



# Near-shore island lizard fauna shaped by a combination of human-mediated and natural dispersal

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## Abstract

**Aim:** Island biotas provide opportunities to study colonization and adaptation to novel environments. Islands, especially near-shore islands, may have a long record of human habitation such that some lineages result from human-assisted introductions. Here, we combine phylogenetic analyses with fossil data and historical specimen records to reconstruct colonization histories, characterize among-island divergence and assess the role of humans in shaping the evolutionary history of lizards inhabiting a near-shore island archipelago.

**Location:** Channel Islands and adjacent mainland of California, United States.

**Taxa:** Western fence lizard (*Sceloporus occidentalis*), southern alligator lizard (*Elgaria multicarinata*), common side-blotched lizard (*Uta stansburiana*).

**Methods:** We sequenced mitochondrial DNA (ND1, cyt-b) from each of three lizard species, covering their entire island distributions plus the adjacent mainland. For each, we estimated diversity within and among each island, obtained maximum likelihood bootstrapped phylogenies, constructed haplotype networks and tested for population expansion. We used museum specimen records and microfossil evidence to infer colonization scenarios.

**Results:** *Sceloporus occidentalis* is characterized by a single island-colonization event, and exhibits the deepest divergences from mainland relatives and the highest among-island divergence. *Elgaria multicarinata* and *Uta stansburiana* each have at least three distinct colonization events, with fossil and historical data indicating that some of these occurred after humans arrived to the islands.

**Main Conclusions:** The evolution of Channel Island lineages for two lizard taxa has been mediated by ancient and contemporary anthropogenic activity, while the evolution of the third is shaped by natural dispersal and vicariance caused by sea-level rise. Genetic divergence corroborates the treatment of *S. occidentalis* as an endemic island species, *Sceloporus becki*. The unique histories of these three taxa are synthesized with other Channel Island lineages highlighting that taxa inhabiting islands with long histories of human activity should be carefully studied to assess the role of people in facilitating colonization and subsequent gene flow.

## KEYWORDS

conservation, divergence, endemism, fossils, island biogeography, museum specimens

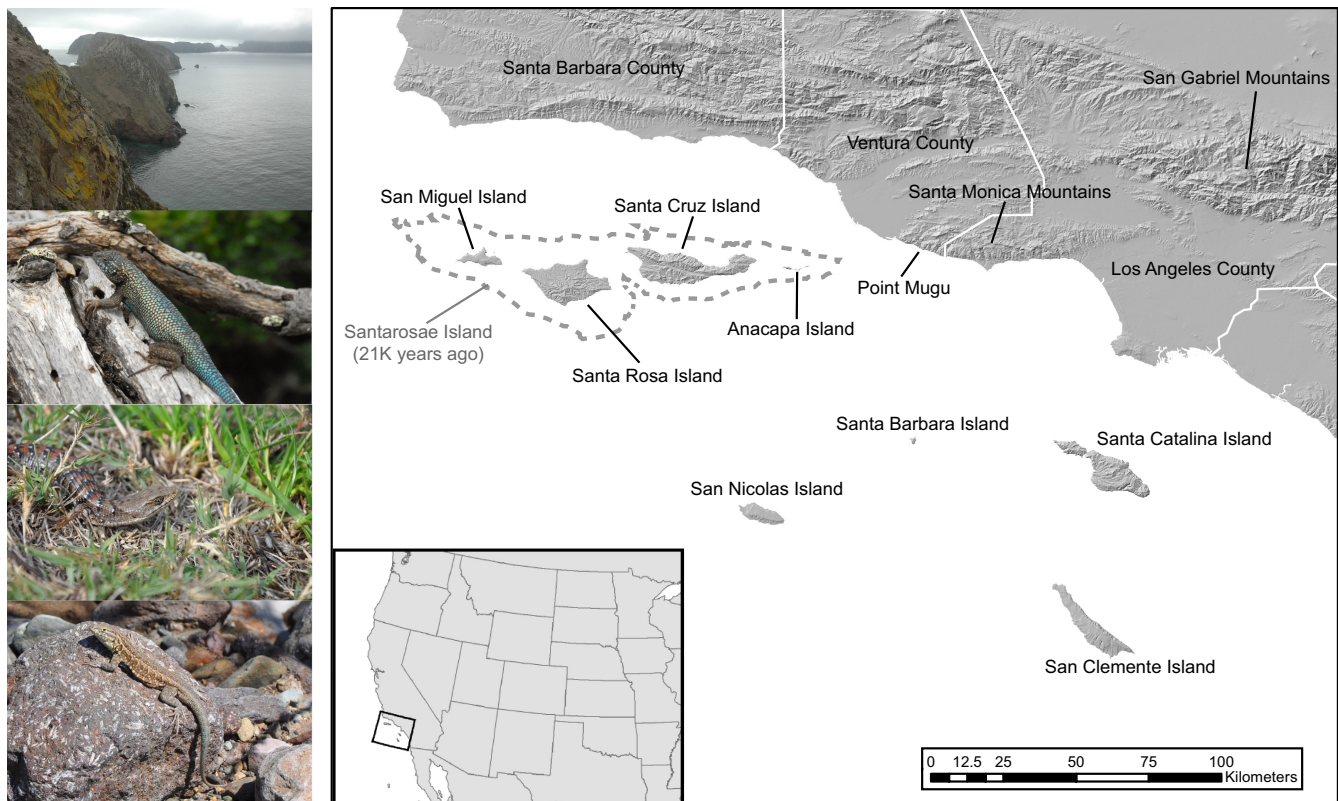
## 1 | INTRODUCTION

Near-shore islands host taxon assemblages that closely mirror mainland communities (Diamond, 1989; Johnson et al., 1968), as opposed to oceanic islands where species diversity and diversification are largely mediated by long-range dispersal and in situ geological and evolutionary processes (Shaw & Gillespie, 2016; Simberloff, 1974). For some taxa, despite the proximity of near-shore islands to the mainland, geographic isolation may be sufficient to reduce dispersal, thereby accelerating lineage divergence from the mainland and leading to the evolution of a unique insular biota (Kier et al., 2009). For other taxa, dispersal and recurring exchange with the mainland results in shallow genetic differentiation between mainland and island populations (e.g. Biaggini et al., 2009). In addition, near-shore islands experience strong anthropogenic pressures, such that the diversity and distribution of many island taxa considered native may instead or additionally reflect human activity on the islands (Hofman & Rick, 2018; Rick et al., 2009). For example, a phylogeographic study of weasel colonization of Mediterranean islands showed that island populations originated from human introductions associated with Bronze Age trade

routes of Eastern civilizations, rather than originating from a nearby mainland source as expected under natural dispersal (Lebarbenchon et al., 2010).

Near-shore island archipelagos, thus, present unique opportunities to examine the role of dispersal, both natural and human-assisted, in colonization history and evolutionary diversification. Furthermore, island systems represent some of the more threatened ecosystems globally. Describing patterns of biological diversity on islands and considering the role of recent, historic and ancient human activities in island systems can lead to important insights about island biodiversity and colonization dynamics, as well as inform conservation efforts (Ficetola & Padoa-Schioppa, 2009; Helmus et al., 2014; Marchán et al., 2020).

The Channel Islands of California are an archipelago of near-shore islands, consisting of four northern and four southern islands (Figure 1). There is no evidence that land bridges ever connected the Channel Islands to the mainland. The islands differ in size, topography and distance to the mainland, and currently are each smaller and farther from the mainland than they were during the last glacial maximum (Porcasi et al., 1999; Reeder-Myers et al., 2015). The islands



**FIGURE 1** Map of the California Channel Islands situated offshore of California, United States. The northern islands of San Miguel, Santa Rosa, Santa Cruz and Anacapa were connected as a single land mass (called Santarosae; dotted line shows island margins at 21 Kya). The county names and mountain ranges in Southern California that are relevant to the phylogeographic study of *Sceloporus occidentalis*, *Elgaria multicarinata* and *Uta stansburiana* are indicated. For the complete mainland range of each species, see Stebbins (2003). Map drawn with topographic relief from DEM hillshade layer (WGS84). Inset of western United States shows the location of islands off the coast of Southern California (USA Contiguous Albers Equal Area Conic USGS). Side panel: A view of East Anacapa Island looking towards Middle and West Anacapa Islands (Northern Channel Islands, California, USA) and the three focal taxa: *Sceloporus becki* (top), *Elgaria multicarinata* (middle), *Uta stansburiana* (bottom).

emerged as recently as 1.2 Mya (San Nicolas Island) to 3.0 Mya (San Clemente Island and all Northern Islands; Muhs et al., 2012, 2014), although more recent analyses suggest some islands may have emerged 5 Mya (D. Muhs, pers. comm). The four Northern Islands (San Miguel, Santa Rosa, Santa Cruz and Anacapa) were connected as a single island, 'Santarosae', as recently as 10–12 Kya (Figure 1) such that movements among present-day islands were once possible via overland dispersal (Reeder-Myers et al., 2015). The Southern Islands have always been isolated from one another (Porcasi et al., 1999), with the two closest islands (San Clemente and Santa Catalina Islands) currently separated by 34 km.

Many California Channel Islands have a long history of human habitation, including one of the oldest recorded human populations in the Americas (ca 13,000 years; Rick et al., 2005). The Chumash (Northern Islands) and the Tongva (Southern Islands) had well-developed trade networks among the islands and to the mainland. More recently, starting with the arrival of Iberian explorer Juan Rodríguez Cabrillo in 1542, Euro-American activities resulted in the introduction of many non-native species including cattle, sheep, goats, rabbits, rats, cats, deer, bison and feral pigs that resulted in severe overgrazing, habitat destruction and erosion (Schoenherr et al., 1999). Most of these non-native species have been eradicated in recent decades, although Santa Catalina Island is still impacted by cats, deer and bison.

The changes in proximity to the mainland, historical island size and connectivity and human habitation have impacted the colonization history and diversification of Channel Island fauna and flora (Rick et al., 2005). Island colonization by terrestrial organisms was likely facilitated by both natural (rafting on vegetation) and human-assisted dispersal. Despite their relatively young age and near-shore position, the California Channel Islands are home to a surprising number of endemic species and subspecies (Adams et al., 2018; Ashley & Wills, 1987; Delaney & Wayne, 2005; Eggert et al., 2004; Gill, 1976; McGlaughlin et al., 2014; Moody, 2000; Noonan et al., 2013; Roemer et al., 2001; Schoenherr et al., 1999; Weissman & Rentz, 1976). Substantial genetic and/or ecological differentiation from mainland ancestors have led to conservation efforts to preserve these unique taxa. In contrast, phylogeographic studies of other California Channel Island taxa (Floyd et al., 2011; Mahoney et al., 2003) have revealed relatively recent colonization from mainland sites with low levels of differentiation from the mainland and among islands. In these cases, observed patterns of differentiation are more likely the result of genetic drift, founder effects and local selection pressures rather than long-term evolutionary isolation. Comparison of the inter- and intra-island diversity, connectivity and diversification among taxonomic groups within the same archipelago provides insight into the myriad evolutionary processes and life-history factors that, combined with human-mediated impacts, shape island biotas.

Our comparative island phylogeographic study focuses on three lizard species that occur within the California Channel Islands archipelago and adjacent mainland: the western fence lizard (*Sceloporus occidentalis*), the southern alligator lizard (*Elgaria*

*multicarinata*) and the common side-blotched lizard (*Uta stansburiana*; see Figure 1). Our goals were to assess colonization history, quantify and compare genetic diversity on each island, infer patterns of connectivity among islands and identify potentially endemic island taxa. We interpret the findings within the framework of both ancient and contemporary human activity and use of near-shore islands.

## 2 | MATERIALS AND METHODS

### 2.1 | Samples and sequences

We obtained sequence data from two mitochondrial loci (cyt-b and ND1) and for three species from the mainland and all islands where they occur: *S. occidentalis* (59 individuals from mainland and three islands), *E. multicarinata* (74 individuals from mainland and six islands, plus one *Elgaria kingii* and one *Elgaria coerulea* to serve as outgroups) and *U. stansburiana* (74 individuals from mainland and five islands, plus one *Urosaurus ornatus* to serve as the outgroup) (Table 1). Our sampling covered as much area per island as possible, given the heterogeneous distribution of suitable habitat for each species, and included dispersed mainland sites in Central and Southern California. All species were captured by hand or lasso and either processed at the site of capture and released (tail tips) or vouchered for museum accession (Appendix S1). DNA was extracted using the DNeasy Blood and Tissue Kit (Qiagen). PCR amplification of mitochondrial regions used previously published primers (ND1: tMet, 16dR, Leaché & Reeder, 2002; cyt-b: IguacytbF2, IguacytbR2, UtaCytbF3, UtaCytbR3, Corl et al., 2010; L14919, Burbrink et al., 2007; Anguis\_cytbREVset1, this study, 5'TTG TCC AAT GAT GAT AAA TGG 3'). Amplicons were sequenced in both directions on capillary sequencers using the same primers used in amplification.

We used Sequencher 5.4 to verify and trim sequences, as well as make contigs and the initial alignment of consensus sequences. We used Mesquite 3.61 (Maddison & Maddison, 1997) to manually inspect the sequence alignments, edit any obvious sequencing and alignment errors, exclude uninformative positions and verify open reading frames of sequenced genes. We estimated the best partitioning scheme for the data with PartitionFinder2 (Lanfear et al., 2016) using an estimated starting tree (Guindon et al., 2010) and the greedy search algorithm (Lanfear et al., 2012).

### 2.2 | Population-level and network inferences

We estimated the number of haplotypes and polymorphic sites, nucleotide diversity,  $\theta_s$ ,  $\pi$  and expected heterozygosity for each island for every species using Arlequin 3.5.2.2 (Excoffier & Lischer, 2010). We determined significance with 10,000 simulations under the null hypothesis of population stability and selective neutrality. Haplotype networks were estimated in TCS

TABLE 1 Haplotype diversity indices and neutrality tests for *Sceloporus occidentalis*, *Elgaria multicarinata* and *Uta stansburiana*

Island	<i>n</i>	# haplotypes	# polymorphic sites	Mean Exp. Heterozygosity	Nucleotide diversity	$\theta_s$	$\pi$	Tajima's <i>D</i>	Fu's $F_s$
<b>Sceloporus</b>									
San Miguel	10	4	3	0.289	0.000422	1.060	0.867	-0.65748 (0.2918)	0.20602 (0.4501)
Santa Rosa	8	7	11	0.344	0.001844	4.242	3.786	-0.53763 (0.3288)	-2.60251* (0.0375)
Santa Cruz	12	10	28	0.404	0.005516	9.271	11.318	0.98940 (0.8823)	-1.12365 (0.2494)
<b>Northern Channel Islands</b>									
San Miguel	7	4	3	0.381	0.000513	1.224	1.143	-0.30187 (0.3847)	-1.21660 (0.0749)
Santa Rosa	11	4	3	0.182	0.000245	1.024	0.545	-1.59996* (0.0445)	-2.04227* (0.0080)
Santa Cruz	6	4	4	0.450	0.000808	1.752	1.800	0.14908 (0.6064)	-0.69169 (0.1907)
Anacapa	15	3	2	0.238	0.000214	0.615	0.476	-0.59419 (0.2638)	-0.51842 (0.2491)
<b>Northern Channel Islands</b>									
Santa Catalina	11	3	7	0.202	0.000637	2.390	1.418	-1.64995* (0.0385)	1.32199 (0.7876)
San Nicolas	6	2	1	0.600	0.000269	0.438	0.600	1.44510 (0.9840)	0.79518 (0.5536)
Santa Cruz	12	9	16	0.175	0.001155	5.298	2.803	-2.03339* (0.0046)	-4.29553* (0.0044)
Anacapa	14	6	5	0.266	0.000548	1.572	1.330	-0.53420 (0.3100)	-0.92406 (0.1992)
<b>Northern Channel Islands</b>									
Santa Catalina	12	10	15	0.167	0.001030	4.967	2.500	-1.71160* (0.0263)	-5.88283* (0.0041)
Santa Catalina	8	5	6	0.339	0.000839	2.314	2.036	-0.56068 (0.3138)	-1.11269 (0.1445)
<b>Santa Catalina + San Clemente Islands</b>									
San Nicolas	9	1	0	—	—	—	—	-2.28928* (0.0013)	-10.37821* (<0.0001)

Note: For each island and species, we show the number of individuals sampled (*n*), number of unique haplotypes, number of polymorphic sites, mean expected heterozygosity, nucleotide diversity,  $\theta_s$ ,  $\pi$ , Tajima's *D* and Fu's  $F_s$ . Asterisks (\*) indicate statistically significant estimates of the neutrality tests Tajima's *D* and Fu's  $F_s$ , which were also estimated for the Northern Channel Islands jointly and for Santa Catalina and San Clemente together (*Uta* only).

(Clement et al., 2000) and visualized with TCS Beautifier (Múrias dos Santos et al., 2016). Missing data can be misleading in haplotype networks (Joly et al., 2007); thus, individuals with missing data were first removed from the dataset (seven *E. multicastrata*, two *U. stansburiana*). The maximum connection steps were set at 19 (*S. occidentalis*, 95% parsimony probability), 30 (*E. multicastrata*, 90% parsimony probability) and 40 steps (*U. stansburiana*, <90% parsimony probability). We also estimated haplotype networks for our data plus the data for *E. multicastrata* and *U. stansburiana* from Mahoney et al. (2003). Alignments were trimmed to the length of the Mahoney et al. dataset (*E. multicastrata* 354 bp; *U. stansburiana* 339 bp). We estimated Fu's  $F_S$  (Fu, 1997) and Tajima's  $D$  (Tajima, 1989a, 1989b) in Arlequin for each species on each island, for each species on the Northern Channel Islands together and for *U. stansburiana* on Santa Catalina plus San Clemente Island.

### 2.3 | Phylogenetic Inference

We obtained maximum likelihood bootstrapped phylogenies using RAxML 8 (Stamatakis, 2014). We ran 1000 long bootstrap iterations and 20 maximum likelihood estimates for each of the three datasets using the best partitions and the GTR+GAMMA model. We additionally estimated uncorrected pairwise distances among major clades inferred in the RaxML tree with MEGAX (Kumar et al., 2018; Stecher et al., 2020) using uniform rates. We conducted additional phylogenetic analyses using reduced versions of our datasets (following the same protocol as above) to compare our sequences with those from recent studies of *E. multicastrata* (Leavitt et al., 2017) and *U. stansburiana* (Corl et al., 2010), both of which used cyt-b but not ND1. We did not conduct divergence time analyses because estimates based only on mitochondrial DNA can be inflated and misleading (e.g. Mulcahy et al., 2012; Zheng et al., 2011).

### 2.4 | Occurrence records

We examined the first date of known occurrence of each species on each island using museum collection records. Specimen occurrence data were downloaded from VertNet for *S. occidentalis*, *E. multicastrata*, *U. stansburiana* and additionally for *Xantusia* and *Plestiodon/Eumeces*. We included these non-focal lizard species to assess overall lizard survey and collection efforts on each of the islands over time. In addition to the genus, we included the search terms 'locality:(Island OR isla OR is.) stateprovince:(California NOT Baja)'. Resulting records were checked manually, deleting records not from the Channel Islands and contacting museums to verify all outlier records. For the verified dataset, we visualized the number of records for each species in each collection year in R (R Core Team, 2022) using the packages DPLYR 1.0.8 (Wickham et al., 2022), GGPlot2 3.3.5 (Wickham, 2016) and RColorBrewer 1.1-3 (Neuwirth, 2022).

## 3 | RESULTS

### 3.1 | Samples and sequences

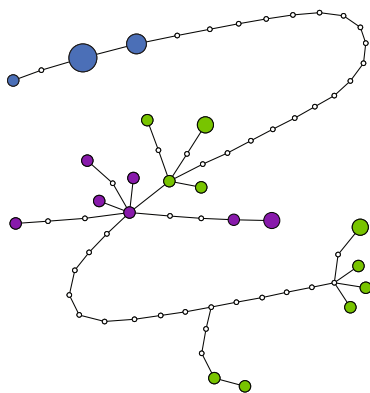
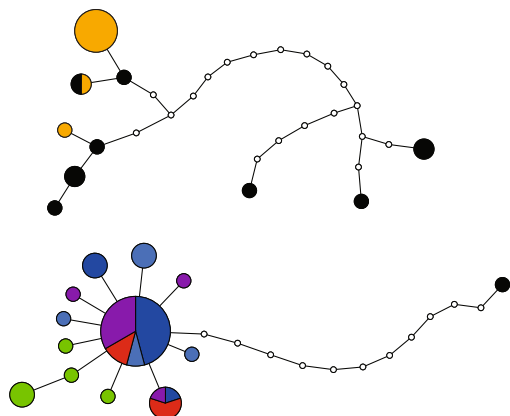
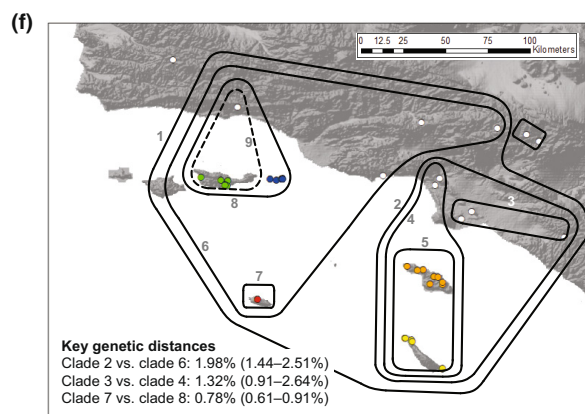
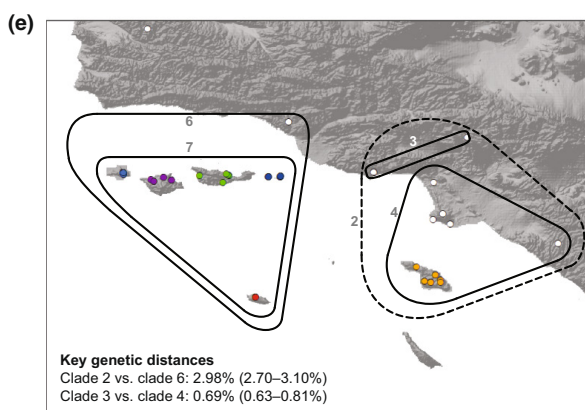
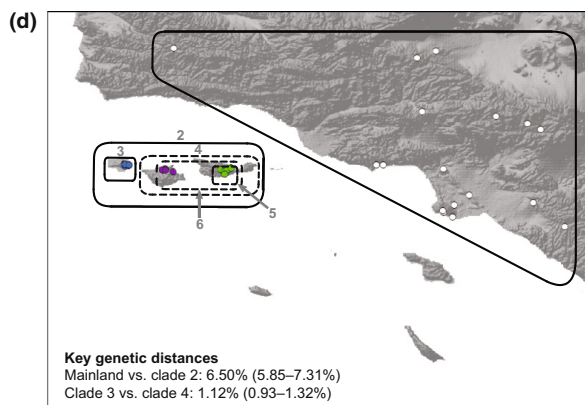
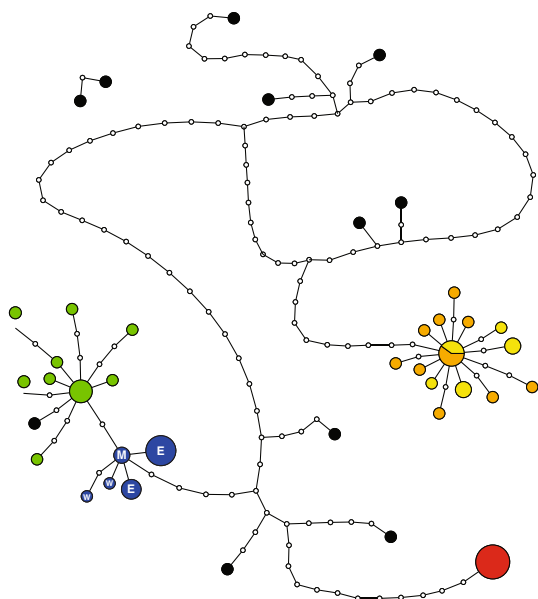
The final sequence alignment for *S. occidentalis* included 59 individuals, 1084 bases for cyt-b and 967 bases for ND1; *E. multicastrata* included 78 individuals, 926 bases for cyt-b and 1301 bases for ND1; and *U. stansburiana* included 75 individuals, 1126 bases for cyt-b and 1300 bases for ND1.

### 3.2 | Population-level and network inferences

The three species differed in patterns of genetic diversity and differentiation across the Channel Islands. *Sceloporus occidentalis* had high variance in population genetic diversity estimates. Santa Cruz Island had the highest diversity across all metrics, while San Miguel Island had the lowest (Table 1). Each *S. occidentalis* haplotype was found on only a single island and island-specific haplotype clusters were divergent from one another (Figure 2a). Santa Cruz Island had the highest nucleotide diversity (Table 1) and the haplotypes fell out in several distinct clusters with one cluster more closely related to Santa Rosa Island haplotypes than to other Santa Cruz Island clusters. San Miguel Island had relatively low diversity. Fu's  $F_S$  was significantly negative for only Santa Rosa Island (Table 1). Tajima's  $D$  was not significantly different from zero for any island, nor the Northern Channel Islands.

In *E. multicastrata*, the number of polymorphic sites ranged between one (San Nicolas Island) and seven (Santa Catalina Island), although the highest diversity metrics were estimated for Santa Cruz Island. Haplotype diversity indices were similar across six island populations of *E. multicastrata* (Table 1). We did not find island-specific haplotype clusters in *E. multicastrata* with the exception of Santa Catalina Island which had haplotypes divergent from other island haplotypes, but identical and/or closely related to multiple mainland haplotypes (Figure 2b). The remaining five islands had haplotypes all belonging to a single haplotype group. A single, common variant was found on four of the five islands with multiple one-step variants primarily found on single islands. The inclusion of data from Mahoney et al. (2003) found congruent results (Appendix S2). Tajima's  $D$  was significantly negative for Santa Catalina Island. Tajima's  $D$  and Fu's  $F_S$  were significantly negative for Santa Rosa Island and the Northern Channel Islands (Table 1).

In *U. stansburiana*, the greatest number of haplotypes and highest nucleotide diversity were estimated for Santa Cruz and Santa Catalina Islands, while San Nicolas Island had the lowest diversity estimates with no polymorphic sites among the 10 sampled individuals. Haplotype diversity was similar across the five island populations of *U. stansburiana* with the exception of San Nicolas Island where all 10 individuals shared a single haplotype not closely related to any other island or mainland samples (Table 1, Figure 2c). Haplotype clusters were largely restricted to single islands with Santa Cruz Islands haplotypes closely related to Anacapa Island

(a) *Sceloporus occidentalis*(b) *Elgaria multicarinata*(c) *Uta stansburiana*

**FIGURE 2** Haplotype networks estimated in TCS and visualized with TCS Beautifier for (a) *Sceloporus occidentalis*, (b) *Elgaria multicarinata* and (c) *Uta stansburiana*. The size of the circle is proportional to the number of individuals with each haplotype. Circle colour refers to the island. Open circles are unsampled haplotypes. Straight line between haplotypes represents a single mutational step. Distribution map of sampling localities on the Southern California mainland (white) and the California Channel Islands (colour coded by island) (WGS84) for (d) *Sceloporus occidentalis*, (e) *Elgaria multicarinata* and (f) *Uta stansburiana*. The major clades from phylogenetic analyses (Appendix S3–S5) are delineated and numbered by node with solid lines (100% bootstrap support) and dashed lines (35%–87% bootstrap support). For the complete mainland range of each species, see Stebbins (2003).

haplotypes. San Clemente and Santa Catalina Island haplotypes formed a single cluster with a single shared haplotype and multiple derived haplotypes unique to each island. Haplotype networks for our data plus data from Mahoney et al. (2003) found similar results though for this short (339 bp) alignment, fewer steps separated island-specific haplotypes and San Nicolas Island haplotypes were identical to three mainland individuals as reported by Mahoney et al. (2003). Tajima's  $D$  and Fu's  $F_s$  were significantly negative for Santa Cruz Island and Santa Catalina Island, for Northern Channel Islands together and for Santa Catalina and San Clemente Islands combined (Table 1).

### 3.3 | Phylogenetic estimates

Estimated phylogenies for the three species largely mirror patterns seen in haplotype networks (Appendices S3–S6). In *S. occidentalis*, we find a single island clade divergent from the mainland (Appendix S3). Individuals from San Miguel Island are monophyletic, while lizards from Santa Cruz Island fall into two clusters, one of which includes lizards from Santa Rosa Island.

In *E. multicolorata*, we find a highly supported clade including the Northern Channel Islands and San Nicolas Island (Appendix S4), with little to no differentiation among islands. This clade is sister to a single mainland specimen from Ventura County (LACM 189908). The Santa Catalina Island samples group with various mainland samples from Orange and Los Angeles Counties. The pairwise divergence between these two main clades is high (2.98%). Additional analyses including data from Leavitt et al. (2017) also support a monophyletic group including Northern Channel Islands plus San Nicolas Island, but this is nested within a clade of individuals from the Central California coast (Monterey to Ventura Counties; Appendix S6). The analysis also highlights that the Santa Catalina Island plus mainland group is nested within a geographically widespread clade spanning Southern California and Baja California.

In *U. stansburiana*, we find island samples generally fall into two mainland/island clades (Appendix S5). One clade contains all San Clemente and Santa Catalina Island samples with little to no differentiation or structure among them. This clade is weakly divergent from two mainland Los Angeles County samples. The other clade contains all samples from San Nicolas, Anacapa and Santa Cruz Islands and three mainland samples from Los Angeles County. Samples from Anacapa and Santa Cruz Islands fall within a highly supported clade with a single mainland sample from Santa Barbara County (LACM 189896). San Nicolas Island samples are a monophyletic group containing a single haplotype. Our analysis including sequences from Corl et al. (2010) recovered a similar inference for the mainland plus Santa Catalina and San Clemente Islands clade (Appendix S7). For the clade including Northern Islands and San Nicolas Island, the added mainland samples from Stunt Ranch (Los Angeles Co.) and Sedgwick Reserve (Santa Barbara Co.; Corl et al., 2010) render these island samples paraphyletic.

### 3.4 | Occurrence records

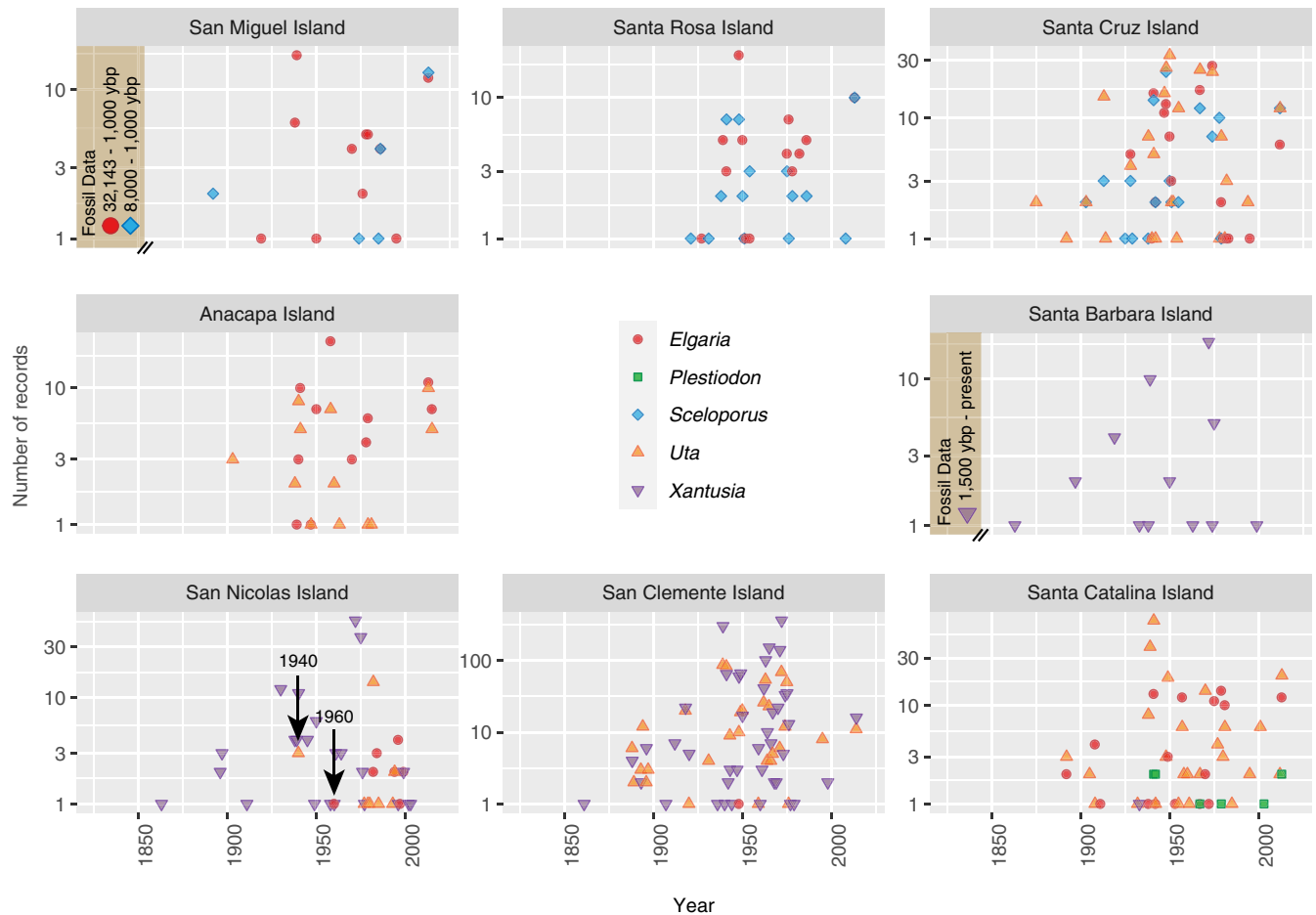
We recovered 3392 reliable occurrence records from VertNet. The earliest occurrence records of lizards on the islands are from the early 1860s (Figure 3). The species currently present on each island have been collected since collections on those islands began, with a few exceptions. *Xantusia* individuals have been collected on San Nicolas Island since 1863, but other species of lizards were not collected on San Nicolas Island until much later (three *U. stansburiana* in 1940 and one *E. multicolorata* in 1960) despite collection efforts in the late 1800s and early 1900s. *Elgaria multicolorata* was not collected on Santa Cruz Island until 1928, 50 years after collections began. There is a single anomalous record of *E. multicolorata* from the northern end of San Clemente Island in 1948, but otherwise, *E. multicolorata* is not known to occur on that island, despite an extensive history of collections prior to 1948 (See Appendix S8 for more information).

## 4 | DISCUSSION

Near-shore islands are considered some of the most fragile ecosystems on Earth, not only because the finite boundaries of islands impose unique physical, ecological and evolutionary pressures but also because many have a long history of human habitation and disturbance (Ficetola & Padoa-Schioppa, 2009; Helmus et al., 2014). The Channel Islands of California have never been connected to the mainland, unlike other near-shore islands (e.g. Caribbean islands: Iturralde-Vinent & MacPhee, 1999; Jowers et al., 2014; Tong et al., 2019; Mediterranean islands: Paulo et al., 2008; Troia et al., 2012), and have a long history of human habitation. Thus, this archipelago presents a unique opportunity to examine the role of human-assisted dispersal. Indeed, we found that both natural over-water dispersal as well as human-assisted migrations have shaped evolutionary divergence for these taxa (Table 2).

Among the three lizard species investigated here, we find only broad similarities in phylogeographic history. The geographic distribution and divergence of all three lizard taxa reflect the long-term isolation of the Northern from the Southern Channel Islands. *Sceloporus occidentalis* is confined to the Northern Channel Islands, and in *E. multicolorata* and *U. stansburiana*, we find a high affinity of the Northern Channel Islands to each other (with affinities to San Nicolas Island resulting from recent introductions). Both *Elgaria* and *Uta* each have at least two independent colonizations of the Southern Islands. This pattern of differentiation between the Northern and Southern Channel Islands is consistent with other studies (e.g. Funk et al., 2016; Hofman et al., 2015; Riley et al., 2016) and highlights how these two geologically distinct groups of islands are largely independent with respect to broad patterns of diversification.

Beyond this shared phylogeographic divergence between the two groups of islands, each taxon exhibits unique histories of colonization, dispersal and divergence rather than a common dispersal route or mechanism. Similar results have been found in other Channel Island studies (e.g. Caterino et al., 2015; Hofman



**FIGURE 3** Known occurrences of the lizard species studied (*Sceloporus occidentalis*, *Elgaria multicarinata* and *Uta stansburiana*) and two additional lizard taxa for comparison (*Xantusia* and *Plestiodon*) on each of the Channel Islands (San Miguel, Santa Rosa, Santa Cruz, Anacapa, Santa Barbara, San Nicolas, San Clemente and Santa Catalina) based on museum collection records (via the VertNet database; see text for details) from 1850 to present. Fossil data are available for only two islands and are indicated on plots. On San Nicolas Island, arrows indicate the first occurrence of *U. stansburiana* and *E. multicarinata*, both of which were observed after monitoring efforts were initiated on the island.

**TABLE 2** Inferences of native status and human-assisted introductions to Northern and Southern Channel Islands for each taxon

	Northern Islands				Southern Islands		
	San Miguel	Santa Rosa	Santa Cruz	Anacapa	Santa Catalina	San Nicolas	San Clemente
<i>Sceloporus occidentalis becki</i>	Native (Endemic)	Native (Endemic)	Native (Endemic)				
<i>Elgaria multicarinata</i>	Native	Native	Native	Native	Possibly Introduced	Introduced	
<i>Uta stansburiana</i>			Possibly Introduced	Possibly Introduced	Uncertain	Introduced	Uncertain/ Possibly Introduced

Open cells indicate not present on island. See text for full description.

et al., 2016), as well as other near-shore island systems (e.g. Marchán et al., 2020). Zamudio et al. (2016) and others (e.g. Papadopoulos & Knowles, 2015; Paz et al., 2015) have emphasized the importance of species-specific traits in diversification. While we were unable to explicitly test the role of life history or ecology on phylogeographic patterns with only three taxa, our data further support the idea that geological processes, colonization and human-assisted movement affect species differently.

#### 4.1 | Island colonization

Evidence of long associations of vertebrate taxa with near-shore islands have been previously described in various systems, reflecting that near-shore islands can hold unique and endemic species despite high opportunity for gene flow (Li et al., 2010; Rodríguez et al., 2017). An example from the Channel Islands is the endemic island scrub-jay, thought to have diverged from their mainland counterpart around



1 Mya (Delaney & Wayne, 2005; McCormack et al., 2011). Our data show that the Channel Island *S. occidentalis* is monophyletic and genetically divergent from mainland counterparts, suggesting a long history of isolation and no contemporary gene flow between island and mainland populations (Figure 2a,d). This degree of mitochondrial divergence suggests that the initial colonization of the Northern Channel Islands likely occurred through natural dispersal before the arrival of humans. Although there is evidence of their continuous occurrence in the fossil record on San Miguel Island from at least 1–8 Kya (Allen, 2013), greater fossil sampling and genomic data could help clarify arrival history.

Human-aided dispersals are a well-documented mechanism of colonization for many near-shore islands. For example, the island fox is estimated to have arrived on the Northern Channel Islands 9200–7100 Ya, and Chumash-aided dispersals likely contributed to both initial and subsequent colonizations (Funk et al., 2016; Hofman et al., 2015; Rick et al., 2009). Other possible introductions to the Channel Islands following human arrival include the western harvest mouse (Ashley, 1989), the spotted skunk (Floyd et al., 2011) and the garden slender salamander (Jockusch et al., 2020). We found evidence of human-assisted migration for some (but not all) island populations of *E. multicastrata* and potentially all *U. stansburiana* island populations (Table 2).

We find support for a single colonization of *E. multicastrata* to the Northern Channel Islands, along with at least one additional colonization event to Santa Catalina Island (Table 2). The colonization event for the Northern Islands originated from a Central California clade (Monterey County southward to Ventura County), whereas the Southern Islands appear to be colonized from the southern mainland clade (Los Angeles County southward into Baja California). Thus, these colonization events originated from distinct, but adjacent mainland phylogeographic regions (Appendix S4; also see figure 2 in Leavitt et al., 2017).

With respect to the timing of colonization of the Northern Islands, microfossil records provide limited, but useful insights nonetheless, and indicate colonization by *E. multicastrata* prior to the break-up of Santarosae and prior to the arrival of humans. Bone remains on San Miguel Island date back to 25,000–38,000 YBP, with bones from site V-10 dating to  $32,143 \pm 787$  years before present (Guthrie, 1993). Fossils from Daisy Cave on San Miguel Island (CA-SMI-261) demonstrate that *E. multicastrata* was present in all strata from 1000 to 10,700 years before present (Allen, 2013; Guthrie, 1993). In contrast, it is not clear when Santa Catalina Island was colonized. Lack of fossil data and genetic similarity between Santa Catalina Island and mainland haplotypes suggests recent colonization, possibly aided by humans. Furthermore, given the paraphyly of Santa Catalina Island haplotypes, we cannot exclude the possibility that *E. multicastrata* may have colonized this island multiple times (Figure 2b, e; see Appendix S8 for details).

Congruent with *S. occidentalis* and *E. multicastrata*, we infer a single colonization of *U. stansburiana* to the Northern Channel Islands. For the Southern Channel Islands, we find support for two separate colonizations from the mainland: one to Santa Catalina and San

Clemente Islands, and one to San Nicolas Island (Table 2). Similar to *E. multicastrata*, the source populations for the colonization of the Southern and Northern Islands come from two distinct phylogeographic clades that exhibit a break in northern Los Angeles County (Figure 2b,e). Given that *U. stansburiana* was not recovered in microfossil studies on San Miguel Island (Allen, 2013; Guthrie, 1993), it seems unlikely that this species was present on Santarosae. Furthermore, the lack of genetic divergence among island and mainland individuals indicates that the arrival of *U. stansburiana* to the Northern and Southern Islands occurred after human arrival, and thus, human-mediated transport to the islands is possible (Table 2).

## 4.2 | Inter-island differentiation

### 4.2.1 | Northern Islands

Patterns of differentiation among islands suggest that the impacts of geological events as well as natural and human-mediated dispersal varied across the focal taxa. Although both *S. occidentalis* and *E. multicastrata* were likely present on the Northern Channel Islands before the break-up of Santarosae, only *S. occidentalis* shows signatures of vicariance (the break-up of Santarosae) as an important process shaping its history and patterns. San Miguel Island *S. occidentalis* form a distinct clade that is moderately diverged from the other two island clades. All haplotypes are unique to each island, though haplotypes on Santa Cruz are paraphyletic with respect to those on Santa Rosa Island. The haplotypes from the Santa Cruz/Santa Rosa clade are found throughout Santa Cruz Island, not only on the western end, which would be the most likely point of exchange. Previous analyses of nuclear microsatellite genotypes from individuals across Santa Cruz Island found a single genetic group and a pattern of isolation by distance (Trumbo et al., 2021). Thus, it is more likely that these lineages are phylogenetically discordant due to incomplete lineage sorting of mtDNA, rather than recent or ongoing gene flow or introgressive hybridization (McGuire et al., 2007).

Despite the long-standing presence of *E. multicastrata* on the Northern Channel Islands (the fossil record dates to c. 38 Kya), this species does not show high levels of among-island divergence and islands contain both unique and shared haplotypes. The fixation of unique haplotypes on each island could be due to decreased gene flow following island separation (break-up of Santarosae). However, we also found support for demographic expansion on Santa Rosa Island as well as on the Northern Channel Islands when treated as a single population (Table 1). Therefore, the retention of shared haplotypes among islands could be due to incomplete lineage sorting following expansion and/or infrequent translocation of animals among the Northern Islands.

*Uta stansburiana* occurs on only two Northern Channel Islands, Santa Cruz and Anacapa. Although we do not find shared haplotypes between these two islands, divergence between the islands is low and they are not monophyletic with respect to mainland samples,

suggesting a moderate history of isolation of these islands. A single mainland sample (LACM 189896) falls within the Santa Cruz Island clade, a finding similar to that of Corl et al. (2010), who found three mainland samples (collected approximately 46 km northwest of LACM 189896) to be highly similar to their Santa Cruz Island samples (Appendix S7). Given the low divergence, the star-shaped haplotype network and evidence for population expansion on Santa Cruz Island as well as Anacapa and Santa Cruz Islands together, it is plausible that these islands were each colonized relatively recently. There is no fossil evidence of *U. stansburiana* on any island; thus, we cannot rule out the colonization of the islands following the separation of Anacapa and Santa Cruz Islands (which happened approximately 10.9–10.3 Kya) and possible human-assisted transport. That said, currently available lizard microfossil data are limited to San Miguel Island, and more fossil data will help to elucidate the colonization and dispersal histories.

#### 4.2.2 | Southern Islands

Of the three lizards included in this study, only *E. multicaudata* and *U. stansburiana* occur on the Southern Channel Islands, and patterns of diversity and divergence hint at a possibly greater role of human-assisted movement compared to the Northern Channel Islands. In both species, individuals on San Nicolas Island are more closely related to the Northern Channel Islands and mainland individuals than they are to the Southern Islands of Santa Catalina and San Clemente, and both cases likely reflect very recent human-assisted introductions. Phylogenetic and haplotype reconstruction and review of museum records indicate that *E. multicaudata* on San Nicolas Island stems from a very recent introduction from the Northern Channel Islands (see Appendix S8 for details).

Similarly, the presence of *U. stansburiana* on San Nicolas Island has long been suggested to be the result of a recent human-assisted introduction (Fellers et al., 2009; Mahoney et al., 2003). The single haplotype among 10 sampled individuals suggests a very recent colonization and/or colonization from a very small founding population (potentially even a single gravid female). Potential sources include ship traffic to support ranching, trade and fishing in the mid-1800s to mid-1900s as well as the US Navy's establishment on the island in 1933 (see Appendix S8 for details). Increased genetic and geographic sampling in mainland Santa Barbara, Ventura and northern Los Angeles Counties will be needed to more precisely identify the source population(s).

Among the other Southern Channel Islands where *U. stansburiana* occurs (Santa Catalina and San Clemente), we find a shared common haplotype and a strong signature of population expansion (Table 1). San Clemente and Santa Catalina Island populations of *U. stansburiana* have been described as divergent from mainland populations in life histories (annual instead of multi-annual reproductive cycles) and body sizes (larger on islands; W. Mautz, pers. comm., Mahoney et al., 2003). Given the low genetic divergences among our sampled individuals, it is likely that these populations

have experienced rapid morphological and ecological evolution after a single colonization of the islands. It is not clear when this colonization event occurred, and we cannot exclude the possibility that lizards were transported from one island to the other by humans (as suggested earlier by Mahoney et al., 2003). If inter-island transport did occur, the direction of movement is more likely to be from Santa Catalina Island to San Clemente Island, because the former has higher reptile diversity (nine species vs two species; Pauly et al., 2021) and is much closer to the mainland (32 km vs 80 km at present).

#### 4.3 | Conservation implications

Our phylogeographic results have important conservation implications for biodiversity on the island archipelago as well as for each of these three lizard species. Here, we were able to identify both native and introduced populations and some that require additional research to conclusively infer their origins (Table 2). This information is critical for deciding how to manage these species on the Channel Islands, all of which are managed at least in part for conservation of biodiversity and natural resources. In particular, San Miguel, Santa Rosa, the eastern third of Santa Cruz, Anacapa and Santa Barbara Islands constitute Channel Islands National Park. The western two-thirds of Santa Cruz Island is owned by The Nature Conservancy, and most of Santa Catalina Island except the town of Avalon is managed by the Santa Catalina Island Conservancy. Finally, San Clemente and San Nicolas Islands are owned by the US Navy. Although they are primarily managed as military installations, the US Navy also monitors and conserves the natural resources of these two islands. Given that these eight islands are not threatened by urbanization and development, there is an exciting opportunity to leverage genetic data to conserve the unique biodiversity free of many of the stressors faced by mainland populations.

For *S. occidentalis*, the monophyly of the Northern Islands and their high sequence divergence from the mainland, combined with previously documented evidence for phenotypic divergence (Bell, 2001; Van Denburgh, 1905), supports the recognition of these populations as a distinct island-endemic species, *S. becki* Van Denburgh, 1905, under various species concepts (general lineage, morphological, evolutionary). As such, *S. becki* would be one of the few Northern Channel Island endemic vertebrates (others include the island scrub-jay [*Aphelocoma insularis*] and the Channel Islands slender salamander [*Batrachoseps pacificus*]), suggesting it merits a high level of conservation prioritization. We are in the process of updating the species description for *S. becki* based on these mtDNA results and additional morphological data. Furthermore, based on low haplotype and nucleotide diversity of *S. becki* on San Miguel Island compared to the other two islands, the San Miguel Island population likely has a very small  $N_e$ . We suspect that contemporary  $N_e$  on San Miguel Island is likely to be much smaller than the c. 200 individuals estimated for Santa Cruz Island based on microsatellite data (Trumbo et al., 2021). If so, then this population would be susceptible

to inbreeding depression and loss of evolutionary potential (Kardos et al., 2021). Additional ecological and genomic research should be a top priority for *S. becki* populations to assess their population status and genome-wide levels of genetic diversity.

With fossils dating back to at least 32 Kya, *E. multicastrata* should be considered a native species on the Northern Channel Islands. The San Nicolas Island population, in contrast, resulted from the recent introduction of multiple individuals from the Northern Channel Islands. *Elgaria multicastrata* is a generalist predator that will consume lizards (Stebbins, 2003); thus, it could have a negative impact on the native *Xantusia riversiana* and its potential prey species, and this warrants ecological monitoring.

*Uta stansburiana* also appears to have been introduced to multiple islands. *Uta stansburiana* was clearly introduced to San Nicolas Island. It was also likely introduced to San Clemente Island from Santa Catalina Island or vice versa; the monophyly and divergence of this clade from the mainland suggest that *U. stansburiana* has long existed on one of these islands, but we are unable to infer to which island it first colonized based on our current results. Further efforts are needed to determine the likely arrival time for *U. stansburiana* on Santa Cruz and Anacapa Islands, but these also likely showed up after arrival of Native Americans to the islands and could result from an introduction event. *Uta stansburiana* consumes a variety of invertebrates, including many species also eaten by *X. riversiana* (Stebbins, 2003). Thus, *U. stansburiana*, as a recent arrival on San Nicolas Island, could negatively impact *X. riversiana* and other native species. Additional fossil and genetic data are needed to better assess arrival times and potential introduction histories on these other islands.

Combining genetic data with microfossil and museum records points to multiple recent movements of both *E. multicastrata* and *U. stansburiana* and indicates that both of these species are prone to intentional or accidental introductions. We urge land managers of these islands to put measures in place to minimize the probability that these lizards are introduced to additional islands or the mainland, where they could compete with or prey upon native species, potentially causing unforeseen cascading effects on these sensitive ecosystems.

## 5 | FUTURE RESEARCH DIRECTIONS

Our results highlight the importance of phylogeographic studies of island taxa to assess their colonization history and the possibility that species long considered to be native to the islands may in fact result from human-assisted introductions. For the Channel Islands, these introductions could have occurred in recent centuries coincident with Euro-American use of the islands (especially during ranching and mining activity) or during the past millennia of Native American transit to, from and among the islands. Although our study includes a high number of individuals both from the islands and the adjacent mainland, we want to highlight the importance of also including a high number of loci in future studies. mtDNA

is matrilineally inherited as a single locus and is likely under various selective pressures. Genomic data in particular could shed light into understanding the complexity of dispersal events in this system, for example, whether any back migrations (island to mainland) have occurred (Bellemain & Ricklefs, 2008), and whether processes such as incomplete lineage sorting, mitochondrial capture and recurrent gene flow mediate the patterns observed herein. Our study also emphasizes the necessity of incorporating other types of data in phylogenetic studies. Microfossil studies provide critical data for determining arrival times and the potential for human-related introduction events, and are therefore an essential research component for assessing the roles of recent human-assisted dispersal, natural dispersal and vicariant events in island systems (see Appendix S9 for more information).

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## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Genbank at <https://www.ncbi.nlm.nih.gov/genbank/>, reference number ON677672 - ON677746; ON691528-ON691645; OP291107-291330. Dryad doi:10.5061/dryad.6djh9w147

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## REFERENCES

- Adams, N. E., Dean, M. D., & Pauly, G. B. (2018). Morphological divergence among populations of *Xantusia riversiana*, a night lizard endemic to the Channel Islands of California. *Copeia*, 106, 550–562.
- Allen, J. A. (2013). Non-cultural deposition in an archaeological site: Microfaunal remains from Cave of the Chimneys (CA-SMI-603), San Miguel Island, California. Master of Arts thesis, California State University, Los Angeles, CA.
- Ashley, M., & Wills, C. (1987). Analysis of mitochondrial DNA polymorphisms among Channel Island deer mice. *Evolution*, 41, 854–863.
- Ashley, M. V. (1989). Absence of differentiation in mitochondrial DNA of island and mainland harvest mice, *Reithrodontomys megalotis*. *Journal of Mammalogy*, 70, 383–386.
- Bell, E. (2001). Taxonomic status of *Sceloporus becki*, the Island Fence Lizard from the Channel Islands, Santa Barbara Co., California. *Bulletin of the Maryland Herpetological Society*, 37, 137–142.
- Bellemain, E., & Ricklefs, R. E. (2008). Are islands the end of the colonization road? *Trends in Ecology & Evolution*, 23, 461–468.
- Biaggini, M., Nulchis, V., Carretero, M. A., Cipolla, R. M., Corti, C., Nappi, A., & Harris, D. J. (2009). Low genetic differentiation between populations of *Podarcis sicula* (Reptilia, Lacertidae) from the Italian islands off the coast of Campania and the mainland. *Belgian Journal of Zoology*, 139, 169–172.
- Burbrink, F. T., Lawson, R., & Slowinski, J. B. (2007). Mitochondrial DNA phylogeography of the polytypic North American rat snake (*Elaphe obsoleta*): A critique of the subspecies concept. *Evolution*, 54, 2107–2118.
- Caterino, M. S., Chatzimanolis, S., & Richmond, M. P. (2015). On the origins of the insect fauna of California's Channel Islands: A comparative phylogeographic study of island beetles. *Monographs of the Western North American Naturalist*, 7, 276–296.
- Clement, M., Posada, D., & Crandall, K. A. (2000). TCS: A computer program to estimate gene genealogies. *Molecular Ecology*, 9, 1657–1659.
- Corl, A., Davis, A. R., Kuchta, S. R., Comendant, T., & Sinervo, B. (2010). Alternative mating strategies and the evolution of sexual size dimorphism in the side-blotched lizard, *Uta stansburiana*: A population-level comparative analysis. *Evolution*, 64, 79–96.
- Delaney, K. S., & Wayne, R. K. (2005). Adaptive units for conservation: Population distinction and historic extinctions in the Island Scrub-Jay. *Conservation Biology*, 19, 523–533.
- Diamond, J. M. (1989). The present, past and future of human-caused extinctions. *Philosophical Transactions of the Royal Society of London B, Biological Sciences*, 325, 469–477.
- Eggert, L. S., Mundy, N. I., & Woodruff, D. S. (2004). Population structure of loggerhead shrikes in the California Channel Islands. *Molecular Ecology*, 13, 2121–2133.
- Excoffier, L., & Lischer, H. E. (2010). Arlequin suite ver 3.5: A new series of programs to perform population genetics analyses under Linux and Windows. *Molecular Ecology Resources*, 10, 564–567.
- Fellers, G. M., Drost, C. A., & Murphey, T. (2009). Status of the Island Night Lizard and two non-native lizards on outlying landing field San Nicolas Island, California. US Geological Survey Open File Report 2008–1371.
- Ficetola, G. F., & Padoa-Schioppa, E. (2009). Human activities alter biogeographical patterns of reptiles on Mediterranean islands. *Global Ecology and Biogeography*, 18, 214–222. <https://doi.org/10.1111/j.1466-8238.2008.00433.x>
- Floyd, C. H., Van Vuren, D. H., Crooks, K. R., Jones, K. L., Garcelon, D. K., Belfiore, N. M., & May, B. (2011). Genetic differentiation of island spotted skunks, *Spilogale gracilis amphiala*. *Journal of Mammalogy*, 92, 148–158.
- Fu, Y. (1997). Statistical tests of neutrality of mutations against population growth, hitchhiking and background selection. *Genetics*, 147, 915–925.
- Funk, W. C., Lovich, R. E., Hohenlohe, P. A., Hofman, C. A., Morrison, S. A., Sillett, T. S., Ghalambor, C. K., Maldonado, J. E., Rick, T. C., Day, M. D., Polato, N. R., Fitzpatrick, S. W., Coonan, T. J., Crooks, K. R., Dillon, A., Garcelon, D. K., King, J. L., Boser, C. L., Gould, N., & Andelt, W. F. (2016). Adaptive divergence despite strong genetic drift: Genomic analysis of the evolutionary mechanisms causing genetic differentiation in the island fox (*Urocyon littoralis*). *Molecular Ecology*, 25, 2176–2194.
- Gill, A. E. (1976). Genetic divergence of insular populations of deer mice. *Biochemical Genetics*, 14, 835–848.
- Guindon, S., Dufayard, J. F., Lefort, V., Anisimova, M., Hordijk, W., & Gascuel, O. (2010). New algorithms and methods to estimate maximum-likelihood phylogenies: Assessing the performance of PhyML 3.0. *Systematic Biology*, 59, 307–321.
- Guthrie, D. A. (1993). New information on the prehistoric fauna of San Miguel Island, California. In F. G. Hochberg (Ed.), *Third California Islands symposium: Recent Advances in Research on the California Islands* (pp. 405–416). Santa Barbara Museum of Natural History.
- Helmus, M. R., Mahler, D. L., & Losos, J. B. (2014). Island biogeography of the Anthropocene. *Nature*, 513, 543–546. <https://doi.org/10.1038/nature13739>
- Hofman, C. A., & Rick, T. C. (2018). Ancient biological invasions and island ecosystems: Tracking translocations of wild plants and animals. *Journal of Archaeological Research*, 26, 65–115. <https://doi.org/10.1007/s10814-017-9105-3>
- Hofman, C. A., Rick, T. C., Hawkins, M. T., Funk, W. C., Ralls, K., Boser, C. L., Collins, P. W., Coonan, T., King, J. L., Morrison, S. A., Newsome, S. D., Sillett, T. S., Fleischer, R. C., & Maldonado, J. E. (2015). Mitochondrial genomes suggest rapid evolution of dwarf California Channel islands foxes (*Urocyon littoralis*). *PLoS One*, 10(2), e0118240.
- Hofman, C. A., Rick, T. C., Maldonado, J. E., Collins, P. W., Erlandson, J. M., Funk, W. C., Fleischer, R. C., Smith, C., Scott Sillett, T., Ralls, K., Teeter, W., Vellanoweth, R. L., & Newsome, S. D. (2016). Tracking the origins and diet of an island canid (*Urocyon littoralis*) across 7300 years of human cultural and environmental change. *Quaternary Science Reviews*, 146, 147–160.
- Iturralde-Vinent, M. A., & MacPhee, R. (1999). Paleogeography of the Caribbean region: Implications for Cenozoic biogeography. *Bulletin of the American Museum of Natural History*, 238, 1–95.
- Jockusch, E. L., Hansen, R. W., Fisher, R. N., & Wake, D. B. (2020). Slender salamanders (genus *Batrachoseps*) reveal Southern California to be a center for the diversification, persistence, and introduction of salamander lineages. *PeerJ*, 8, e9599.
- Johnson, M. P., Mason, L. G., & Raven, P. H. (1968). Ecological parameters and plant species diversity. *American Naturalist*, 102(926), 297–306.
- Joly, S., Stevens, M. I., & van Vuuren, B. J. (2007). Haplotype networks can be misleading in the presence of missing data. *Systematic Biology*, 56, 857–862.
- Jowers, M. J., Lehtinen, R. M., Downie, R. J., Georgiadis, A. P., & Murphy, J. C. (2014). Molecular phylogenetics of the glass frog *Hyalinobatrachium orientale* (Anura: Centrolenidae): Evidence for Pliocene connections between mainland Venezuela and the island of Tobago. *Mitochondrial DNA*, 26, 613–618. <https://doi.org/10.3109/19401736.2014.880888>
- Kardos, M., Armstrong, E. E., Fitzpatrick, S. W., Hauser, S., Hedrick, P. W., Miller, J. M., & Funk, W. C. (2021). The crucial role of genome-wide genetic variation in conservation. *Proceedings of the National Academy of Sciences of the USA*, 118(48), e2104642118.
- Kier, G., Kreft, H., Lee, T. M., Jetz, W., Ibsch, P. L., Nowicki, C., Mutke, J., & Barthlott, W. (2009). A global assessment of endemism and species richness across island and mainland regions. *Proceedings of the National Academy of Sciences of the USA*, 106, 9322–9327.
- Kumar, S., Stecher, G., Li, M., Knyaz, C., & Tamura, K. (2018). MEGA X: Molecular evolutionary genetics analysis across computing platforms. *Molecular Biology and Evolution*, 35, 1547–1549.
- Lanfear, R., Calcott, B., Ho, S. Y., & Guindon, S. (2012). PartitionFinder: Combined selection of partitioning schemes and substitution

- models for phylogenetic analyses. *Molecular Biology and Evolution*, 29, 1695–1701.
- Lanfear, R., Frandsen, P. B., Wright, A. M., Senfeld, T., & Calcott, B. (2016). PartitionFinder 2: New methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Molecular Biology and Evolution*, 34, 772–773.
- Leaché, A. D., & Reeder, T. W. (2002). Molecular systematics of the eastern fence lizard (*Sceloporus undulatus*): A comparison of parsimony, likelihood, and Bayesian approaches. *Systematic Biology*, 51, 44–68.
- Leavitt, D. H., Marion, A. B., Hollingsworth, B. D., & Reeder, T. W. (2017). Multilocus phylogeny of alligator lizards (*Elgaria*, Anguillidae): Testing mtDNA introgression as the source of discordant molecular phylogenetic hypotheses. *Molecular Phylogenetics and Evolution*, 110, 104–121.
- Lebarbenchon, C., Poitevin, F., Arnal, V., & Montgelard, C. (2010). Phylogeography of the weasel (*Mustela nivalis*) in the western-Palaearctic region: Combined effects of glacial events and human movements. *Heredity*, 105, 449–462. <https://doi.org/10.1038/hdy.2009.186>
- Li, J.-W., Yeung, C. K. L., Tsai, P.-W., Lin, R.-C., Yeh, C.-F., Yao, C.-T., Han, L., Hung, I. M., Ding, P., Wang, Q., & Li, S. H. (2010). Rejecting strictly allopatric speciation on a continental island: Prolonged postdivergence gene flow between Taiwan (*Leucodipteron taiwanus*, Passeriformes Timaliidae) and Chinese (*L. canorum canorum*) hwameis. *Molecular Ecology*, 19, 494–507.
- Maddison, W. P., & Maddison, D. R. (1997). Mesquite: A modular system for evolutionary analysis. Version 3.61.
- Mahoney, M. J., Parks, D. S. M., & Fellers, G. M. (2003). *Uta stansburiana* and *Elgaria multicarinata* on the California Channel Islands: Natural dispersal or artificial introduction? *Journal of Herpetology*, 37, 586–591.
- Marchán, D. F., Hedde, M., Lapied, E., Maggia, M.-E., Nova, M., Domínguez, J., & Decaëns, T. (2020). Contrasting phylogeographic patterns of earthworms (Crassidellata, Lumbricidae) on near-shore Mediterranean islands. *European Journal of Soil Biology*, 101, 103242.
- McCormack, J. E., Heled, J., Delaney, K. S., Peterson, A. T., & Knowles, L. L. (2011). Calibrating divergence times on species trees versus gene trees: Implications for speciation history of *Aphelocoma* jays. *Evolution*, 65, 184–202.
- McGlaughlin, M. E., Wallace, L. E., Wheeler, G. L., Bresowar, G., Riley, L., Britten, N. R., & Helenurm, K. (2014). Do the island biogeography predictions of MacArthur and Wilson hold when examining genetic diversity on the near mainland California Channel Islands? Examples from endemic *Acmispon* (Fabaceae). *Botanical Journal of the Linnean Society*, 174, 289–304.
- McGuire, J. A., Linkem, C. W., Koo, M. S., Hutchinsons, D. W., Lappin, A. K., Orange, D. I., & Jaeger, J. R. (2007). Mitochondrial introgression and incomplete lineage sorting through space and time: Phylogenetics of crotaphytid lizards. *Evolution*, 61, 2879–2897.
- Moody, A. (2000). Analysis of plant species diversity with respect to island characteristics on the Channel Islands, California. *Journal of Biogeography*, 27, 711–723.
- Muhs, D. R., Simmons, K. R., Schumann, R. R., Groves, L. T., DeVogel, S. B., Minor, S. A., & Laurel, D. (2014). Coastal tectonics on the eastern margin of the Pacific Rim: Late Quaternary sea-level history and uplift rates, Channel Islands National Park, California, USA. *Quaternary Science Reviews*, 105, 209–238.
- Muhs, D. R., Simmons, K. R., Schumann, R. R., Groves, L. T., Mitrovica, J. X., & Laurel, D. (2012). Sea-level history during the Last Interglacial complex on San Nicolas Island, California: Implications for glacial isostatic adjustment processes, paleozoogeography and tectonics. *Quaternary Science Reviews*, 37, 1–25.
- Mulcahy, D. G., Noonan, B. P., Moss, T., Townsend, T. M., Reeder, T. W., Sites, J. W., Jr., & Wiens, J. J. (2012). Estimating divergence dates and evaluating dating methods using phylogenomic and mitochondrial data in squamate reptiles. *Molecular Phylogenetics and Evolution*, 65(3), 974–991. <https://doi.org/10.1016/j.ympev.2012.08.018>
- Múrias dos Santos, A., Cabezas, M. P., Tavares, A. I., Xavier, R., & Branco, M. (2016). tcsBU: A tool to extend TCS network layout and visualization. *Bioinformatics*, 32, 627–628.
- Neuwirth, E. (2022). RColorBrewer: ColorBrewer Palettes. R package version 1.1–3. <https://CRAN.R-project.org/package=RColorBrewer>
- Noonan, B. P., Pramuk, J. B., Bezy, R. L., Sinclair, E. A., de Queiroz, K., & Sites, J. W., Jr. (2013). Phylogenetic relationships within the lizard clade Xantusiidae: Using trees and divergence times to address evolutionary questions at multiple levels. *Molecular Phylogenetics and Evolution*, 69, 109–122.
- Papadopoulou, A., & Knowles, L. L. (2015). Species-specific responses to island connectivity cycles: Refined models for testing phylogeographic concordance across a Mediterranean Pleistocene Aggregate Island Complex. *Molecular Ecology*, 24, 4252–4268. <https://doi.org/10.1111/mec.13305>
- Paulo, O. S., Pinheiro, J., Miraldo, A., Bruford, M. W., Jordan, W. C., & Nichols, R. A. (2008). The role of vicariance vs. dispersal in shaping genetic patterns in ocellated lizard species in the western Mediterranean. *Molecular Ecology*, 17, 1535–1551. <https://doi.org/10.1111/j.1365-294X.2008.03706.x>
- Pauly, G. B., Knapp, D. A., & Etter, K. (2021). Assessing the history of reptile and amphibian specimen collecting on California's Channel Islands. Unpublished final report prepared for The Nature Conservancy by the Natural History Museum of Los Angeles County, Los Angeles, California.
- Paz, A., Ibanez, R., Lips, K. R., & Crawford, A. J. (2015). Testing the role of ecology and life history in structuring genetic variation across a landscape: A trait-based phylogeographic approach. *Molecular Ecology*, 24, 3723–3737.
- Porcasi, P., Porcasi, J. F., & O'Neill, C. (1999). Early Holocene coastlines of the California Bight: The Channel Islands as first visited by humans. *Pacific Coast Archaeological Society Quarterly*, 35, 1–24.
- R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Reeder-Myers, L., Erlandson, J. M., Muhs, D. R., & Rick, T. C. (2015). Sea level, paleogeography, and archeology on California's Northern Channel Islands. *Quaternary Research*, 83, 263–272.
- Rick, T. C., Erlandson, J. M., Vellanoweth, R. L., & Braje, T. J. (2005). From Pleistocene mariners to complex hunter-gatherers: The archaeology of the California Channel Islands. *Journal of World Prehistory*, 19, 169–228.
- Rick, T. C., Erlandson, J. M., Vellanoweth, R. L., Braje, T. J., Collins, P. W., Guthrie, D. A., & Stafford, T. W. (2009). Origins and antiquity of the island fox (*Urocyon littoralis*) on California's Channel Islands. *Quaternary Research*, 71, 93–98.
- Riley, L., McGlaughlin, M. E., & Helenurm, K. (2016). Narrow water barriers prevent multiple colonizations and limit gene flow among California Channel Island wild buckwheats (*Eriogonum*: Polygonaceae). *Botanical Journal of the Linnean Society*, 181, 246–268.
- Rodríguez, V., Buades, J. M., Brown, R. P., Terrasa, B., Pérez-Mellado, V., Corti, C., Delauger, M., Castro, J. A., Picornell, A., & Ramon, M. M. (2017). Evolutionary history of *Podarcis tiliguerta* on Corsica and Sardinia. *BMC Evolutionary Biology*, 17, 27. <https://doi.org/10.1186/s12862-016-0860-4>
- Roemer, G. W., Coonan, T. J., Garcelon, D. K., Bascompte, J., & Laughrin, L. (2001). Feral pigs facilitate hyperpredation by golden eagles and indirectly cause the decline of the island fox. *Animal Conservation*, 4, 307–318.
- Schoenherr, A. A., Feldmeth, C. R., & Emerson, M. J. (1999). *Natural History of the Channel Islands*. University of California Press.
- Shaw, K. L., & Gillespie, R. G. (2016). Comparative phylogeography of oceanic archipelagos: Hotspots for inferences of evolutionary

- process. *Proceedings of the National Academy of Sciences of the USA*, 113, 7986–7993.
- Simberloff, D. S. (1974). Equilibrium theory of island biogeography and ecology. *Annual Review of Ecology and Systematics*, 5, 161–182.
- Stamatakis, A. (2014). RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, 30, 1312–1313.
- Stebbins, R. C. (2003). *Western Reptiles and Amphibians* (3rd ed.). Houghton Mifflin Company.
- Stecher, G., Tamura, K., & Kumar, S. (2020). Molecular evolutionary genetics analysis (MEGA) for macOS. *Molecular Biology and Evolution*, 37, 1237–1239.
- Tajima, F. (1989a). Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. *Genetics*, 123, 585–595.
- Tajima, F. (1989b). The effect of change in population size on DNA polymorphism. *Genetics*, 123, 597–601.
- Tong, Y., Binford, G., Rheims, C. A., Kuntner, M., Liu, J., & Agnarsson, I. (2019). Huntsmen of the Caribbean: Multiple tests of the GAARlandia hypothesis. *Molecular Phylogenetics and Evolution*, 130, 259–268.
- Troia, A., Raimondo, F. M., & Geraci, A. (2012). Does genetic population structure of *Ambrosina bassii* L. (Araceae, Ambrosineae) attest a post-Messinian land-bridge between Sicily and Africa? *Flora – Morphology, Distribution, Functional Ecology of Plants*, 207(9), 646–653. <https://doi.org/10.1016/j.flora.2012.06.017>
- Trumbo, D. R., Funk, W. C., Pauly, G. B., & Robertson, J. M. (2021). Conservation genetics of an island-endemic lizard: Low  $N_e$  and the critical role of intermediate temperatures for genetic connectivity. *Conservation Genetics*, 22, 783–797.
- Van Denburgh, J. (1905). The reptiles and amphibians of the islands of the Pacific Coast of North America from the Farallons to Cape San Lucas and the Revilla Gigedos. *Proceedings of the California Academy of Sciences of the USA*, 4(1), 1–40.
- Weissman, D. B., & Rentz, D. C. (1976). Zoogeography of the grasshoppers and their relatives (Orthoptera) on the California Channel Islands. *Journal of Biogeography*, 3, 105–114.
- Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag.
- Wickham, H., François, R., Henry, L., & Müller, K. (2022). dplyr: A grammar of data manipulation. R package version 1.0.8. <https://CRAN.R-project.org/package=dplyr>
- Zamudio, K. R., Bell, R. C., & Mason, N. A. (2016). Phenotypes in phylogeography: Species' traits, environmental variation, and vertebrate diversification. *Proceedings of the National Academy of Sciences of the USA*, 113(29), 8041–8048.
- Zheng, Y., Peng, R., Kuro-o, M., & Zeng, X. (2011). Exploring patterns and extent of bias in estimating divergence time from mitochondrial DNA sequence data in a particular lineage: A case study of

salamanders (Order Caudata). *Molecular Biology and Evolution*, 28(9), 2521–2535. <https://doi.org/10.1093/molbev/msr072>

## BIOSKETCH

The authors study the evolutionary and colonization histories of the Channel Island biota and are committed to having their work inform conservation and management of this island archipelago. W. C. Funk, J. M. Robertson and G. B. Pauly have each been working on the Channel Islands for over a decade. L. M. Chan and P. E. Salerno joined the research team more recently. L. M. Chan will increase focus on the Channel Islands with her move to California Polytechnic State University, San Luis Obispo in 2023. P. E. Salerno also continues to work on Channel Islands but is generally committed to studying insular species and ecosystems. All authors are committed to the broader Channel Islands Rediscovery initiative including increasing the number of specimens, tissues and datasets that will be available for biologists and land managers of the future to use in making informed conservation decisions.

**Author contributions:** W.C.F., G.B.P and J.M.R. conceived the ideas and conducted the fieldwork; L.M.C and J.M.R. collected the molecular data; L.M.C and P.E.S. analysed the molecular data; L.M.C. and G.B.P. conducted the analysis of occurrence records; and all authors contributed to writing and revising the manuscript.

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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## SUPPORTING INFORMATION

### Appendix S1.

Locality data and GenBank accession numbers for all individuals sequenced for this study. Abbreviations are as follows: LACM = Natural History Museum of Los Angeles County, LACM-TC = Natural History Museum of Los Angeles County Tissue Collection, CD = Personal collection of Charles Drost, WCF = Personal collection of W. Chris Funk.

Species	Sample ID	Island or Mainland County	Latitude	Longitude	Specific Locality	Cyt-b GenBank	ND1 GenBank
<i>Elgaria coerulea</i>	LACM 189205	USA, California, Mono County	37.768510	-118.526020	East-central Sierra Nevada, SSE of Silver Lake, along Nevada Street 0.53 road km NNW of CA-158 intersection	-	OP291312
<i>Elgaria kingii</i>	LACM 178638	Mexico			N/A	ON677719	OP291302
<i>Elgaria multica rinata</i>	CD 0312	San Nicolas Island			Humphreys Sump	ON677672	OP291255
<i>Elgaria multica rinata</i>	CD 0313	San Nicolas Island			Humphreys Sump	ON677673	OP291256
<i>Elgaria multica rinata</i>	CD 0314	San Nicolas Island			Theodolite	ON677674	OP291257
<i>Elgaria multica rinata</i>	CD 0315	San Nicolas Island			Theodolite	ON677675	OP291258
<i>Elgaria multica rinata</i>	CD 0323	San Nicolas Island			Greenhouse	ON677676	OP291259
<i>Elgaria multica rinata</i>	CD 0324	San Nicolas Island			Greenhouse	-	OP291260
<i>Elgaria multica rinata</i>	CD 0351	San Nicolas Island			Monroe	ON677677	OP291261
<i>Elgaria multica rinata</i>	CD 0352	San Nicolas Island			Central STIPA	ON677678	OP291262
<i>Elgaria multica rinata</i>	CD 0353	San Nicolas Island			Central STIPA 880	ON677679	OP291263
<i>Elgaria multica rinata</i>	CD 1200	San Nicolas Island				-	OP291264
<i>Elgaria multica rinata</i>	LACM 131208	Santa Catalina Island	33.450286	-118.511367	Cherry Valley	ON677718	OP291301
<i>Elgaria multica rinata</i>	LACM 183662	San Miguel Island	34.038510	-120.351900	Ranger Station	ON677680	OP291265
<i>Elgaria multica rinata</i>	LACM 183673	San Miguel Island	34.029300	-120.342930	Brooks fox pens	ON677681	OP291266
<i>Elgaria multica rinata</i>	LACM 183674	San Miguel Island	34.029300	-120.342930	Brooks fox pens	ON677682	OP291267
<i>Elgaria multica rinata</i>	LACM 183675	San Miguel Island	34.029300	-120.342930	Brooks fox pens	ON677683	OP291268
<i>Elgaria multica rinata</i>	LACM 183691	San Miguel Island	34.037680	-120.342690	Ranger Station fox pens	ON677684	OP291269
<i>Elgaria multica rinata</i>	LACM 183692	San Miguel Island	34.037680	-120.342690	Ranger Station fox pens	ON677685	OP291270
<i>Elgaria multica rinata</i>	LACM 183693	San Miguel Island	34.037680	-120.342690	Ranger Station fox pens	ON677686	OP291271

Species	Sample ID	Island or Mainland County	Latitude	Longitude	Specific Locality	Cyt-b GenBank	ND1 GenBank
<i>Elgaria multicolorinata</i>	LACM 183703	Anacapa Island	34.015400	-119.363590	East Anacapa Island	ON677687	OP291272
<i>Elgaria multicolorinata</i>	LACM 183704	Anacapa Island	34.015400	-119.363590	East Anacapa Island	ON677688	OP291273
<i>Elgaria multicolorinata</i>	LACM 183705	Anacapa Island	34.014550	-119.365720	East Anacapa Island	ON677689	OP291274
<i>Elgaria multicolorinata</i>	LACM 183706	Anacapa Island	34.013690	-119.365950	East Anacapa Island	ON677690	OP291275
<i>Elgaria multicolorinata</i>	LACM 183707	Anacapa Island	34.013690	-119.365950	East Anacapa Island	ON677691	OP291276
<i>Elgaria multicolorinata</i>	LACM 183708	Anacapa Island	34.015950	-119.363590	East Anacapa Island	ON677692	OP291277
<i>Elgaria multicolorinata</i>	LACM 183709	Anacapa Island	34.015950	-119.363590	East Anacapa Island	ON677693	OP291278
<i>Elgaria multicolorinata</i>	LACM 183710	Anacapa Island	34.015160	-119.361950	East Anacapa Island	ON677694	OP291279
<i>Elgaria multicolorinata</i>	LACM 183711	Anacapa Island	34.015310	-119.361830	East Anacapa Island	ON677695	OP291280
<i>Elgaria multicolorinata</i>	LACM 183712	Anacapa Island	34.015310	-119.361830	East Anacapa Island	ON677696	OP291281
<i>Elgaria multicolorinata</i>	LACM 183736	Santa Catalina Island	33.358810	-118.461280	Middle Ranch fox pens	ON677697	OP291282
<i>Elgaria multicolorinata</i>	LACM 183737	Santa Catalina Island	33.358810	-118.461280	Middle Ranch fox pens	ON677698	OP291283
<i>Elgaria multicolorinata</i>	LACM 183760	Santa Catalina Island	33.368440	-118.361630	Toyon Canyon	ON677699	OP291284
<i>Elgaria multicolorinata</i>	LACM 183761	Santa Catalina Island	33.368640	-118.362660	Toyon Canyon	ON677700	OP291285
<i>Elgaria multicolorinata</i>	LACM 183762	Santa Catalina Island	33.352040	-118.361490	Haypress Reservoir	ON677701	OP291286
<i>Elgaria multicolorinata</i>	LACM 183812	Santa Catalina Island	33.398480	-118.394400	0.3 km SW of Echo Lake	ON677702	OP291287
<i>Elgaria multicolorinata</i>	LACM 183813	Santa Catalina Island	33.398480	-118.394400	0.3 km SW of Echo Lake	ON677703	OP291288
<i>Elgaria multicolorinata</i>	LACM 183814	Santa Catalina Island	33.352570	-118.422640	Skull Canyon	ON677704	OP291289
<i>Elgaria multicolorinata</i>	LACM 183815	Santa Catalina Island	33.352570	-118.422640	Skull Canyon	ON677705	OP291290
<i>Elgaria multicolorinata</i>	LACM 183816	Santa Catalina Island	33.352560	-118.422100	Skull Canyon	ON677706	OP291291
<i>Elgaria multicolorinata</i>	LACM 183820	USA, California, Los Angeles County	34.037170	-118.778550	Escondido Canyon, Santa Monica Mountains	ON677707	OP291292
<i>Elgaria multicolorinata</i>	LACM 183821	USA, California, Los Angeles County	34.040200	-118.779530	Escondido Canyon, Santa Monica Mountains	ON677708	OP291293
<i>Elgaria multicolorinata</i>	LACM 183822	USA, California, Los Angeles County	34.040200	-118.779530	Escondido Canyon, Santa Monica Mountains	ON677709	OP291294
<i>Elgaria multicolorinata</i>	LACM 183873	USA, California, Los Angeles County	33.744890	-118.408830	Alta Vicente Reserve, Palos Verdes Peninsula	ON677710	OP291295
<i>Elgaria multicolorinata</i>	LACM 183874	USA, California, Los Angeles County	33.744890	-118.408830	Alta Vicente Reserve, Palos Verdes Peninsula	ON677711	OP291296



Species	Sample ID	Island or Mainland County	Latitude	Longitude	Specific Locality	Cyt-b GenBank	ND1 GenBank
<i>Elgaria multicolorata</i>	LACM 183882	USA, California, Los Angeles County	34.259380	-118.196360	Angeles Crest Highway	ON677712	OP291297
<i>Elgaria multicolorata</i>	LACM 184174	USA, California, Los Angeles County	33.717480	-118.301880	3169 S. Leland St., San Pedro	ON677713	OP291298
<i>Elgaria multicolorata</i>	LACM 186034	Santa Rosa Island	33.993710	-120.045850	along Cherry Creek Trail	ON677736	OP291320
<i>Elgaria multicolorata</i>	LACM 186035	Santa Rosa Island	33.993710	-120.045850	along Cherry Creek Trail	ON677737	OP291321
<i>Elgaria multicolorata</i>	LACM 186036	Santa Rosa Island	33.993710	-120.045850	along Cherry Creek Trail	ON677738	OP291322
<i>Elgaria multicolorata</i>	LACM 186037	Santa Rosa Island	34.011180	-120.094020	Lobo Canyon	ON677739	OP291323
<i>Elgaria multicolorata</i>	LACM 186038	Santa Rosa Island	34.010970	-120.092830	Lobo Canyon	ON677740	OP291324
<i>Elgaria multicolorata</i>	LACM 186039	Santa Rosa Island	33.986080	-120.154540	corral along Arlington Canyon	ON677741	OP291325
<i>Elgaria multicolorata</i>	LACM 186040	Santa Rosa Island	33.986080	-120.154540	corral along Arlington Canyon	ON677742	OP291326
<i>Elgaria multicolorata</i>	LACM 186041	Santa Rosa Island	33.986080	-120.154540	corral along Arlington Canyon	ON677743	OP291327
<i>Elgaria multicolorata</i>	LACM 186042	Santa Rosa Island	33.986080	-120.154540	corral along Arlington Canyon	ON677744	OP291328
<i>Elgaria multicolorata</i>	LACM 186758	USA, California, Los Angeles County	33.781200	-118.348650	Rawhide Lane, 102 m NE of Palos Verdes Drive, Rolling Hills Estates	ON677723	OP291306
<i>Elgaria multicolorata</i>	LACM 187795	Anacapa Island	34.013210	-119.439640	West Anacapa Island	ON677724	OP291307
<i>Elgaria multicolorata</i>	LACM 187797	Anacapa Island	34.013000	-119.438390	West Anacapa Island	ON677725	OP291308
<i>Elgaria multicolorata</i>	LACM 187799	Anacapa Island	34.013080	-119.437940	West Anacapa Island	ON677726	OP291309
<i>Elgaria multicolorata</i>	LACM 187800	Anacapa Island	34.013020	-119.437720	West Anacapa Island	ON677727	OP291310
<i>Elgaria multicolorata</i>	LACM 187801	Anacapa Island	34.013020	-119.436950	West Anacapa Island	ON677728	OP291311
<i>Elgaria multicolorata</i>	LACM 189908	USA, California, Ventura County	34.354710	-119.312860	along Casitas Vista Road, vicinity of Foster Park	ON677714	OP291299
<i>Elgaria multicolorata</i>	LACM 189923	USA, California, Santa Barbara County	34.939490	-120.193350	along Colson Canyon Road (off Tepusquet Rd.), Sierra Madre Mountains	ON677715	-
<i>Elgaria multicolorata</i>	LACM 189935	USA, California, Orange County	33.595570	-117.628070	vicinity of lower Tijeras Canyon, W of Antonio Parkway, N of Oso Parkway, Las Flores	ON677716	OP291300
<i>Elgaria multicolorata</i>	LACM 189947	USA, California, San Diego County	32.854150	-116.575310	along Old Hwy 80, W of Guatay	ON677717	-
<i>Elgaria multicolorata</i>	LACM 190289	Santa Cruz Island	34.021582	-119.868920	vicinity of Christy Ranch	ON677729	OP291313
<i>Elgaria multicolorata</i>	LACM 190290	Santa Cruz Island	33.976002	-119.722360	along Coches Prietos Road	ON677735	OP291319
<i>Elgaria multicolorata</i>	LACM 190291	Santa Cruz Island	34.022640	-119.691282	along Pelican Bay Trail	ON677731	OP291315

Species	Sample ID	Island or Mainland County	Latitude	Longitude	Specific Locality	Cyt-b GenBank	ND1 GenBank
<i>Elgaria multicolorata</i>	LACM 190292	Santa Cruz Island	34.022640	-119.691282	along Pelican Bay Trail	ON677732	OP291316
<i>Elgaria multicolorata</i>	LACM 190293	Santa Cruz Island	34.022640	-119.691282	along Pelican Bay Trail	ON677733	OP291317
<i>Elgaria multicolorata</i>	LACM 190294	Santa Cruz Island	34.031924	-119.701169	vicinity of Pelican Bay	ON677734	OP291318
<i>Elgaria multicolorata</i>	LACM 190295	Santa Cruz Island	34.019142	-119.683885	Prisoners Harbor	ON677730	OP291314
<i>Elgaria multicolorata</i>	LACM-TC 1689	USA, California, Los Angeles County	33.976360	-118.406290	Bluff Creek Trail, Playa Vista	ON677720	OP291303
<i>Elgaria multicolorata</i>	LACM-TC 1806	USA, California, Napa County	38.485270	-122.149700	Quail Ridge Ecological Preserve, off Hwy 128	ON677721	OP291304
<i>Elgaria multicolorata</i>	LACM-TC 1853	USA, California, Sutter County	38.929870	-121.583820	Bobelaine Audubon Preserve, E end of Laurel Ave off Hwy 99/70, S of Yuba city, along Feather Rvier	ON677722	OP291305
<i>Elgaria multicolorata</i>	WCF 6492	Santa Rosa Island	33.997150	-120.173070	Tecelote Canyon	ON677745	OP291329
<i>Elgaria multicolorata</i>	WCF 6493	Santa Rosa Island	33.986080	-120.154540	corral along Arlington Canyon	ON677746	OP291330
<i>Sceloporus occidentalis</i>	LACM 183676	San Miguel Island	34.029300	-120.342930	Brooks fox pens	ON691528	ON691587
<i>Sceloporus occidentalis</i>	LACM 183677	San Miguel Island	34.029300	-120.342930	Brooks fox pens	ON691529	ON691588
<i>Sceloporus occidentalis</i>	LACM 183678	San Miguel Island	34.029300	-120.342930	Brooks fox pens	ON691530	ON691589
<i>Sceloporus occidentalis</i>	LACM 183679	San Miguel Island	34.029830	-120.320860	Willow Canyon	ON691531	ON691590
<i>Sceloporus occidentalis</i>	LACM 183680	San Miguel Island	34.035620	-120.318340	Willow Canyon	ON691532	ON691591
<i>Sceloporus occidentalis</i>	LACM 183695	San Miguel Island	34.038510	-120.351900	Ranger Station	ON691533	ON691592
<i>Sceloporus occidentalis</i>	LACM 183696	San Miguel Island	34.038510	-120.351900	Ranger Station	ON691534	ON691593
<i>Sceloporus occidentalis</i>	LACM 183697	San Miguel Island	34.037680	-120.342690	Ranger Station fox pens	ON691535	ON691594
<i>Sceloporus occidentalis</i>	LACM 183698	San Miguel Island	34.037680	-120.342690	Ranger Station fox pens	ON691536	ON691595
<i>Sceloporus occidentalis</i>	LACM 183702	San Miguel Island	34.035620	-120.318340	Willow Canyon	ON691537	ON691596
<i>Sceloporus occidentalis</i>	LACM 183824	USA, California, Los Angeles County	34.034970	-118.775990	Escondido Canyon, Santa Monica Mountains	ON691538	ON691597
<i>Sceloporus occidentalis</i>	LACM 183825	USA, California, Los Angeles County	34.034970	-118.776710	Escondido Canyon, Santa Monica Mountains	ON691539	ON691598
<i>Sceloporus occidentalis</i>	LACM 183830	USA, California, Los Angeles County	34.035310	-118.733250	Corral Canyon, Santa Monica Mountains	ON691540	ON691599
<i>Sceloporus occidentalis</i>	LACM 183831	USA, California, Los Angeles County	34.035310	-118.733250	Corral Canyon, Santa Monica Mountains	ON691541	ON691600
<i>Sceloporus occidentalis</i>	LACM 183862	USA, California, Los Angeles County	34.746770	-118.406650	Alta Vicente Reserve, Palos Verdes Peninsula	ON691542	ON691601

Species	Sample ID	Island or Mainland County	Latitude	Longitude	Specific Locality	Cyt-b GenBank	ND1 GenBank
<i>Sceloporus occidentalis</i>	LACM 183863	USA, California, Los Angeles County	33.740270	-118.359770	Portuguese Bend Reserve, Palos Verdes Peninsula	ON691543	ON691602
<i>Sceloporus occidentalis</i>	LACM 183871	USA, California, Los Angeles County	33.749040	-118.361940	Portuguese Bend Reserve, Palos Verdes Peninsula	ON691544	ON691603
<i>Sceloporus occidentalis</i>	LACM 184187	USA, California, Los Angeles County	33.784180	-118.291590	Lake Machado, Ken Malloy Harbor Regional Park	ON691545	ON691604
<i>Sceloporus occidentalis</i>	LACM 184188	USA, California, Los Angeles County	33.711700	-118.303490	cliffs below W Paseo Del Mar, San Pedro	ON691546	ON691605
<i>Sceloporus occidentalis</i>	LACM 184189	USA, California, Los Angeles County	33.711700	-118.303490	cliffs below W Paseo Del Mar, San Pedro	ON691547	ON691606
<i>Sceloporus occidentalis</i>	LACM 186026	Santa Rosa Island	33.992780	-120.044460	Water Canyon downstream of campground	ON691579	ON691638
<i>Sceloporus occidentalis</i>	LACM 186027	Santa Rosa Island	34.006180	-120.090560	Lobo Canyon	ON691580	ON691639
<i>Sceloporus occidentalis</i>	LACM 186028	Santa Rosa Island	34.010970	-120.092830	Lobo Canyon	ON691581	ON691640
<i>Sceloporus occidentalis</i>	LACM 186029	Santa Rosa Island	34.010880	-120.093170	Lobo Canyon	ON691582	ON691641
<i>Sceloporus occidentalis</i>	LACM 186030	Santa Rosa Island	34.001900	-120.110600	Verde Canyon corral	ON691583	ON691642
<i>Sceloporus occidentalis</i>	LACM 186031	Santa Rosa Island	34.002890	-120.094830	between Lobo and Cow Canyons	ON691584	ON691643
<i>Sceloporus occidentalis</i>	LACM 186032	Santa Rosa Island	34.002890	-120.094830	between Lobo and Cow Canyons	ON691585	ON691644
<i>Sceloporus occidentalis</i>	LACM 186033	Santa Rosa Island	34.002890	-120.094830	between Lobo and Cow Canyons	ON691586	ON691645
<i>Sceloporus occidentalis</i>	LACM 186715	USA, California, Los Angeles County	34.365750	-118.492860	Whitney Canyon Park	ON691552	ON691611
<i>Sceloporus occidentalis</i>	LACM 186734	USA, California, Los Angeles County	34.291020	-117.835170	vicinity of San Gabriel Canyon Road at Alpine Canyon	ON691553	ON691612
<i>Sceloporus occidentalis</i>	LACM 186746	USA, California, Los Angeles County	33.845360	-118.200350	SE corner of vacant lot along Oregon Ave, 125 m S of Del Amo Blvd, Long Beach	ON691554	ON691613
<i>Sceloporus occidentalis</i>	LACM 186808	USA, California, Los Angeles County	34.339350	-118.030140	1.8 km NW of 3N21 on 3N14, Chilao Campground area, Angeles National Forest	ON691555	ON691614
<i>Sceloporus occidentalis</i>	LACM 186847	USA, California, Los Angeles County	34.257410	-117.753460	East Fork San Gabriel River Canyon	ON691556	ON691615
<i>Sceloporus occidentalis</i>	LACM 186903	USA, California, Kern County	35.297520	-118.614007	Tollhouse Ranch, off Caliente-Bodfish Rd, Caliente	ON691557	ON691616
<i>Sceloporus occidentalis</i>	LACM 186906	USA, California, Los Angeles County	34.702090	-118.524360	vicinity of Lower Shake Public Campground, 50 m S. of Pine Canyon Road at intersection of Pine Canyon Road and Pacific Crest Trail	ON691558	ON691617
<i>Sceloporus occidentalis</i>	LACM 187275	USA, California, Orange County	33.800561	-117.800412	4939 E. Lomita Avenue, E of Rancho Santiago Blvd., Orange	ON691560	ON691619
<i>Sceloporus occidentalis</i>	LACM 187276	USA, California, Orange County	33.798780	-117.799470	E. Bond Avenue at N. Bridle Path, Orange	ON691561	ON691620

Species	Sample ID	Island or Mainland County	Latitude	Longitude	Specific Locality	Cyt-b GenBank	ND1 GenBank
<i>Sceloporus occidentalis</i>	LACM 188006	USA, California, Mono County	37.492650	-118.568050	Volcanic Tablelands, Gorge Road/Owens Gorge Pipeline Road, 6.7 road km NNE of CA-395 intersection	ON691562	ON691621
<i>Sceloporus occidentalis</i>	LACM 188050	USA, California, San Bernardino County	35.726580	-115.915540	Kingston Peak summit, Kingston Mountains	ON691563	ON691622
<i>Sceloporus occidentalis</i>	LACM 188771	USA, California, San Luis Obispo County	35.056050	-119.781870	Caliente Ridge Trail, Carrizo Plain	ON691564	ON691623
<i>Sceloporus occidentalis</i>	LACM 188779	USA, California, Santa Barbara County	34.762360	-120.041600	Grass Mountain Peak, off Figueroa Mountain Road	ON691565	ON691624
<i>Sceloporus occidentalis</i>	LACM 188806	USA, California, Riverside County	33.710570	-117.534044	Santiago Peak, Santa Ana Mtns, Orange-Riverside County line	ON691548	ON691607
<i>Sceloporus occidentalis</i>	LACM 188807	USA, California, Orange County	33.649639	-117.603317	O'Neill Regional Park	ON691566	ON691625
<i>Sceloporus occidentalis</i>	LACM 189905	USA, California, San Luis Obispo County	35.311674	-120.828907	NW corner of Fairchild Way at Los Osos Valley Rd, Los Osos	ON691549	ON691608
<i>Sceloporus occidentalis</i>	LACM 189944	USA, California, San Diego County	32.855100	-116.578670	along Old Hwy 80, W of Guatay	ON691550	ON691609
<i>Sceloporus occidentalis</i>	LACM 190297	Santa Cruz Island	34.006918	-119.746067	Cascada	ON691568	ON691627
<i>Sceloporus occidentalis</i>	LACM 190298	Santa Cruz Island	33.976490	-119.722700	along Coches Prietos Road	ON691576	ON691635
<i>Sceloporus occidentalis</i>	LACM 190299	Santa Cruz Island	33.976490	-119.722700	along Coches Prietos Road	ON691577	ON691636
<i>Sceloporus occidentalis</i>	LACM 190300	Santa Cruz Island	34.011532	-119.692977	along Cañada del Puerto	ON691570	ON691629
<i>Sceloporus occidentalis</i>	LACM 190301	Santa Cruz Island	34.014220	-119.685073	along Cañada del Puerto	ON691578	ON691637
<i>Sceloporus occidentalis</i>	LACM 190302	Santa Cruz Island	34.016480	-119.683563	along Cañada del Puerto	ON691571	ON691630
<i>Sceloporus occidentalis</i>	LACM 190303	Santa Cruz Island	34.002386	-119.709931	along Cañada del Puerto	ON691575	ON691634
<i>Sceloporus occidentalis</i>	LACM 190304	Santa Cruz Island	34.003892	-119.705833	along Cañada Del Puerto Road	ON691572	ON691631
<i>Sceloporus occidentalis</i>	LACM 190305	Santa Cruz Island	34.003892	-119.705833	along Cañada Del Puerto Road	ON691573	ON691632
<i>Sceloporus occidentalis</i>	LACM 190306	Santa Cruz Island	34.003892	-119.705833	along Cañada Del Puerto Road	ON691574	ON691633
<i>Sceloporus occidentalis</i>	LACM 190307	Santa Cruz Island	34.003622	-119.745106	Road between Cascada pools and UC Field Station	ON691567	ON691626
<i>Sceloporus occidentalis</i>	LACM 190308	Santa Cruz Island	33.997009	-119.724729	UC Field Station	ON691569	ON691628
<i>Sceloporus occidentalis</i>	LACM-TC 2204	USA, California, Riverside County	33.561040	-116.514000	Santa Rosa Mountain Truck Trail	ON691551	ON691610
<i>Sceloporus occidentalis</i>	LACM-TC 2676	USA, California, Los Angeles County	34.010930	-118.358200	Kenneth Hahn State Recreation Area	ON691559	ON691618
<i>Urosaurus ornatus</i>	LACM 188126	USA, Nevada, Clark County	35.310790	-114.862050	Pianka Searchlight field site; SE of intersection of Loran Station Road and Hwy 95	OP291162	OP291237

Species	Sample ID	Island or Mainland County	Latitude	Longitude	Specific Locality	Cyt-b GenBank	ND1 GenBank
<i>Uta stansburiana</i>	CD 1	San Nicolas Island			Beach Boxthorn	-	OP291181
<i>Uta stansburiana</i>	CD 200.2	San Nicolas Island			Beach Boxthorn	OP291107	OP291182
<i>Uta stansburiana</i>	CD 200.3	San Nicolas Island			Beach Boxthorn	OP291108	OP291183
<i>Uta stansburiana</i>	CD 3000.3	San Nicolas Island			Tranquility 845	OP291110	OP291185
<i>Uta stansburiana</i>	CD 3000.4	San Nicolas Island			SE Choya	OP291111	OP291186
<i>Uta stansburiana</i>	CD 3000.5	San Nicolas Island			Ocean Coreopsis	OP291112	OP291187
<i>Uta stansburiana</i>	CD 3000.6	San Nicolas Island			Ocean Coreopsis	OP291113	OP291188
<i>Uta stansburiana</i>	CD 3500	San Nicolas Island			Theodolites	OP291114	OP291189
<i>Uta stansburiana</i>	CD 4000	San Nicolas Island			Central STIPA	OP291115	OP291190
<i>Uta stansburiana</i>	CD 3000.2	San Nicolas Island			Theodolites	OP291109	OP291184
<i>Uta stansburiana</i>	LACM 183330	Santa Catalina Island	33.444800	-118.482910	USC Wrigley Marine Science Center at Big Fisherman's Cove	OP291116	OP291191
<i>Uta stansburiana</i>	LACM 183331	Santa Catalina Island	33.445170	-118.482470	USC Wrigley Marine Science Center at Big Fisherman's Cove	OP291117	OP291192
<i>Uta stansburiana</i>	LACM 183714	Anacapa Island	34.013570	-119.370790	East Anacapa Island	OP291118	OP291193
<i>Uta stansburiana</i>	LACM 183715	Anacapa Island	34.013570	-119.370790	East Anacapa Island	OP291119	OP291194
<i>Uta stansburiana</i>	LACM 183716	Anacapa Island	34.013570	-119.370790	East Anacapa Island	OP291120	OP291195
<i>Uta stansburiana</i>	LACM 183717	Anacapa Island	34.013570	-119.370790	East Anacapa Island	OP291121	OP291196
<i>Uta stansburiana</i>	LACM 183718	Anacapa Island	34.015390	-119.363210	East Anacapa Island	OP291122	OP291197
<i>Uta stansburiana</i>	LACM 183719	Anacapa Island	34.014780	-119.362720	East Anacapa Island	OP291123	OP291198
<i>Uta stansburiana</i>	LACM 183720	Anacapa Island	34.014780	-119.362720	East Anacapa Island	OP291124	OP291199
<i>Uta stansburiana</i>	LACM 183721	Anacapa Island	34.014780	-119.362720	East Anacapa Island	OP291125	OP291200
<i>Uta stansburiana</i>	LACM 183722	Anacapa Island	34.014780	-119.362720	East Anacapa Island	OP291126	OP291201
<i>Uta stansburiana</i>	LACM 183723	Anacapa Island	34.014780	-119.362720	East Anacapa Island	OP291127	OP291202
<i>Uta stansburiana</i>	LACM 183734	Santa Catalina Island	33.356590	-118.442030	Middle Ranch	OP291128	OP291203
<i>Uta stansburiana</i>	LACM 183735	Santa Catalina Island	33.356590	-118.442030	Middle Ranch	OP291129	OP291204
<i>Uta stansburiana</i>	LACM 183742	Santa Catalina Island	33.441560	-118.520450	Silver Peak Rd. west of Catalina Harbor	OP291130	OP291205
<i>Uta stansburiana</i>	LACM 183744	Santa Catalina Island	33.466870	-118.583650	west of Silver Peak on Silver Peak Rd.	OP291131	OP291206

Species	Sample ID	Island or Mainland County	Latitude	Longitude	Specific Locality	Cyt-b GenBank	ND1 GenBank
<i>Uta stansburiana</i>	LACM 183747	Santa Catalina Island	33.468490	-118.582890	west of Silver Peak on Silver Peak Rd.	OP291132	OP291207
<i>Uta stansburiana</i>	LACM 183753	Santa Catalina Island	33.403150	-118.415340	Catalina Island airport	OP291133	OP291208
<i>Uta stansburiana</i>	LACM 183754	Santa Catalina Island	33.403150	-118.415340	Catalina Island airport	OP291134	OP291209
<i>Uta stansburiana</i>	LACM 183756	Santa Catalina Island	33.352040	-118.361490	Haypress Reservoir	OP291135	OP291210
<i>Uta stansburiana</i>	LACM 183757	Santa Catalina Island	33.368010	-118.362390	Toyon Canyon	OP291136	OP291211
<i>Uta stansburiana</i>	LACM 183758	Santa Catalina Island	33.400410	-118.390820	Echo Lake	OP291137	OP291212
<i>Uta stansburiana</i>	LACM 183832	USA, California, Los Angeles County	34.036290	-118.734120	Corral Canyon	OP291138	OP291213
<i>Uta stansburiana</i>	LACM 185309	San Clemente Island	33.005000	-118.553940	ca. 340 m east of Wilson Cove Navy dock	OP291146	OP291221
<i>Uta stansburiana</i>	LACM 185310	San Clemente Island	32.995960	-118.551980	vicinity of Natural Resource Office	OP291147	OP291222
<i>Uta stansburiana</i>	LACM 185311	San Clemente Island	32.995860	-118.551730	vicinity of Natural Resource Office	OP291148	OP291223
<i>Uta stansburiana</i>	LACM 185312	San Clemente Island	33.016530	-118.596980	West Cove	OP291149	OP291224
<i>Uta stansburiana</i>	LACM 185314	San Clemente Island	33.016230	-118.597220	West Cove	OP291150	OP291225
<i>Uta stansburiana</i>	LACM 185316	San Clemente Island	33.018160	-118.593770	ca. 100 m S of runway, near West Cove	OP291151	OP291226
<i>Uta stansburiana</i>	LACM 185317	San Clemente Island	32.826140	-118.361080	southern terminus of main road	OP291152	OP291227
<i>Uta stansburiana</i>	LACM 185319	San Clemente Island	32.827720	-118.363040	250 m NW of southern terminus of main road	OP291153	OP291228
<i>Uta stansburiana</i>	LACM 186650	USA, California, San Bernardino County	35.792340	-115.976200	wash, NE side of Kingston Mtns, along Excelsior Mine Rd.	OP291145	OP291220
<i>Uta stansburiana</i>	LACM 186721	USA, California, Los Angeles County	34.365910	-118.494970	Whitney Canyon Park	OP291154	OP291229
<i>Uta stansburiana</i>	LACM 186756	USA, California, Los Angeles County	34.291740	-117.839030	Cold Brook Campground, along San Gabriel Canyon Road	OP291155	OP291230
<i>Uta stansburiana</i>	LACM 186807	USA, California, Los Angeles County	34.332450	-118.020960	0.5 km NW of 3N21 on 3N14, Chilao Campground area, Angeles National Forest	OP291156	OP291231
<i>Uta stansburiana</i>	LACM 186843	USA, California, Los Angeles County	34.017250	-118.380330	Baldwin Hills Scenic Overlook	OP291143	OP291218
<i>Uta stansburiana</i>	LACM 186845	USA, California, Los Angeles County	34.250260	-117.759430	East Fork San Gabriel River Canyon	OP291157	OP291232
<i>Uta stansburiana</i>	LACM 186978	USA, California, San Bernardino County	34.146850	-115.836420	Pianka Twentynine Palms field site; vicinity of Hollywood Lane, S. of Amboy Rd.	OP291158	OP291233
<i>Uta stansburiana</i>	LACM 187365	Anacapa Island	34.005440	-119.401070	Middle Anacapa Island	OP291141	OP291216
<i>Uta stansburiana</i>	LACM 187367	Anacapa Island	34.005070	-119.402050	Middle Anacapa Island	OP291142	OP291217

Species	Sample ID	Island or Mainland County	Latitude	Longitude	Specific Locality	Cyt-b GenBank	ND1 GenBank
<i>Uta stansburiana</i>	LACM 187802	Anacapa Island	34.013260	-119.439700	West Anacapa Island	OP291160	OP291235
<i>Uta stansburiana</i>	LACM 187803	Anacapa Island	34.013110	-119.439480	West Anacapa Island	OP291161	OP291236
<i>Uta stansburiana</i>	LACM 188039	USA, California, Mono County	37.666430	-118.518570	Volcanic Tablelands, 250 m E of Morris Mine Road, 1.25 road km N of Chidago Canyon Road intersection	OP291159	OP291234
<i>Uta stansburiana</i>	LACM 188537	USA, California, Los Angeles County	33.763901	-118.244409	Vicinity of Pier S200, Terminal Island, San Pedro	OP291164	OP291239
<i>Uta stansburiana</i>	LACM 188644	USA, California, Orange County	33.648476	-117.603203	O'Neill Regional Park	OP291163	OP291238
<i>Uta stansburiana</i>	LACM 188756	USA, California, Los Angeles County	33.809793	-118.181378	E 29th St, 60 m W of California Ave	OP291165	-
<i>Uta stansburiana</i>	LACM 188773	USA, California, San Luis Obispo County	35.035900	-119.760950	NW slope of Caliente Peak, Carrizo Plain	OP291166	OP291240
<i>Uta stansburiana</i>	LACM 188776	USA, California, Santa Barbara County	34.760670	-120.049430	Grass Mountain Trail, off Figueroa Mountain Road	OP291167	OP291241
<i>Uta stansburiana</i>	LACM 189066	USA, California, Kern County	35.085620	-118.148780	Pianka Mojave field site; NE of town of Mojave	OP291168	OP291242
<i>Uta stansburiana</i>	LACM 189896	USA, California, Santa Barbara County	34.464750	-119.643573	Cold Spring Trails, Los Padres National Forest (above Montecito)	OP291139	OP291214
<i>Uta stansburiana</i>	LACM 189945	USA, California, San Diego County	33.231290	-117.035760	along Canyon Road, uphill from Valley Center Road, Valley Center	OP291140	OP291215
<i>Uta stansburiana</i>	LACM 190309	Santa Cruz Island	34.006918	-119.746067	Cascada pools	OP291169	OP291243
<i>Uta stansburiana</i>	LACM 190310	Santa Cruz Island	34.006918	-119.746067	Cascada pools	OP291170	OP291244
<i>Uta stansburiana</i>	LACM 190311	Santa Cruz Island	34.023176	-119.871680	vicinity of Christy Ranch	OP291171	OP291245
<i>Uta stansburiana</i>	LACM 190312	Santa Cruz Island	33.971439	-119.707358	along Coches Prietos Road	OP291174	OP291248
<i>Uta stansburiana</i>	LACM 190313	Santa Cruz Island	33.971439	-119.707358	along Coches Prietos Road	OP291175	OP291249
<i>Uta stansburiana</i>	LACM 190314	Santa Cruz Island	33.975883	-119.721220	along Coches Prietos Road	OP291176	OP291250
<i>Uta stansburiana</i>	LACM 190315	Santa Cruz Island	33.975887	-119.721858	along Coches Prietos Road	OP291180	OP291254
<i>Uta stansburiana</i>	LACM 190316	Santa Cruz Island	33.975887	-119.721858	along Coches Prietos Road	OP291177	OP291251
<i>Uta stansburiana</i>	LACM 190317	Santa Cruz Island	33.976490	-119.722700	along Coches Prietos Road	OP291178	OP291252
<i>Uta stansburiana</i>	LACM 190318	Santa Cruz Island	33.976490	-119.722700	along Coches Prietos Road	OP291179	OP291253
<i>Uta stansburiana</i>	LACM 190319	Santa Cruz Island	34.003892	-119.705833	along Cañada Del Puerto Road	OP291172	OP291246
<i>Uta stansburiana</i>	LACM 190320	Santa Cruz Island	34.003892	-119.705833	along Cañada Del Puerto Road	OP291173	OP291247
<i>Uta stansburiana</i>	LACM-TC 2152	USA, California, Los Angeles County	33.975460	-118.408201	Bluff Creek Trail, Playa Vista	OP291144	OP291219

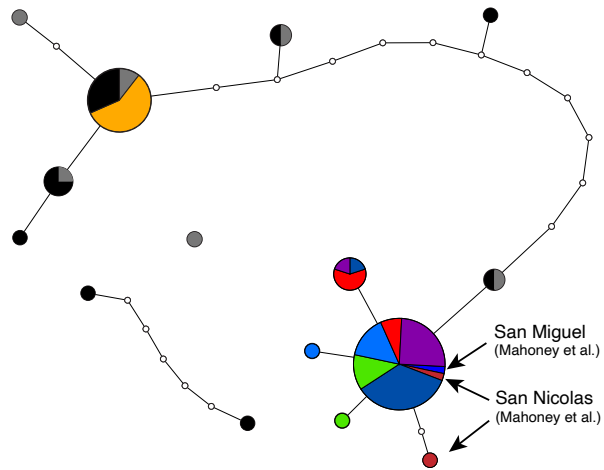




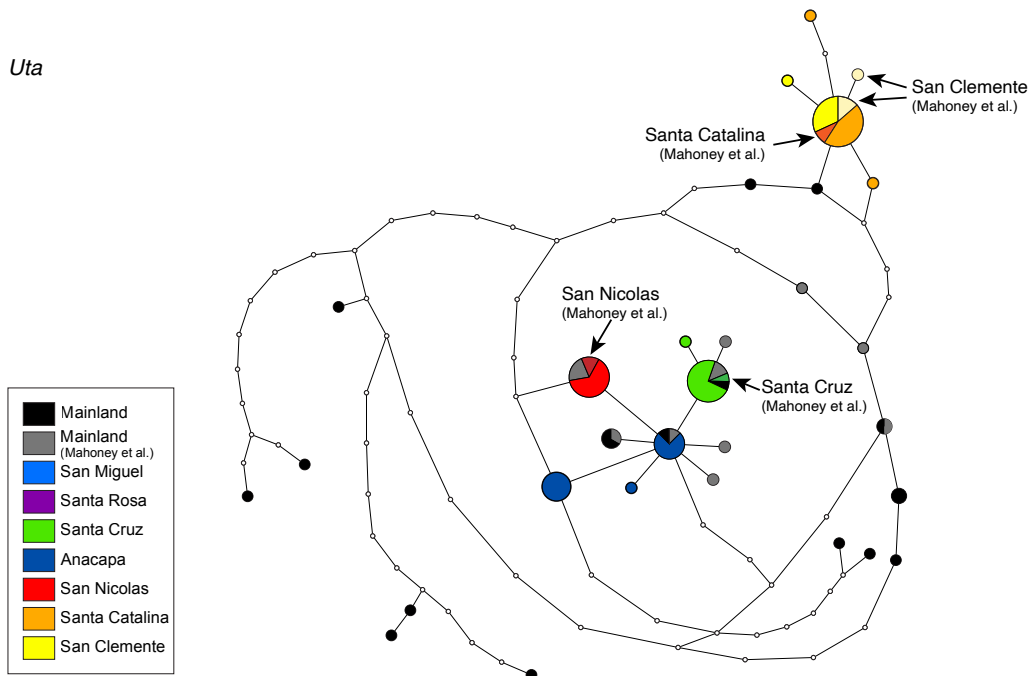
## Appendix S2.

Haplotype network for trimmed sequences from our datasets combined with sequences from an existing study (Mahoney et al., 2003) for *Elgaria multicarinata* and *Uta stansburiana*.

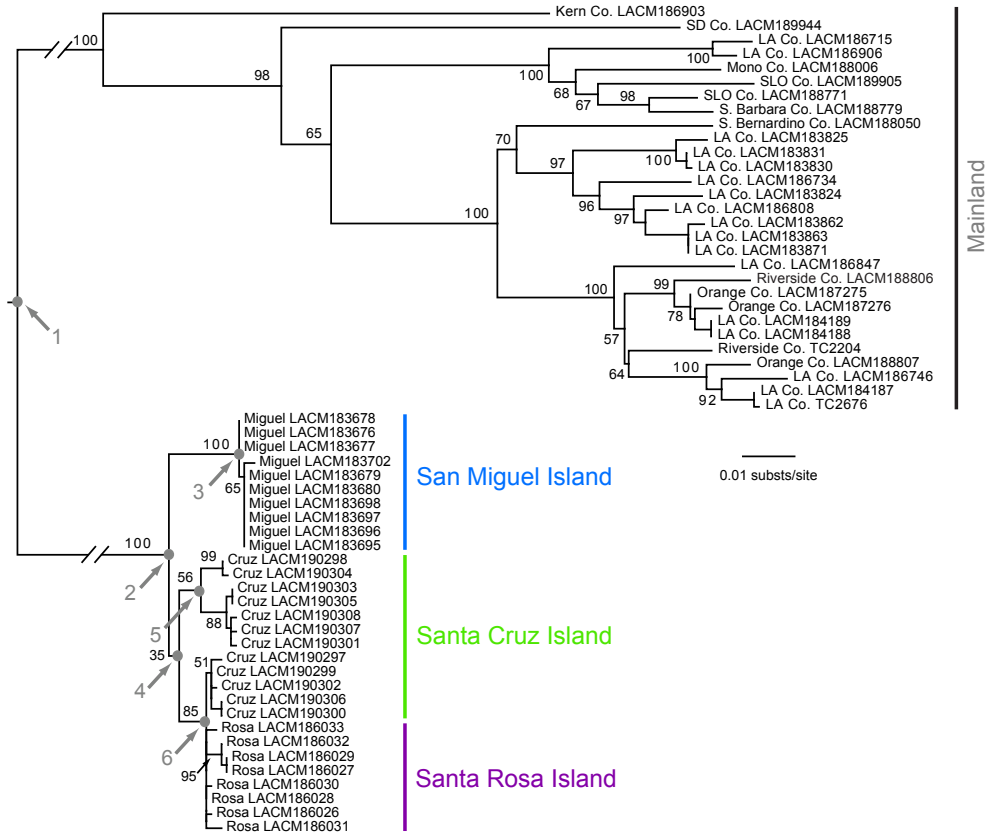
*Elgaria*



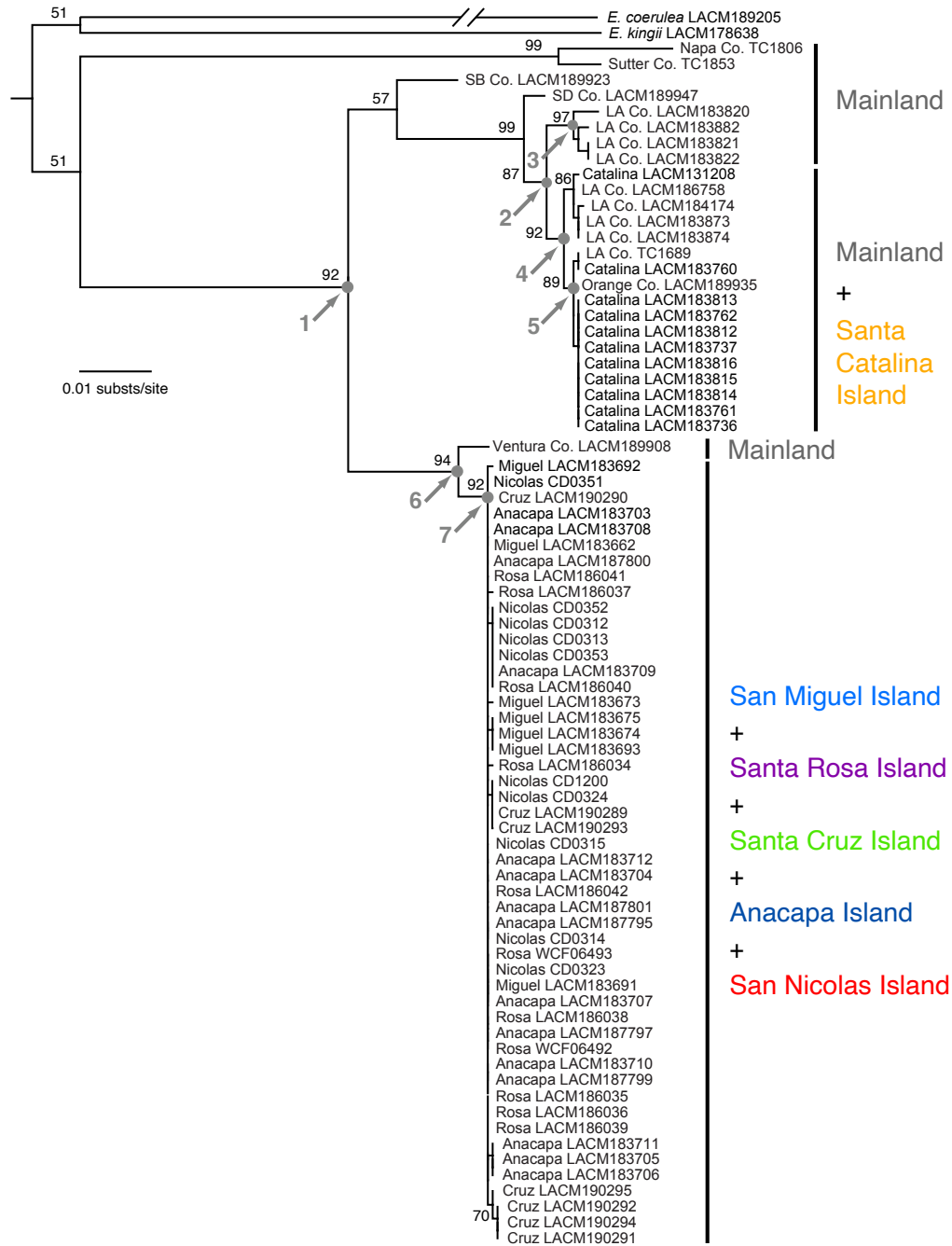
*Uta*



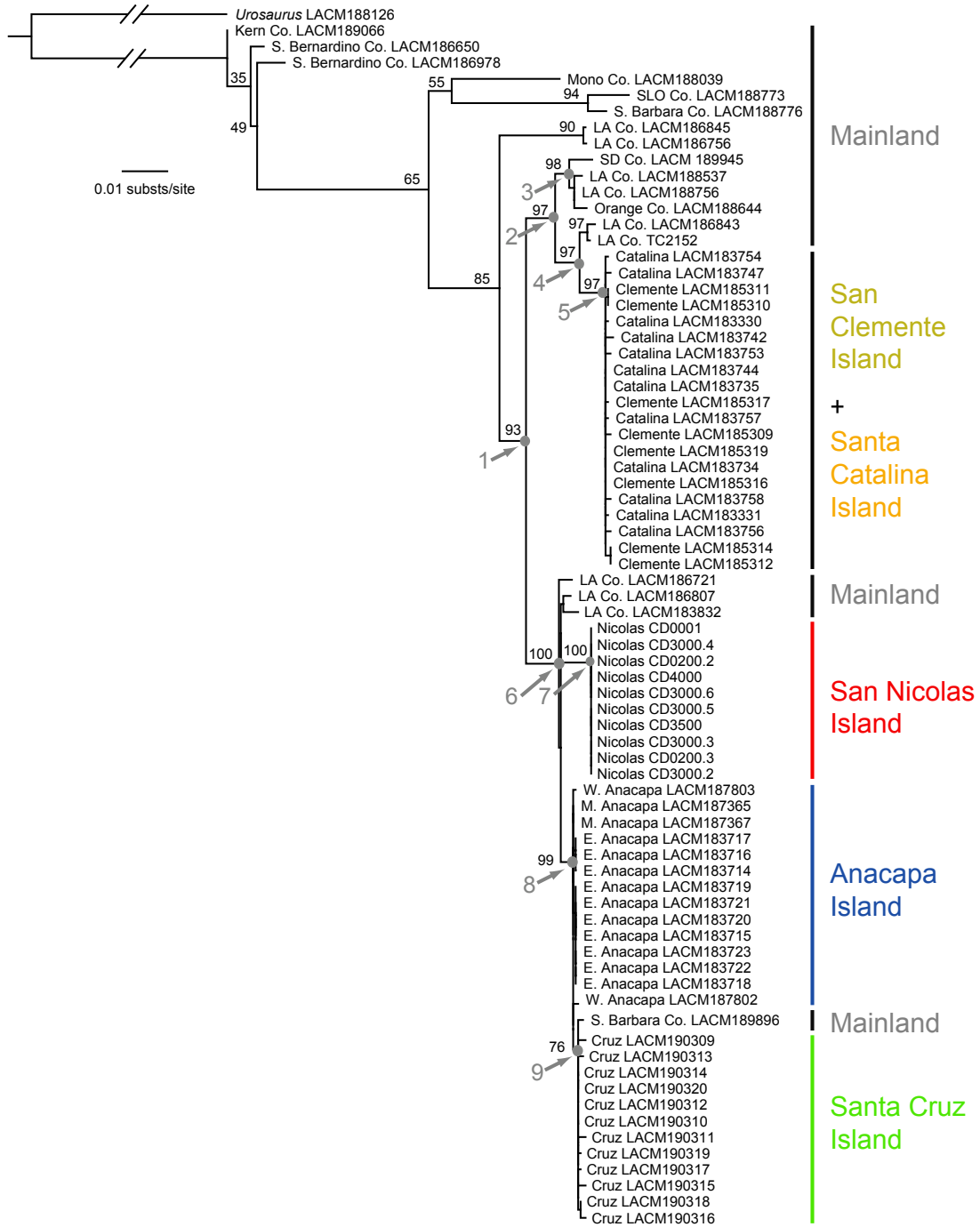
Appendix S3. Phylogenetic analyses of *Sceloporus occidentalis* from the Northern Channel Islands and nearby California mainland. RAxML maximum likelihood phylogeny with bootstrap values.



Appendix S4. Phylogenetic analyses of *Elgaria multicarinata* from the Channel Islands and nearby California mainland. RAxML maximum likelihood phylogeny with bootstrap values.



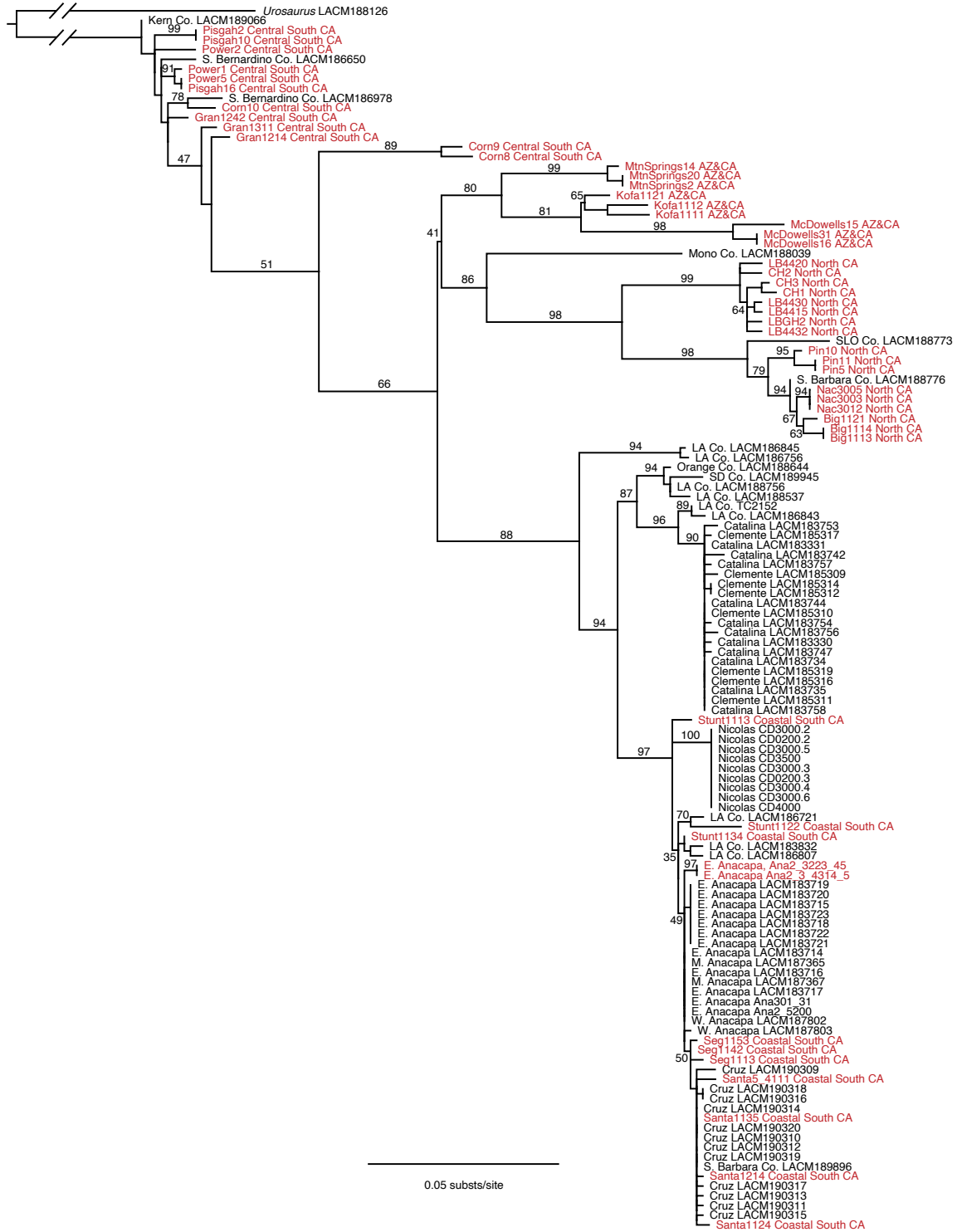
Appendix S5. Phylogenetic analyses of *Uta stansburiana* from the Channel Islands and nearby California mainland. RAxML maximum likelihood phylogeny with bootstrap values.



Appendix S6. Phylogenetic analyses using a reduced version of our dataset (see text for methods) to compare our sequences with those from an existing study of *E. multicastrata* (Leavitt et al., 2017; sequences in red).



Appendix S7. Phylogenetic analyses using a reduced version of our dataset (see text for methods) to compare our sequences with those from an existing study of *U. stansburiana* (Corl et al., 2010; sequences in red).



Appendix S8. Further details on introductions of *E. multicolorata* and *U. stansburiana*

### ***E. multicolorata* on Santa Catalina Island**

It is not clear when Santa Catalina Island was colonized by *E. multicolorata*. Lack of fossil data and genetic similarity between Santa Catalina Island and mainland haplotypes suggests recent colonization, possibly aided by humans. Furthermore, given the paraphyly of Santa Catalina Island haplotypes, we cannot exclude the possibility that *E. multicolorata* may have colonized this island multiple times (Fig. 2B, E). The most divergent Santa Catalina Island sample (LACM 131208; Appendix S5), is most similar to other mainland samples from the Los Angeles area and is our only sample from west of a narrow isthmus that connects the smaller western end of the island with the majority of Santa Catalina Island's land mass. The divergent specimen was collected in an area with several camps with high use by mainland residents; thus, it is possible that the lizard was introduced. Additional sampling from the west end of the island will clarify whether these alligator lizards might represent a separate colonization event.

### ***E. multicolorata* on San Nicolas Island**

Previous studies have attempted to identify the source population of *E. multicolorata* on San Nicolas Island. Banta and Wilson (1976) noted similar color patterns among *E. multicolorata* on San Nicolas Island and the Northern Channel Islands. Some have suggested the most likely routes of introduction to San Nicolas Island are through the movement of supplies by the military, which was particularly active on San Miguel and Santa Rosa Islands or from a mainland military base (Point Mugu) (Fellers et al., 1998, 2009; Mahoney et al., 2003). Our increased sampling relative to Mahoney et al. (2003) reveals that the two mtDNA haplotypes on San Nicolas also occur on Santa Rosa and Anacapa Islands. We suspect that Santa Rosa Island is the likely source population for the introduced San Nicolas Island *E. multicolorata*. The first San Nicolas Island *E. multicolorata* specimen was collected in 1960 (MVZ 70339; Fig. 3) consistent with the timing of military activity at the Santa Rosa Island Air Force Station with introduction in the 1950s and first detection in 1960. Fellers et al. (2009) documented the introduction and spread of *E. multicolorata* on San Nicolas Island between 1995 and 2007, further supporting a recent introduction to the island.

### ***E. multicolorata* on San Clemente Island**

Note that although *E. multicolorata* was reportedly collected from San Clemente Island in 1948 (Fig. 3), it has not been documented since, despite continued collection efforts, suggesting that this single specimen may have been a labeling error or a single introduction that was unable to establish a reproductive population. Thus, *E. multicolorata* is confined to only two Southern Channel Islands with no apparent connectivity between them.

### ***U. stansburiana on San Nicolas Island***

Mahoney et al. (2003) suggested *U. stansburiana* was transported to San Nicolas Island from Point Mugu Naval Air Station as stowaways in naval cargo shipments. However, the earliest *U. stansburiana* individuals collected on San Nicolas are from 1940 (LACM 5360–5362; Fig. 3), two years prior to the establishment of Point Mugu Naval Air Station. The documented rapid expansion of this island population between 1940 and 2007 (Fellers et al., 2009), suggests the introduction is likely to have taken place shortly before Point Mugu Naval Air Station was established. Our increased sampling relative to Mahoney et al. (2003) reveals that the San Nicolas Island individuals are highly divergent from both mainland and island samples (Fig. 2C, F; see Appendix S6), and additional sampling is needed to identify the mainland source population.



## Appendix S9.

### The utility of microfossil data on resolving colonization patterns for California Channel Island Biogeography

The only microfossil studies relevant to our three focal taxa were conducted on San Miguel Island (Allen, 2013; Guthrie, 1993, 2005). Because of the long history of human habitation on the islands, middens and other Late Pleistocene and Holocene sites have drawn a lot of attention from archaeologists and paleontologists. Unfortunately, sorting of this material often uses screen sizes that do not keep skeletal remains of smaller vertebrates (Allen, 2013). Thus, increased effort is needed to obtain a better understanding of the history of many of the smaller Channel Islands vertebrates. With respect to our focal species, microfossil studies on additional islands would help to determine when *E. multicolorata* first arrived to Santa Catalina Island, when *U. stansburiana* first arrived to Santa Catalina and San Clemente Islands (and hence whether one might result from transfer from the other), when *U. stansburiana* first arrived to Anacapa and Santa Cruz Islands, and whether *S. occidentalis* was once present on Anacapa Island. These results could also clarify whether the arrival of some of these species postdates human colonization of the islands, as was determined for the island fox (Rick et al., 2009).

## References

- Allen, J. A. (2013). Non-cultural deposition in an archaeological site: Microfaunal remains from Cave of the Chimneys (CA-SMI-603), San Miguel Island, California. *Master of Arts thesis, California State University, Los Angeles, California.*
- Banta, B. H., & Wilson, R. L. (1976). On the occurrence of *Gerrhonotus multicoloratus* on San Nicolas Island, Ventura County, California. *Bulletin of the Maryland Herpetological Society, 12*, 99–100.
- Corl, A., Davis, A. R., Kuchta, S. R., Comendant, T., & Sinervo, B. (2010). Alternative mating strategies and the evolution of sexual size dimorphism in the side-blotched lizard, *Uta stansburiana*: A population-level comparative analysis. *Evolution, 64*, 79–96.
- Fellers, G. M., Drost, C. A., Mautz, W. J., & Murphey, T. (1998). Ecology of the Island Night Lizard, *Xantusia riversiana*, on San Nicolas Island, California. U.S. Navy report.
- Fellers, G. M., Drost, C. A., & Murphey, T. (2009). Status of the Island Night Lizard and two non-native lizards on outlying landing field San Nicolas Island, California. *US Geological Survey Open File Report 2008–1371.*
- Guthrie, D. A. (1993). New information on the prehistoric fauna of San Miguel Island, California. In F. G. Hochberg (Eds.), *Third California Islands symposium: Recent Advances in Research on the California Islands* (pp. 405–16). Santa Barbara, CA: Santa Barbara Museum of Natural History.

- Guthrie, D. A. (2005). Distribution and provenance of fossil avifauna on San Miguel Island. In D. K. Garcelon & C. A. Schwemm (Eds.), *Proceedings of the Sixth California Islands Symposium. National Park Service Technical Publication CHIS-05-01* (pp. 35–42). Institute for Wildlife Studies, Arcata.
- Leavitt, D. H., Marion, A. B., Hollingsworth, B. D., & Reeder, T. W. (2017). Multilocus phylogeny of alligator lizards (*Elgaria*, Anguinae): testing mtDNA introgression as the source of discordant molecular phylogenetic hypotheses. *Molecular Phylogenetics and Evolution*, *110*, 104–121.
- Mahoney, M. J., Parks, D. S. M., & Fellers, G. M. (2003). *Uta stansburiana* and *Elgaria multicarinata* on the California Channel Islands: natural dispersal or artificial introduction? *Journal of Herpetology*, *37*, 586–591.
- Rick, T. C., Erlandson, J. M., Vellanoweth, R. L., Braje, T. J., Collins, P. W., Guthrie, D. A., & Stafford, T. W. (2009). Origins and antiquity of the island fox (*Urocyon littoralis*) on California's Channel Islands. *Quaternary Research*, *71*, 93–98.