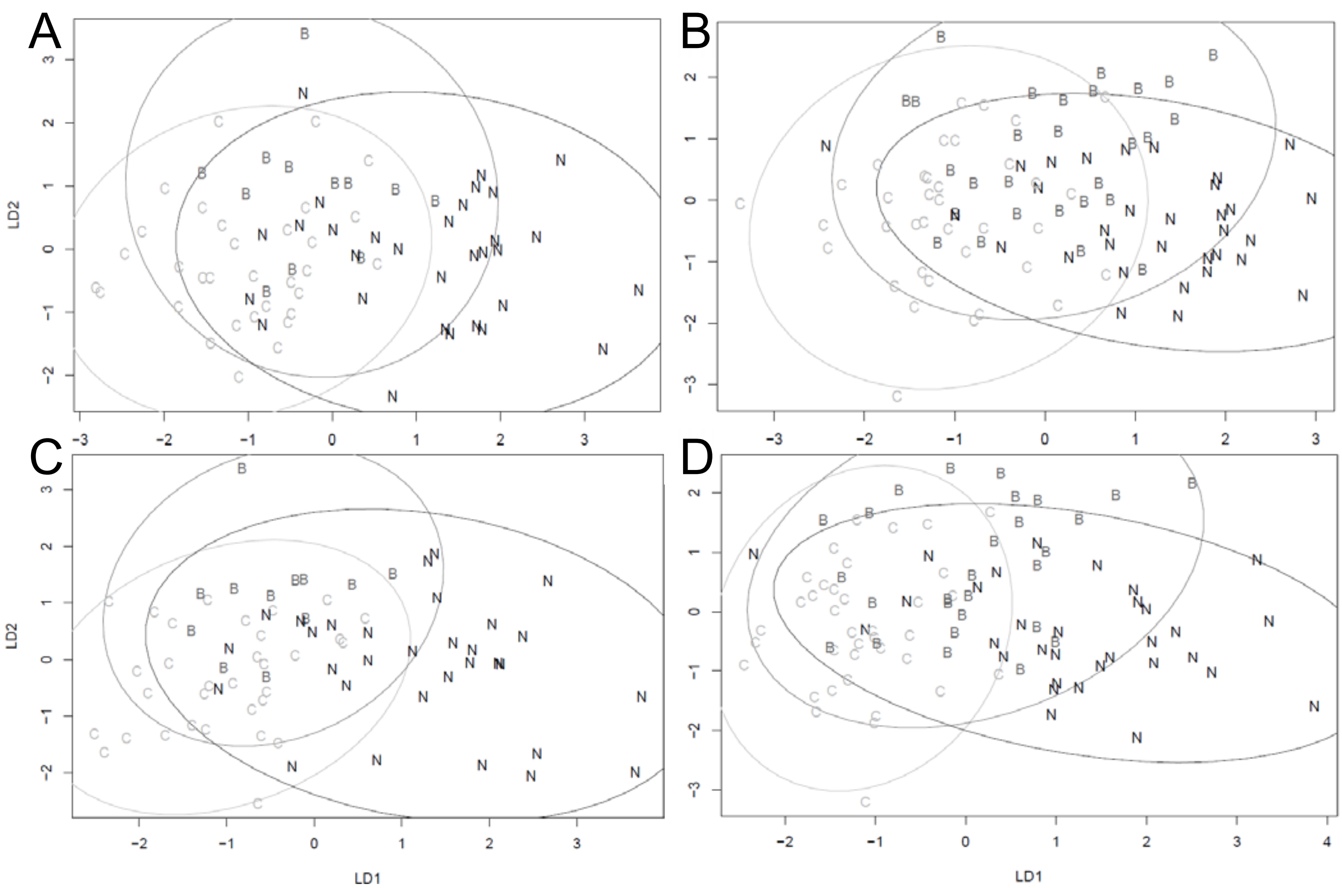

A
B
C
D
LD1
LD2

Table 1. Mean ± 1 SD for 15 morphological traits for males and females for each island. For each trait, we list the raw measurements (mm) ± 1 SD with the ranges in parentheses. For the morphometric characters, we also list the median residuals ± 1 SD from regressions of log10 trait values on log10 SVL in square brackets.

	Santa Barbara (*X. r. reticulata*)		San Clemente (*X. r. reticulata*)		San Nicolas (*X. r. riversiana*)	
	F (n = 28)	M (n = 12)	F (n = 37)	M (n = 32)	F (n = 32)	M (n = 31)
SVL	85.17 ± 6.57 (75.65 – 101.06)	81.78 ± 6.49 (75.88 – 97.77)	85.97 ± 5.16 (78.11 - 97.93)	82.63 ± 4.73 (71.69 – 91.65)	91.08 ± 7.69 (75.17 – 105.02)	87.37 ± 7.07 (75.52 – 106.29)
Head length	29.78 ± 2.87 (23.36 – 35.47) [0.004 ± 0.026]	29.86 ± 2.38 (25.95 – 35.16) [0.006 ± 0.023]	30.25 ± 2.13 (26.07 – 34.56) [0.002 ± 0.018]	29.93 ± 1.84 (24.81 – 32.96) [0.002 ± 0.015]	32.20 ± 2.40 (26.74 – 36.05) [3.22x10^{-4} ±0.015]	32.31 ± 2.68 (27.60 – 38.33) [-4.83x10^{-4} ± 0.013]
Head width	14.37 ± 0.99 (12.87 – 16.51) [2.09x10^{-4} ± 0.018]	14.49 ± 0.92 (13.32 – 16.43) [0.002 ± 0.012]	14.96 ± 1.05 (13.43 – 17.12) [0.004 ± 0.018]	15.04 ± 1.02 (13.18 – 17.00) [-0.001 ± 0.017]	15.62 ± 1.27 (13.07 – 18.73) [-0.002 ± 0.013]	15.75 ± 1.63 (12.26 – 20.31) [0.001 ± 0.017]
Head depth	9.32 ± 0.72 (7.96 – 10.71) [-0.003 ± 0.019]	9.28 ± 0.67 (8.47 – 10.70) [9.73x10^{-4} ± 0.012]	9.48 ± 0.59 (8.49 – 11.22) [-0.002 ± 0.014]	9.34 ± 0.51 (8.18 – 10.32) [3.69x10^{-4} ± 0.009]	10.14 ± 0.89 (8.29 – 11.61) [0.004 ± 0.023]	10.32 ± 1.15 (8.59 – 12.60) [-1.87x10^{-4} ± 0.028]
Snout length	5.91 ± 0.38 (5.18 – 6.81) [7.35x10^{-4} ± 0.012]	5.83 ± 0.38 (5.51 – 6.75) [0.004 ± 0.013]	5.82 ± 0.31 (5.06 – 6.36) [3.38x10^{-5} ± 0.013]	5.81 ± 0.37 (5.00 – 6.34) [-0.002 ± 0.013]	6.42 ± 0.47 (5.12 – 7.05) [0.004 ± 0.014]	6.38 ± 0.51 (5.51 – 7.54) [4.58x10^{-4} ± 0.016]
Interorbital distance	9.00 ± 0.68 (7.79 – 10.01) [0.009 ± 0.025]	9.01 ± 0.48 (8.04 – 10.13) [-0.005 ± 0.014]	8.93 ± 0.51 (8.16 – 9.87) [-0.004 ± 0.016]	8.94 ± 0.51 (8.04 – 10.22) [0.001 ± 0.017]	9.74 ± 0.88 (8.09 – 11.21) [1.12x10^{-4} ±0.020]	9.91 ± 1.00 (7.51 – 12.25) [-0.002 ± 0.023]

Forelimb length	18.77 ± 0.96 (16.18 – 20.10) [0.001 ± 0.014]	18.44 ± 1.04 (16.54 – 20.66) [0.003 ± 0.012]	18.79 ± 1.16 (16.55 – 21.24) [0.002 ± 0.015]	18.79 ± 0.99 (16.80 – 20.36) [-2.04×10^{-4} ±0.015]	19.85 ± 1.26 (16.60 – 22.08) [2.69×10^{-5} ±0.013]	19.63 ± 1.21 (17.27 – 22.47) [0.002 ± 0.012]
Hind limb length	24.11 ± 1.29 (21.18 – 26.53) [-0.001 ± 0.018]	23.54 ± 1.49 (20.72 – 26.46) [7.97×10^{-4} ± 0.019]	23.97 ± 1.40 (20.77 – 26.27) [0.002 ± 0.018]	23.82 ± 1.32 (20.80 – 25.83) [-3.74×10^{-4} ±0.013]	25.39 ± 1.67 (21.28 – 30.23) [-0.004 ± 0.016]	25.57 ± 1.79 (21.14 – 29.43) [-0.001 ± 0.015]
Pectoral width	13.55 ± 1.10 (11.96 – 15.70) [2.33×10^{-4} ± 0.016]	13.13 ± 0.95 (11.73 – 15.10) [6.16×10^{-4} ± 0.018]	13.98 ± 1.02 (12.28 – 16.87) [0.003 ± 0.016]	13.60 ± 1.13 (11.43 – 15.46) [0.006 ± 0.021]	14.80 ± 1.29 (11.99 – 17.07) [-0.002 ± 0.019]	14.62 ± 1.32 (11.77 – 17.19) [0.001 ± 0.018]
Tail length	72.64 ± 12.19 (51.42 – 97.01) [0.006 ± 0.054]	69.70 ± 7.93 (56.05 – 79.20) [-0.005 ± 0.047]	68.59 ± 6.28 (56.50 – 80.39) [-0.001 ± 0.030]	70.85 ± 8.18 (43.34 – 83.98) [0.008 ± 0.052]	83.93 ± 8.79 (68.44 – 98.50) [-8.3×10^{-4} ±0.037]	83.09 ± 5.01 (74.12 – 88.95) [-5.23×10^{-4} ± 0.029]
Ventral scales	34.30 ± 1.10 (32 – 36)	34.00 ± 1.21 (32 – 36)	33.51 ± 0.93 (32 – 36)	33.34 ± 0.83 (31 – 35)	33.06 ± 1.05 (31 – 35)	32.90 ± 1.19 (31 – 35)
Gular scales	50.96 ± 3.11 (45 – 57)	50.91 ± 2.47 (45 – 54)	48.43 ± 2.24 (43 – 52)	48.63 ± 2.55 (43 – 55)	43.63 ± 2.12 (38 – 47)	45.07 ± 2.51 (40 – 51)
Preanal scales	5.19 ± 0.96 (3 – 7)	5.08 ± 0.79 (4 – 6)	4.78 ± 0.82 (3 – 7)	5.59 ± 1.01 (4 – 7)	4.28 ± 0.96 (3 – 6)	4.94 ± 0.78 (4 – 7)
Femoral pores	10.57 ± 0.79 (9 – 12)	10.75 ± 0.45 (10 – 11)	10.35 ± 0.82 (8 – 13)	10.81 ± 0.54 (10 – 12)	10.63 ± 0.71 (9 – 12)	10.61 ± 0.97 (9 – 13)
4th toe lamellae	23.38 ± 0.94 (22 – 25)	22.91 ± 1.04 (22 – 25)	22.68 ± 1.18 (20 – 25)	22.31 ± 1.18 (20 – 25)	21.59 ± 1.41 (19 – 24)	21.45 ± 1.35 (19 – 25)

Table 2. Results of univariate analyses on all individuals and for *X. r. reticulata* only (which excludes specimens from San Nicolas Island) with island and sex as factors. Body characters were log10 transformed data corrected for size, meristic characters were untransformed but corrected for size. Statistical significance indicated by **bold** values (from ANOVAs for log10 SVL and ANCOVAs for all other traits with log10 SVL as a covariate).

		P				
		Island	Subspecies	Sex	Sex (Island)	Sex (Subspecies)
SVL	All individuals	**1.42×10^{-5}**	**2.41×10^{-6}**	**4.62×10^{-3}**	**4.13×10^{-4}**	**5.15×10^{-4}**
	X. r. reticulata	0.74		**2.69×10^{-3}**	**5.95×10^{-4}**	
Head length	All individuals	**6.72×10^{-3}**	**2.51×10^{-3}**	**1.67×10^{-6}**	**1.54×10^{-6}**	**9.69×10^{-7}**
	X. r. reticulata	0.39		**6.09×10^{-4}**	**8.11×10^{-4}**	
Head width	All individuals	**7.93×10^{-6}**	0.147	**2.80×10^{-11}**	**2.14×10^{-11}**	**3.74×10^{-12}**
	X. r. reticulata	**6.90×10^{-6}**		**2.31×10^{-6}**	**2.07×10^{-6}**	
Head depth	All individuals	**7.66×10^{-6}**	**1.80×10^{-6}**	**8.61×10^{-7}**	**9.82×10^{-7}**	**6.17×10^{-7}**
	X. r. reticulata	0.18		**5.54×10^{-4}**	**5.42×10^{-4}**	
Snout length	All individuals	**4.43×10^{-16}**	**1.45×10^{-15}**	**2.55×10^{-7}**	**2.25×10^{-7}**	**2.47×10^{-6}**
	X. r. reticulata	**0.01**		**4.32×10^{-5}**	**4.15×10^{-5}**	

Interorbital distance	All individuals	**7.15 x 10^{-8}**	**1.91 x 10^{-8}**	**2.98 x 10^{-7}**	**2.76 x 10^{-7}**	**7.88 x 10^{-7}**
	X. r. reticulata	0.29		**2.03 x 10^{-3}**	**1.93 x 10^{-3}**	
Forelimb length	All individuals	**6.41 x 10^{-3}**	**2.75 x 10^{-3}**	**6.31 x 10^{-5}**	**5.97 x 10^{-5}**	**3.96 x 10^{-5}**
	X. r. reticulata	0.30		**8.81 x 10^{-4}**	**8.57 x 10^{-4}**	
Hind limb length	All individuals	**3.97 x 10^{-5}**	**6.79 x 10^{-6}**	**8.62 x 10^{-5}**	**8.65 x 10^{-5}**	**7.99 x 10^{-5}**
	X. r. reticulata	0.79		**0.04**	**0.04**	
Pectoral width	All individuals	**7.53 x 10^{-4}**	**0.03**	**0.01**	**0.01**	**5.77 x 10^{-3}**
	X. r. reticulata	**2.03 x 10^{-3}**		0.16	0.16	
Tail length	All individuals	**1.41 x 10^{-5}**	**2.66 x 10^{-6}**	0.57	0.56	0.67
	X. r. reticulata	0.57		0.67	0.67	
Ventral scales	All individuals	**3.94 x 10^{-7}**	**5.83 x 10^{-5}**	0.24	0.24	0.11
	X. r. reticulata	**1.42 x 10^{-4}**		0.43	0.43	
Gular scales	All individuals	**< 2 x 10^{-16}**	**< 2 x 10^{-16}**	**0.02**	**0.02**	0.08
	X. r. reticulata	**2.09 x 10^{-5}**		0.45	0.45	
Preanal scales	All individuals	**0.03**	**8.56 x 10^{-3}**	**8.48 x 10^{-4}**	**9.77 x 10^{-4}**	**1.01 x 10^{-3}**
	X. r. reticulata	0.94		**0.03**	**0.03**	

Femoral pores	All individuals	0.87	0.71	0.07	0.07	0.08
	X. r. reticulata	0.69		**0.01**	**0.01**	
4th toe lamellae	All individuals	**2.25×10^{-11}**	**2.72×10^{-10}**	0.36	0.36	0.18
	X. r. reticulata	**3.56×10^{-3}**		0.15	0.14	

Table 3. Multivariate analyses of variance (MANOVAs) for various character sets (all characters, body measurements only, and scale characters only) and groups of specimens (all individuals or *X. r. reticulata* only). Statistical significance indicated by **bold** values. Does not include tail length.

			DF	Residuals	Approx. F	*P*
All characters, All individuals		Subspecies	1	169	13.72	**3.19×10^{-16}**
		Island	2	168	8.96	**$< 2.2 \times 10^{-16}$**
		Sex (subspecies)	1	169	11.33	**1.23×10^{-13}**
		Sex (island)	1	168	10.89	**3.93×10^{-13}**
All characters, *X. r. reticulata* only		Island	1	106	5.21	**8.77×10^{-6}**
		Sex	1	106	6.06	**9.99×10^{-7}**
Body measurements, All individuals	Male	Subspecies	1	73	7.09	**4.5×10^{-7}**
		Island	2	72	3.60	**1.03×10^{-5}**
	Female	Subspecies	1	95	6.58	**4.16×10^{-7}**
		Island	2	94	4.97	**5.44×10^{-9}**
Body measurements, *X. r. reticulata* only	Male	Island	1	42	1.93	0.080
	Female	Island	1	63	3.97	**0.001**

Body measurements, All individuals, size removed	Male	Subspecies	1	73	8.08	**6.28×10^{-8}**
		Island	2	72	4.27	**4.81×10^{-7}**
	Female	Subspecies	1	95	7.34	**6.94×10^{-8}**
		Island	2	94	5.39	**7.16×10^{-10}**
Body measurements, *X. r. reticulata* only, size removed	Male	Island	1	42	2.24	**0.043**
	Female	Island	1	63	4.90	**7.96×10^{-5}**
Scale counts, All individuals	Male	Subspecies	1	70	10.16	**3.02×10^{-7}**
		Island	2	69	4.79	**7.33×10^{-6}**
	Female	Subspecies	1	88	23.00	**1.78×10^{-14}**
		Island	2	87	9.24	**4.18×10^{-12}**
Scale counts, *X. r. reticulata* only	Male	Island	1	40	2.05	0.095
	Female	Island	1	56	3.90	**0.004**

DF = degrees of freedom.

Table 4. Posterior probabilities of correct island assignment from four Linear Discriminant Analyses. Values indicate the median and range (in parentheses) of posterior probabilities for correct island assignment.

		X. r. reticulata		*X. r. riversiana*
		Santa Barbara	San Clemente	San Nicolas
Body measurements	Male	0.50 (0.40 - 0.91)	0.80 (0.40 - 0.98)	0.83 (0.46 - 1.00)
	Female	0.62 (0.40 - 0.84)	0.79 (0.45 - 0.98)	0.80 (0.36 - 0.99)
Body measurements,	Male	0.53 (0.40 - 0.95)	0.76 (0.39 - 0.99)	0.88 (0.43 - 1.00)
Size removed	Female	0.62 (0.41 - 0.89)	0.80 (0.37 - 0.98)	0.82 (0.47 - 1.00)