CALIFORNIA STATE UNIVERSITY, NORTHRIDGE

Genetic Consequences of Landscape Heterogeneity and Isolation for an Island-Endemic Lizard

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For the degree of Master of Science in Biology

By

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Table of Contents

Signature Page…………………………………………………………………………………….ii

Acknowledgements……………………………………………………………………….……...iii

List of Tables …………………………………………………………………………………….v

List of Figures…………………………………………………………………………………….vi

Abstract ……………………………………………………………………………………….....vii

Introduction ………………………………………………………………………………………1

Methods ……………………………………………………………………………………….….4

Results …………………………………………………….……………………………………..10

Discussion …………………………………………………………………………………….....13

Literature Cited ………………………………………………………………………………… 20

Appendix A: Tables…………………………………………………………………………….. 28

Appendix B: Figures …………………………………………………………………………… 36

List of Tables

Table 1….………………………………………………………………………………28

Table 2….………………………………………………………………………………29

Table 3………………………………………………………………………………….31

Table 4………………………………………………………………………………….31

Table 5………………………………………………………………………………….31

Table 6………………………………………………………………………………….32

Table 7………………………………………………………………………………….34

Table 8………………………………………………………………………………….35

List of Figures

Figure 1….………………………………………………………………………………36

Figure 2….………………………………………………………………………………36

Figure 3….………………………………………………………………………………37

Figure 4….………………………………………………………………………………38

Figure 5….………………………………………………………………………………39

Figure 6….………………………………………………………………………………40

Abstract  
Genetic Consequences of Landscape Heterogeneity and Isolation for an Island Endemic Lizard

By

Rachel Esther Gutner

Master of Science in Biology

Landscape genetics uses population genetics and landscape ecology to make inferences about microevolutionary forces affecting species and the way they interact with their environment. The Island Fence Lizard (*Sceloporus occidentalis becki)* exhibits deep divergence from its mainland cousin, *S. occidentalis*, suggesting that the subspecies *S. o. becki* is likely an endemic taxon, *S. becki*. The Northern Channel Islands (Anacapa, San Miguel, Santa Rosa, Santa Cruz Islands) lie 20-44 km off the southern coast of California. These four Northern Islands were connected as a single island, ‘Santarosae,’ as recently as 10-12 ka, allowing historical overland dispersal among areas that are now present-day islands. Islands differ in solar radiation, cloud cover, and substrate type, contributing towards their variable climate. Our goals were to quantify genetic diversity and connectivity within and among islands and understand how the complex geologic history and landscape composition of its habitat has impacted this organism’s natural history and future. We used RAD sequencing to create a SNP dataset. Population genetic analyses revealed strong genetic structure and low levels of admixture among islands with varying levels of diversity on each island. We used linear mixed effects models with individual-based genetic data to test each landscape variable in a spatial graph-theoretic framework. Landscape genetics analyses emphasized the role of climate in driving population structure and dynamics. Combined, our analyses show that the island endemic has been deeply influenced by geologic and landscape changes, as well as human habitation.

**Introduction**

Compared to the mainland, island populations are often small and isolated, with low levels of genetic diversity, which can increase the risk of extinction (Carson and Templeton, 1984; Lynch 1995; Frankham 1998; Frankham 2002). Island biota are shaped by their geologic history as well as their abiotic and biotic interactions. Ectotherms are particularly good study organisms for landscape genetics because they rely on bioclimatic conditions for physiological processes, predator avoidance, competition, and dispersal (Christian and Tracy, 1981; Pafilis et al. 2006; Amarasekara and Coutinho, 2014; Andriuzzi, 2025). Naturally, these organisms will respond to changes in temperature, substrate, and vegetation.

The Channel Islands of California are an archipelago of eight near-shore islands, consisting of four northern and four southern islands (Schoenherr et al. 1999). The Northern Islands (Anacapa (Anyapakh), Santa Cruz (Limuw), Santa Rosa (Wi’ma), and San Miguel (Tuqan)) lie 20-44 km off the coast of California (Schoenherr et al. 1999). The northern Channel Islands of California have a complex geologic history, with repeated submersions and immersions into the Pacific Ocean (Schoenherr et al. 1999; Muhs et al. 2014). These four Northern Islands were connected as a single island, ‘Santarosae,’ as recently as 10-12 ka, allowing historical overland dispersal among areas that are now present-day islands (Reeder-Myers et al, 2015). Additionally, the islands have a legacy of human habitation dating back to at least 13,000 years (human bones on Santa Rosa Island; Johnson et al. 2007); Europeans visited and inhabited these islands on and off from the 1500s to the 1800s (Braje et al. 2021), followed by the arrival of ranchers in the 1800s (Braje et al. 2021). Biota of the Northern Channel Islands have undoubtedly been influenced by this human habitation, proximity to the mainland, historical island size and topography, and connectivity.

The Island Fence Lizard (*S. o. becki)* exhibits deep divergence from its mainland cousin, *S. occidentalis*, (Salerno et al. 2023) suggesting that the endemic subspecies *S. o. becki* (Grinnell and Camp 1917) should be elevated to its own species, *S. becki* (Van Denburgh 1905; Bell 2001; Salerno et al. 2023). Morphological work suggests significant phenotypic divergence (Pauly et al. unpublished); therefore, we treat it here as a distinct species (*S. becki*). The Island Fence Lizard inhabits three out of the four Northern Channel Islands of California: Santa Cruz Island (Limuw), Santa Rosa Island (Wi’ma), and San Miguel Island (Tuqan). This severely range-restricted organism (total habitable area: ca. 502 km2) recently experienced a bottleneck and has a low effective population size, likely making it a taxon of conservation concern (Trumbo et al. 2021). Islands vary in air temperature, surface temperature, precipitation, topography, and size. Previous work showed that temperature variables are greatest drivers of connectivity for *S. becki* on Santa Cruz Island, (Trumbo et al. 2021). However, no population genetic or landscape genetic studies have been conducted for populations on the other two islands that they inhabit. Here, we quantify neutral genetic diversity metrics and estimate the impact of landscape factors on diversity and population structure across the range of the island endemic lizard, *Sceloporus becki*.

Landscape genetics uses population genetics and landscape ecology to make inferences about microevolutionary forces affecting species and the way they interact with their environment (Holdregger and Wagner, 2006). Functional landscape connectivity is the degree to which an organism can move through the landscape (Calabrese and Fagan, 2004). If connectivity is high relative to habitat size, then there may be no population structure (Galligan et al. 2012). If connectivity is low and dispersal distances are small relative to habitat size, we expect a pattern of isolation by distance, where genetic distance follows patterns of geographic distance, across islands (Langin et al. 2015). In a heterogenous landscape, we expect associations between genetic connectivity and environmental variation (Hamilton et al. 2006). Though data on *S. becki* are limited, its closest relative, *S. occidentalis*, has been well-studied in aspects of dispersal, thermal biology, behavior, and disease ecology (Adolph, 1990; Sheldahl and Martins, 2000; Massot et al. 2003; Swei et al. 2011). Closely related sceloporine lizards have a narrow range of preferred body temperatures (*Sceloporus occidentalis* seasonal mean field body temperatures of 30.4-35.9˚C, McGinnis, 1966; *Uta stansburiana* 35-38˚C. Waldschmidt and Tracy, 1983; *Sceloporus undulatus* 32-34˚C, Angiletta et al. 2000, Angiletta 2001) therefore, we expect average air and surface temperatures to impact gene flow between populations of *S. becki*. The annual mean air temperature on the Channel Islands ranges from 11°C in cooler months to 21°C in warmer months. Each island varies in solar radiation, cloud cover, and substrate type, contributing to variable ground temperatures. Therefore, we expect variables related to temperature to heavily impact patterns of dispersal for *S. becki*.

Reduced-representation genomic sequencing, like the RADseq methods implemented in this study, are increasingly used to examine the demographic history for non-model organisms. We ask **(1)** are these recently connected island populations genetically differentiated, **(2)** how do effective population sizes vary by island, and **(3)** what landscape factors are mediating connectivity within islands?

**Methods**

We collected lizards via lasso or hand on the three Channel Islands where *S. becki* occurs (Figure 1). Our sampling strategy prioritized individual sampling across the breadth of environments that *S. becki* may inhabit (e.g., across potential barriers such as canyons, rivers, and mountains) as recommended for landscape genetic studies (Storfer et al. 2018). Along with nonlethal tissue sampling (tail tips), we also collected 10 voucher specimens from each island. Tissues were stored in cryovials in 95% EtOH. Non-vouchered lizards were released at the site of capture and vouchers and tissues were deposited in the herpetology collection at the Museum of Natural History, Los Angeles County (LACM XXXX–XXXX). At each capture site, we recorded the latitude and longitude with a handheld GPS device (WGS 84 datum; ± 14 m or less; Garmin inReach Explorer+, Olathe, Kansas, United States).

We extracted nuclear DNA from lizard tissues using a Qiagen DNeasy Blood & Tissue Kit (Qiagen, Hilden, Germany). We used RAD sequencing (Baird et al. 2008) to create a SNP dataset following the BestRAD library preparation protocol (Ali et al. 2016). First, we digested 10 ng/µl of genomic DNA from each tissue sample with the restriction enzyme Sbf1. Then, we ligated unique BestRAD barcodes onto each sample, pooled each set of 96 samples into a single library, sonicated the library (Covaris M220, Woburn, Massachusetts, United States) to shear the sequences to 400–600 bp, and ligated sequencing adaptors. Last, we used PCR to amplify sequences and AMPure XP Beads (Beckman Coulter Life Sciences, Indianapolis, Indiana, United States) to clean the amplified product of any impurities and very small fragments (e.g., unincorporated dNTPs, primers, salts, etc.). Libraries were sent to Admera Health (South Plainfield, New Jersey, United States) and pooled in equimolar concentrations for sequencing on a single lane of Illumina NovaSeq X. We included technical replicates from two localities (SCI n=2, SRI n=2) across libraries to account for library effects (Miermans 2015).

*Bioinformatics*

We used Stacks v. 2.66 (Catchen et al. 2013) to demultiplex and filter raw sequence reads (i.e., remove RAD barcodes, bases below a minimum mapping quality of 10). We aligned sequences to a reference genome of the sister taxon (*S. occidentalis*; Bishop et al. 2023) using BWA-MEM (Li and Durbin 2010). We made a catalog using gstakcs, then called SNP variants using the *populations* command in Stacks v. 2.66 (Catchen et al. 2013) and filtered them with VCFtools v. 0.1.16 (Danecek et al. 2011) to remove loci with poor depth, individuals with high missingness, and linked SNPs. Because we expect each island be genetically distinct, we one dataset and separated each population for intraisland analyses, following recommendations from Hemstrom et al. (2024). We minimized errors resulting from library preparation following recommendations from O’ Leary et al. (2018). Specifically, we increased confidence in genotypes and minimized allele dropout by restricting minimum read depth (minDP) per genotype to 4 and maximum read depth per genotype (maxDP) to 120. We removed loci with less than 90% completeness and individuals with more than 50% missing data. Loci within a certain number of base pairs of each other are often physically linked (Miyashita and Langley, 1988; Hohenlohe et al. 2012), so we thinned SNPs to retain only one SNP from each contig using VCFtools v. 0.1.16 (Danecek et al. 2011). We filtered loci significantly out of Hardy-Weinberg equilibrium for each population using dartR (Gruber et al. 2018). Our final dataset was converted to a genepop file (dartR; Gruber et al. 2018) and into a genetic Euclidean distance matrix for downstream analyses using dist.genpop (adegenet; Jombart 2008).

*Population Genetic Analyses*

We estimated standard metrics of population genetic diversity using the function “gl.report.heterozygosity” in dartR (Gruber et al. 2018). To estimate initial population structure and clustering, we created a PCA for each island using dartR (Gruber et al. 2018; Fig. 2). Then, we converted the variant call format (VCF) files to a plink file using *populations* from Stacks v. 2.66 (Catchen et al. 2013). Next, we used Admixture v. 1.3.0 (Alexander et al. 2020) to infer the number of genetic demes and their distributions within and across islands. We visualized assignment probabilities with R v 4.2.3 (R Core Team, 2023).

To estimate contemporary Ne, we used NeEstimator v. 2.1 (Do et al. 2014) with the LD method, implemented in the package snpR (Hemstrom and Jones 2023). Because we had sample sizes ranging from n=27 to 144, we selected Ne at two different *P*crit values. For San Miguel Island (n=27), we used *P*crit = 0.03 to exclude only alleles that occur in a single copy, as recommended by Do and Waples (2010). Our other two populations (SCI, n=144 and SRI, n=103), we used *P*crit = 0.02 to exclude alleles that occur in a single copy (Do and Waples, 2014). We measured patterns of isolation by distance using proportion of shared alleles, calculated from the inverse of Hamming distance using the function poppr::bitwise.dist (Kamvar et al. 2014) and geographic Euclidean distances.

*Landscape Genetic Analyses*

For our landscape genetics analyses, we selected landscape variables that we considered to be ecologically relevant to *S. becki*, and its’ nearest cousin*, S. occidentalis* (Table 2). Landscape data came from the 2024 National Land Cover Database (USGS, 2024), Shuttle Radar Topography Mission (SRTM, Farr et al., 2007) digital elevation model (USGS EROS Data Center), and WorldClim climate data (Fick and Hijmans, 2017; data resolutions in Table 2).

We performed landscape genetic analyses with five landscape predictor variables and three bioclimatic variables per island, as well as a null topographic distance model corrected for topographic complexity (topoDist; Wang, 2019). To select bioclimatic variables, we used a PCA and selected the variables most strongly correlated with the top three PC axes (79.3% of variance explained), as they should explain climatic variance for our defined extent (Lanes et al. 2018, Carvalho et al. 2020). To examine the factors mediating functional connectivity, we selected landscape variables that likely impact the natural history and ecology of *S. becki* at several scales. For each island, we tested three bioclimatic variables, topographic distance, percent shrub cover, percent tree canopy cover, percent bare ground, and heat load index, which takes elevation, slope, and aspect into account as a proxy for ground temperatures (Table 2).

We resampled all rasters to achieve a 30 m resolution. We calculated heat load index (McCune and Keon, 2002) from the digital elevation model (USGS EROS Data Center) using the spatialEco version 1.3-6 package in R version 3.6.2 (Evans and Murphy, 2021). For all vegetation layers, we used data from the year 2009, which exhibits the least deviation from average annual rainfall in Ventura County, the closest continental county (35-year average rainfall = 14.67 in/yr; 2009 average = 11.78 in/yr, Ventura County Public Works Agency – Watershed Protection Hydrologic Data Server).

We used linear mixed effects models with individual-based genetic data as the response variable to test each landscape variable in a spatial graph-theoretic gravity model framework (Murphy et al. 2010) using the R package GeNetIt 0.1-6 (Evans and Murphy, 2023). Gravity models use points (individual lizard tissue samples) and edges (straight lines between points) to form a spatial interaction network. Edges do not represent movement paths, but instead sample the landscape conditions between points and are predictors for the genetic response variable (Murphy et al. 2010). We treated landscape variables and topographic distance as fixed effects and sites as random effects.

To prepare the rasters, we created a covariate file using selected layers (Table 5) and used the R package terra (Hijmans, 2025) to reproject each raster from WGS84 to UTM and clipped them to the same extent, then stacked them. Then, we used our full genetic distance matrices to create a fully saturated graph for each island population, with each individual as a sampling site. We calculated statistical moments (mean, minimum, maximum, variance, median) for all environmental variables using base R functions (R Core Team, 2023) and added them to our graph. Between-site variables were represented as median values of the edges. We selected the median value because it is more robust to skew and outliers. To evaluate collinearity, we created a data frame of all edge statistics, then log-transformed them and calculated correlations, but none met the collinearity threshold (0.8).

We generated between 39 and 55 candidate models for each island (SCI=39, SRI=54, SMI=55 models) using all possible variables and compared all candidate models using ML methods. We comparedAIC scores to get the best-fit model. Then, we fit our final models and calculated effect sizes. We used restricted maximum likelihood (REML) to calculate parameter estimates (Zuur et al. 2009) and confidence intervals under the best-fit model (Lakens, 2013). We scaled all variables, so effect sizes can be directly compared, and effect sizes indicate directionality of each variable in the final model.

We predict that on Santa Cruz Island gene flow will be highest a) through areas with high heat load index, b) high densities of shrub, c) moderate percent tree canopy cover, and d) medium percent bare ground. On Santa Rosa Island, we predict that the greatest gene flow will occur a a) through areas with high heat load index, b) high densities of shrub habitat, c) low to moderate percent tree canopy cover, and d) medium percent bare ground. On San Miguel Island, we predict that gene flow will occur most a) through areas with high heat load index, b) moderate densities of shrub habitat, c) low percent tree canopy cover, and d) medium percent bare ground.

**Results**

We sequenced a total number of 353 *S. becki*. Our island sampling was as follows: Santa Cruz (SCI; *n*=181), Santa Rosa (SRI; *n*=130), and San Miguel (SMI; *n* =32) Islands from 2013–2024 (Fig. 1). BestRAD libraries for the 353 individual lizards in our study generated 4,198,889 raw loci. We removed loci with less than 90% completeness, as well as 73 individuals with high missing data (>50%). After filtering loci out of Hardy-Weinberg Equilibrium by population, we were left with 31,925 loci and 274 individuals (SCI, *n*=143; SRI, *n*=105; SMI, *n*=26 (Table 1)).

*Population Assignment*

In PC Space, samples were clustered by island with no overlap. PC1 explained 20.5% of variation and PC2 explains 4.3% of variation (Figure 1). Admixture analyses reveal that signatures of genetic admixture between Santa Cruz and Santa Rosa Islands, as well as Santa Rosa and San Miguel Islands (Figure 2). Cross validation error results indicate that the most likely number of populations is *K=4*. When four ancestral populations were assumed, each island (Santa Cruz Island, Santa Rosa Island, and San Miguel) comprised individual clusters, with substructure emerging on Santa Cruz. At *K = 5*, substructure also emerges on Santa Rosa Island along a northwest and southeast axis. Some western individuals on Santa Cruz Island share ancestry from individuals on Santa Rosa Island (SOC0124-0128, SOC0167-0177) and some western individuals on Santa Rosa Island contained ancestry from San Miguel Island (LACM-TC7501-7505, LACM-TC7507) and Santa Cruz Island. At *K =6*, substructure on Santa Cruz Island is emphasized (Figure 3), along a distance gradient, but patterns of structure on the other two islands remain the same. Using a subset with only Santa Cruz Island data, we found support for *K = 2* (cross validation error = 0.304; Figure 3) and similar estimates of support for *K = 3* (cross validation error = 0.307; Figure 3). In both cases, substructure on Santa Cruz follows an east-west axis. In summary, each island is a distinct population, affirming results found with mtDNA (Salerno et al. 2021).

*Population Genetic Metrics*

Heterozygosity estimates can be used as a general indicator of genetic diversity. We found that expected heterozygosity (HE) and observed heterozygosity (HO) highest on Santa Cruz Island, followed by Santa Rosa Island, then by San Miguel (Table 3). However, the inbreeding statistic, FIS, was highest on Santa Rosa Island, followed by Santa Cruz, then by San Miguel (Table 3). In Table 3, we see the highest genetic differentiation between the two most distant islands: Santa Cruz and San Miguel (FST = 0.371). We find that Santa Cruz and Santa Rosa Islands have an FST = 0.207, indicating high to moderate genetic differentiation. Santa Rosa and San Miguel Islands have a similar level of differentiation with an FST=0.209 (Table 3). Broadly, genetic differentiation between each island population is high and heterozygosity is low.

All populations exhibit statistically significant relationships between proportion of shared alleles (Dps) and geographic distance. San Miguel Island is the only population that does not have a negative relationship between Dps and geographic distance (y=0.0000002). Effective population sizes (Ne) are low on all islands. Estimates were separated by subgroups on Santa Cruz Island to account for the Wahlund effect and are low within each subgroup (Ne east=176.2, Ne west=151.2; Table 4). Estimates of Ne on Santa Rosa Island and San Miguel Island are low (Ne=283.3, Ne=455.6 respectively). While finite jackknife confidence intervals were estimated for both Santa Cruz and Santa Rosa Islands, the upper limit of the confidence interval for San Miguel Island is considered infinite (Table 4).

*Landscape Genetics*

We tested the same landscape variables for each island to test whether the landscape variables that mediate gene flow for *S. becki* are generally similar, however, abiotic variables varied by island (Table 5). On Santa Cruz Island, we find that the best fit model is the global model, which includes all respective variables for this island. Specifically, we foundtree canopy cover, heat load index, temperature annual range, topography, and length all significantly (p < 0.05) impact functional connectivity on Santa Cruz Island (Table 6). Variables included in the best fit model which did not significantly affect connectivity were percent cover bare ground, annual mean temperature, and annual precipitation.On Santa Rosa Island, we found that the best fit model was composed of three abiotic and one biotic variable: annual mean temperature, temperature during the coldest quarter, length, and percent bare ground cover. All these variables were statistically significant in predicting functional connectivity (Table 7).On San Miguel Island, we found that the best fit model was a global model, including all respective variables. We find that percent bare ground over, percent tree canopy cover, mean temperature of the warmest quarter, annual precipitation, temperature annual range, topography, and length all significantly impact connectivity. However, percent shrub cover and heat load index do not significantly impact connectivity (Table 8).

**Discussion**

We found that each island is genetically distinct, with low levels of admixture among neighboring islands and strong patterns of isolation by distance within islands. Santa Cruz Island contains two subgroups, with a signature of isolation by distance, and the remaining two islands contain a single deme each. Santa Cruz Island populations have the highest heterozygosity, and Santa Rosa has the highest level of inbreeding (FIS). San Miguel exhibits low heterozygosity and low FIS. Each island is highly differentiated from each other, with San Miguel and Santa Cruz being the most different from each other. Landscape genetic analyses revealed that each island population is influenced differently by the landscape, with each best fit model containing different predictors. Temperature variables were important on all islands. However, no significant environmental variables were shared among island populations, emphasizing that lizard populations should be considered distinct on each island for management. We discuss these population and landscape genetic results with respect to near-shore island evolution and conservation.

*Near-shore Island Evolution*

Island biogeography predicts that the largest and closest islands to continents should have the largest populations with the greatest richness (Simberloff, 1976; Frankham, 1996; Montgomery et al. 2000), often with highest levels of diversity and highest Ne (Vellend, 2005). For example, the island fox (*Urocyon littoralis*) has the lowest heterozygosity and Ne on the smallest island it inhabits, San Miguel (Robinson et al. 2016). In many archipelagos, this pattern is observed across taxa (Simberloff, 1976; Cole et al. 2012; Larrue, 2024). We expected Santa Cruz, the largest and closest island in this archipelago to continental California, to have highest heterozygosity, followed by Santa Rosa and then San Miguel. This is partially true in our study: Santa Cruz has the highest genetic diversity and two genetic groups, Santa Rosa is intermediate in heterozygosity, and San Miguel has the lowest heterozygosity, but effective population sizes deviate from expectations.

*Population Genetics*

Population genetic metrics indicate that *Sceloporus becki* on all islands have a very low level of heterozygosity, low effective population sizes, and are highly differentiated between each island. Our results are consistent with the strong pattern of isolation by distance (IBD; Figure 6) observed previously for *S. becki* on Santa Cruz Island using 15 microsatellites (Trumbo et al. 2021). In fact, the patterns of IBD meet our expectations for all islands given their relative sizes and shapes of each island, as well as the distribution of lizards. For example, there is a statistically significant relationship between Dps and geographic distance for all populations. On Santa Cruz Island, there is a minor, but significant, relationship between relatedness and distance following an east-west axis through the central valley, which is bound by two steep ridges on the north and south sides. On Santa Rosa, we found very shallow negative slope (Figure 6), likely due to the radial canyon structure which may facilitate connectivity and dispersal. Additionally, we find two smaller groups of individuals falling away from Santa Rosa that have high proportions of shared alleles across 25 km. The number of groups which fall out in our IBD plots mirror the same groups which fall out of our admixture plots at *K = 5*, explained by a northwest-southeast break in ancestry within Santa Rosa. We expect that this break is due to climatic relationships, as the northwest side of Santa Rosa is often more shrouded in fog (Rastogi et al. 2016). Lizards on San Miguel have a small, significant slope that may be reflective of distributions – lizards are primarily concentrated on the eastern half of the island (ca. 18 km).

One of our questions addressed the extent of admixture between populations on Santa Rosa and Santa Cruz Island to better understand the paraphyly revealed with mtDNA (Salerno et al. 2023). Of the four islands which made up ‘Santarosae’, these two islands were most recently connected. The genetic legacy of historical gene flow between Santa Rosa and Santa Cruz does not appear to be forgotten, as indicated by ancestry plots (Figure 3). Admixture results show that some individuals have mixed ancestry, primarily between Santa Rosa and Santa Cruz Islands, which were connected more recently than Miguel to Santa Rosa.

Prior field expeditions led us to believe that Santa Cruz Island, with such dense populations in the central valley, would have high genetic diversity estimates, low inbreeding, and high effective population sizes. However, it seems that although *S. becki* are most concentrated in the central valley of the island, the population density is scattered elsewhere (Figure 1). This could be due to a variety of the following reasons: cooccurrence with another common basking lizard (*Uta stansburiana*, Baird and Gerard, 1852), who inhabits similar habitats on the mainland with *S. becki*’s mainland relative, *S. occidentalis* (David and Verbeek, 1972), improper climatic and abiotic conditions, predation, or inadequate habitat. *S. becki* on Santa Rosa and San Miguel face no competition from lizards with a similar life history and have fewer predators, however, environmental conditions vary on each island.

*Landscape Connectivity*

The patterns of genetic diversity and differentiation observed for *S. becki* requires an understanding of the landscape history of this environment. Over the last 20,000 years these islands have lost more than 75% of their landmass, converting the super-island “Santarosae” into an archipelago of four smaller islands. With this, there were accompanying changes in temperature and precipitation, and thus, altered vegetation regimes. If *S. becki* has the same habitat preferences for woody trees and rocky outcrops as mainland *S. occidentalis*, we expect that increased temperature after the last glacial maximum reduced habitat due to loss of land and loss of woody vegetation on all islands. However, islands vary in landscape and climate, which may have created different patterns of habitat loss and population dynamics across the archipelago.

Previous work established that the strongest predictor of gene flow on Santa Cruz Island is intermediate values of maximum temperature during the warmest month (Trumbo et al. 2021). We tested this variable and found it to be highly collinear with another bioclimatic variable (Temperature Annual Range) and so we dropped it from analysis, as we considered Temperature Annual Range to be more informative, and it was an important predictor in our model. Personal observations led us to expect that *S. becki* may be more oak associated on Santa Cruz Island, where oaks and other woody vegetation are abundant, than on Santa Rosa or San Miguel Islands. Indeed, we found that percent tree canopy cover is a significant predictor of functional connectivity on Santa Cruz Island for *S. becki*. The only other island where percent tree canopy cover is significant is San Miguel Island, where percent tree canopy cover hinders connectivity. Indeed, observations from our field work on San Miguel suggest high associations with bare ground (basking data, G. Pauly et al. unpublished).

On Santa Rosa, we encountered *S. becki* on nearly every terrestrial surface, including oak trees, upper intertidal rocks, and grasslands. We uncovered relatively high genetic diversity with weak population genetic structure (*K = 1*). Our landscape genetics analyses revealed that bare ground impedes connectivity. Climatic predictors were all significant: annual mean temperature, mean temperature of the coldest quarter, and annual temperature range all impede connectivity. We also see a strong, positive relationship between topographic distance and genetic distance, indicating a pattern of isolation-by-distance. We expected percent tree canopy cover to be an important predictor on Santa Rosa Island because we have observed S. becki on downed branches and in leaf litter. However, as part of our data collection, we frequently describe vegetation regimes associated with *S. becki*, and on Santa Rosa Island we have primarily found associations with *Baccharis*, *Eriogonum*, *Coreopsis*, and *Artemisia*. We suggest that lizards on Santa Rosa Island may be using small forms of woody vegetation than trees to disperse.

On San Miguel, distributions are restricted, and we believe this is mostly due to lack of suitable habitat, such as relatively cooler temperatures and other bioclimatic variables (i.e., fog and cloud cover). Our dataset includes the western-most *S. becki* ever encountered, which was basking on a northeast-facing rock. On San Miguel, we often find these lizards basking on the ground on organic-matter rich soils, presumably because they hold more heat than the whitish chalky rock which makes up most of the island. The most strongly supported model included only climatic variables: mean temperature of the warmest quarter, annual precipitation, and temperature annual range. Our results indicate that a higher mean temperature of the warmest quarter and a higher annual precipitation have a direct, positive relationship. Temperature annual range is negatively related to genetic distance, indicating that temperature annual range facilitates connectivity.

For ectotherms, genetic connectivity is closely tied to climatic patterns. On all three islands, lizards must rely on woody vegetation, rocks, and cracks in the ground as retreat sites from predators, thus tree canopy and bare ground should lead to the same genetic patterns on each island. Specifically, Santa Rosa and Santa Cruz populations experience the same direct relationship with bare ground and inverse relationship with tree canopy cover. However, the density and distribution of trees varies greatly across the two islands.

Notably, each island has a different set of bioclimatic variables which influence patterns of connectivity for *S. becki*. Though not measured here, the presence and duration of cloud cover and fog varies among islands and is expected to influence temperature and vegetation patterns on each island. San Miguel Island experiences the greatest amount of cloud cover and with wind sweeping the western half (Rastogi et al. 2016), it is no surprise that the range of *S. becki* does not extend westward from the center of the island. On Santa Rosa, the north side of the island is most often cloaked in clouds (Rastogi et al. 2016), reflected by the temperature annual range data for this island. The south side of Santa Rosa is warmer, due in part to the warm Davidson Current which runs from the south against Santa Rosa Island. Finally, Santa Cruz Island exhibits complex topography, an interior valley, and multiple open areas on the west and east end. Cloud cover and fog banks on Santa Cruz are most prevalent on the western side of the island (Rastogi et al. 2016).

On the continent, *S. occidentalis* is an opportunistic generalist, so it is unsurprising that *S. becki* can exploit the diverse substrates available on each island. We found that bare ground is abundant on San Miguel Island, intermediate on Santa Rosa Island, and minimal on Santa Cruz Island (calculated statistical moments from analyses).Similarly, trees are widely distributed on Santa Cruz Island, but nearly absent on San Miguel Island. On each island, the legacy of ranching history remains – there is a massive amount of the landscape covered by invasive grasses on all islands, with native vegetation destroyed by cattle and sheep, and woody vegetation recruitment disrupted by feral pigs and deer, with the last deer being removed from the islands in 2011. Given these conditions, *S. becki* may be responding to altered climate and vegetation regimes, as well as island size, differently.

*Conservation Implications*

Effective population sizes determine the rate at which a population loses genetic diversity due to drift, which is amplified in small, isolated populations. Minimum Ne sizes for population maintenance of genetic diversity are Ne = 500 for long term maintenance and minimum Ne for short-term population maintenance is 50 (Franklin, 1980). Estimating Ne can be an important tool in the assessment of vulnerable populations (Mace and Lande, 1991). With effective population sizes all below 500 (Table 5), it is clear this taxon should be considered for conservation priority via monitoring and be managed separately on each island.

As temperatures continue to rise with our changing climate, habitable area for *S. becki* will continue to decrease, making landscape genetic analyses important for conservation. Because we have observed lizards on Santa Rosa Island using small woody vegetation as patches among seas of invasive grasses, we believe that efforts to promote shrubs may benefit *S. becki*.

Effective population sizes of *S. becki* on these islands is generally low, similar to other island endemics. For example, the Island Fox, *Urocyon littoralis* (Baird, 1857), using the LD method, has an Ne size of 64 and 133 individuals on San Nicolas and San Miguel Islands, respectively, during more than 93% of the last 500 generations (Robinson et al. 2016). Similarly, the Island Night Lizard, *Xantusia riversiana*, is estimated to have an Ne of 170.6 individuals (O’Donnell et al. 2018). The Island Scrub Jay, *Aphelocoma insularis*, found only on Santa Cruz Island, has a long-term Ne of 1603 individuals (Delaney and Wayne, 2005). These three endemic species have long been recognized as species of conservation concern, and it is now clear the Island Fence Lizard is also an endemic and merits concern, as well.

*Conclusion*

This is one endemic species that occurs on three islands and is highly differentiated from each other. Based on genetic differentiation, landscape genetic results, personal observations and other datasets that highlight differences in basking sites and morphologies associated with those differences, these populations should be managed as distinct units. This study has advanced our understanding of the patterns of genetic diversity within and among populations of the Island Fence Lizard, and the landscape features that facilitate connectivity. Some questions regarding their persistence and distribution remains. Specifically, which species interactions (competition, predation) drive low densities on Santa Cruz and high densities on Santa Rosa? How do populations on San Miguel persist given habitat and climate unsuitability? Research in thermal physiology, local adaptation and behavior is paramount to its conservation and should be considered in future studies of this island endemic.

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**Appendix A: Tables**

**Table 1.** Single nucleotide polymorphisms (SNPs) recovered for *S. becki*, organized by dataset, with details of filtering parameters and number of individuals retained.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Dataset | SNP filtering | Individual filtering | Individuals retained | # SNPs recovered |
| (1) Santa Cruz Island + Santa Rosa Island + San Miguel Island | --minDP 4  --maxDP 120  --mac 3  --max-missing 90  --thin 100 | Missing <10% | 274 | 31925 |

**Table 2.** Landscape variables used for testing linear mixed effects models, predicted effects, and brief ecological justifications for the effect on functional connectivity *of Sceloporus becki*. Landscape processes are independent hypotheses and are tested in individual models. Data sources are open source, and the corresponding resolution of each variable is included.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Variable** | **Data source** | **Resolution** | **Populations** | **Prediction** | **Ecological Justification** |
| Topography | DEM (SRTM) | 30m | Santa Cruz Island | + | *Sceloporus* lizards are large-bodied and likely to use topographic complexity to their advantage when dispersing. This layer was only used on Santa Cruz Island because there are two mountain ranges with a large valley, so it is exceedingly complex for these islands. |
| Bare ground | NLCD 2009 | 30 m | Santa Cruz Island  Santa Rosa Island  San Miguel Island | -  -  + | *Sceloporus* lizards prefer vegetation for basking in hotter climates (David and Verbeek, 1972). However, on San Miguel Island, the climate is much cooler, and there are zero trees. |
| Tree | NLCD 2009 | 30 m | Santa Cruz Island  Santa Rosa Island  San Miguel Island | +  -  - | *Sceloporus* lizards prefer vegetation for basking in hotter climates (David and Verbeek, 1972). Tree canopy is reduced on Santa Rosa and nil on San Miguel Island. |
| Shrub | NLCD 2009 | 30 m | Santa Cruz Island  Santa Rosa Island  San Miguel Island | +  +  + | *Sceloporus* lizards prefer vegetation for basking in hotter climates (David and Verbeek, 1972). Small vegetation is abundant and may be relied on by Sceloporus lizards as climate refuge or basking sites. |
| Annual Mean Temperature | WorldClim  1970-2000 | 1 km | Santa Cruz Island  Santa Rosa Island | +  + | Ectotherms require a range of temperatures for physiological and reproductive processes. |
| Mean Temperature of Coldest Quarter | WorldClim  1970-2000 | 1 km | Santa Rosa Island | - | Ectotherm dispersal is heavily impacted by cool temperatures. |
| Mean Temperature of Warmest Quarter | WorldClim  1970-2000 | 1 km | San Miguel Island | + | Ectotherm dispersal is heavily impacted by warm temperatures. |
| Annual Precipitation | WorldClim  1970-2000 | 1 km | Santa Cruz Island  San Miguel Island | +  + | Sceloporus lizards often rely on vegetation, and therefore water. |
| Temperature Annual Range | WorldClim  1970-2000 | 1 km | Santa Cruz Island  Santa Rosa Island  San Miguel Island | +  +  + | Extreme temperatures restrict gene flow (Adolph 1990; Kearney et al. 2009; Buckley et al. 2010; Sinervo 2010; Dominguez-Guerrero et al. 2019), making the full range informative. |
| Heat load index | DEM (SRTM) | 30 m | Santa Cruz Island  Santa Rosa Island  San Miguel Island | +  +  + | Ectotherms require warmth to perform. |
| Length |  |  | Santa Cruz Island  Santa Rosa Island  San Miguel Island | -  -  - | Isolation by distance. |

**Table 3.** Expected heterozygosity (He), observed heterozygosity (Ho), and inbreeding statistic (FIS) estimates for *S. becki* on each island.

|  |  |  |  |
| --- | --- | --- | --- |
|  | He | Ho | FIS |
| Santa Cruz Island | 0.104 | 0.098 | 0.059 |
| Santa Rosa Island | 0.084 | 0.077 | 0.085 |
| San Miguel Island | 0.059 | 0.059 | 0.017 |

**Table 4.** Pairwise differentiation (FST) between each population of *S. becki*, delineated by island.

|  |  |  |
| --- | --- | --- |
|  | Santa Cruz Island | Santa Rosa Island |
| Santa Cruz Island | - | - |
| Santa Rosa Island | 0.207 | - |
| San Miguel Island | 0.371 | 0.209 |

**Table 5.** Effective population sizes for *S. becki* on each island.

|  |  |  |
| --- | --- | --- |
|  | Ne | 95% CI (Jackknife) |
| Santa Cruz Island (SCI)  East  West | 197.3  158.9 | 149.6-282.1  90.2-500 |
| Santa Rosa Island (SRI) | 283.3 | 212-416 |
| San Miguel Island (SMI) | 455.6 | 104.3-Infinite |

**Table 6.** Parameter estimates based on Cohen's D for variables included in the final model for *S. becki* on Santa Cruz Island. Effect sizes with confidence intervals that span zero + are considered insignificant. Effect size direction is the same direction as in “Cohen’s d” column for each variable and can be interpreted directly.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Variable** | **t-value** | **df** | **Cohen’s d** | **p-value** | **Lower CI** | **Upper CI** | **Interpretation** |
| Bare ground | 1.4865 | 11906 | 0.0272 | 0.1371 | 0.0018 | 0.0526 | Percent bare ground cover has no significant impact on connectivity. |
| Tree canopy cover | -3.9689 | 11906 | -0.0727 | 0.0000 | -0.0981 | -0.0473 | Tree canopy cover facilitates connectivity. |
| Heat load index | -2.4335 | 11906 | -0.0446 | 0.0149 | -0.0700 | -0.0191 | Heat load index facilitates connectivity. |
| Annual Mean Temperature | -1.3806 | 11906 | -0.0253 | 0.1674 | -0.0507 | 0.0001 | Annual Mean Temperature has no significant impact on connectivity. |
| Annual Precipitation | 1.8260 | 11906 | 0.0334 | 0.0678 | 0.0080 | 0.0588 | Annual Precipitation has no significant impact on connectivity. |
| Temperature Annual Range | -8.3471 | 11906 | -0.1529 | 0.0000 | -0.1784 | -0.1275 | Temperature Annual Range facilitates connectivity. |
| Topography | -3.1178 | 11906 | -0.0571 | 0.0018 | -0.0825 | -0.0317 | Topography facilitates connectivity. |
| Length | 42.2153 | 11906 | 0.7737 | 0.0000 | 0.7474 | 0.8001 | Length hinders connectivity. |

**Table 7.** Parameter estimates based on Cohen's D for variables included in the final model for *S. becki* Santa Rosa Island. Effect sizes with confidence intervals that span zero + are considered insignificant. Effect size direction is the same direction as in “Cohen’s d” column for each variable and can be interpreted directly.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Variable** | **t-value** | **df** | **Cohen’s d** | **p-value** | **Lower CI** | **Upper CI** | **Interpretation** |
| Annual Mean Temperature | 3.1826 | 8077 | 0.0708 | 0.0014 | 0.0399 | 0.1016 | Intermediate annual Mean Temperature significantly hinders connectivity. |
| Mean Temperature of the Coldest Quarter | -5.0492 | 8077 | -0.1123 | 0.0000 | -0.1432 | -0.0814 | Mean Temperature of the Coldest Quarter significant facilitates connectivity. |
| Bare ground | 15.3997 | 8077 | 0.3427 | 0.0000 | 0.3116 | 0.3737 | Percent cover bare ground significant hinders connectivity. |
| Length | 14.6492 | 8077 | 0.3260 | 0.0000 | 0.2949 | 0.3570 | Length significantly hinders connectivity. |

**Table 8.** Parameter estimates based on Cohen's D for variables included in the final model for *S. becki* San Miguel Island. Effect sizes with confidence intervals that span zero + are considered insignificant. Effect size direction is the same direction as in “Cohen’s d” column for each variable and can be interpreted directly.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Variable** | **t-value** | **df** | **Cohen’s d** | **p-value** | **Lower CI** | **Upper CI** | **Interpretation** |
| Percent bare ground cover | -2.3171 | 540 | -0.1994 | 0.0208 | -0.3192 | -0.0796 | Percent bare ground cover significantly facilitates connectivity. |
| Percent shrub cover | 0.4180 | 540 | 0.0359 | 0.6761 | -0.0835 | 0.1555 | Percent shrub cover does not significantly impact connectivity. |
| Percent tree canopy cover | 2.5077 | 540 | 0.2158 | 0.0124 | 0.0959 | 0.3357 | Tree canopy cover significantly hinders connectivity. |
| Mean Temperature of the Warmest Quarter | 5.8886 | 540 | 0.5068 | 0.0000 | 0.3853 | 0.6282 | Mean temperature of the warmest quarter significantly hinders connectivity. |
| Annual Precipitation | 5.3415 | 540 | 0.4597 | 0.0000 | 0.3386 | 0.5808 | Annual precipitation significantly hinders connectivity. |
| Temperature Annual Range | -2.1247 | 540 | -0.1828 | 0.0340 | -0.3026 | -0.0630 | Temperature annual range significantly facilitates connectivity. |
| Heat load index | -0.1132 | 540 | -0.0097 | 0.9098 | -0.1292 | 0.1097 | Heat load index does not significantly impact connectivity |
| Topography | -3.6549 | 540 | -0.3145 | 0.0002 | -0.4348 | -0.1943 | Topography significantly facilitates connectivity. |
| Length | 8.0055 | 540 | 0.6890 | 0.0000 | 0.5659 | 0.8120 | Length significantly hinders connectivity. |

**Appendix B: Figures**

A satellite image of land

Description automatically generated

**Figure 1.** *Sceloporus becki* sampling sites and delineation of populations according to Salerno et al. (2023).

A graph with different colored dots

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**Figure 2.** Clustering of samples of S. becki with XXX from each island.

A screenshot of a graph

Description automatically generated

**Figure 3**. Population genetic structure (K = 4) of Sceloporus becki in the context of spatial relationships among individuals. Individuals on the west side of Santa Rosa share ancestry with San Miguel, and individuals on the west side of Santa Cruz share ancestry with Santa Rosa. We show K=5 and K=6 to show how ancestry estimates change with each number of populations.

**Figure 4.** Population genetic structure (K = 2) of Sceloporus becki in the context of spatial relationships among individuals on Santa Cruz Island.

**Figure 5.** Population genetic structure (K = 3) of Sceloporus becki in the context of spatial relationships among individuals on Santa Cruz Island.

A graph of different colored dots

Description automatically generated

**Figure 6.** Test of isolation by distance for *Sceloporus becki* using proportion of shared alleles to pairwise geographic distances (m) for each individual.