Western North American Naturalist 85(2), © 2025, pp. 293–309

Phylogenetics of Channel Island deer mice based on the cytochrome *b* gene sheds light on multiple colonization events and supports current taxonomy

Madeleine A. Becker[1,2,3,*], Cesar Carrasco[2,4], Andreas F. Kautt[5], Susette Castañeda-Rico[1,2,3], John L. Orrock[6], Jesús E. Maldonado[2,3], and Cody W. Edwards[1,3]

[1]*Smithsonian-Mason School of Conservation, Front Royal, VA*
[2]*Center for Conservation Genomics, Smithsonian's National Zoo and Conservation Biology Institute, Washington, DC*
[3]*College of Science, George Mason University, Fairfax, VA*
[4]*Department of Chemistry and Biochemistry, California State University Los Angeles, Los Angeles, CA*
[5]*Department of Organismic & Evolutionary Biology, Harvard University, Cambridge, MA*
[6]*Department of Integrative Biology, University of Wisconsin–Madison, Madison, WI*

Abstract.—The *Peromyscus maniculatus* species complex is a diverse North American group comprising multiple wide-ranging clades and insular endemic forms, including Channel Island deer mice. This study employs complete mitochondrial cytochrome *b* sequences of 75 mice from all 8 California Channel Islands to better understand their origins and to test the phylogenetic placement of Channel Island deer mice within the broader context of the *P. maniculatus* species group for the first time. We recover a well-resolved clade within *P. gambelii* (Baird 1858) that includes mice from the Northern Channel Islands (Anacapa, Santa Cruz, Santa Rosa, and San Miguel), Santa Barbara Island, and San Nicolas Island. The resulting patterns of genetic structure are indicative of natural biogeographic processes on the Northern Channel Islands and suggest translocation via Chumash trade routes to San Nicolas Island. Notably, Santa Catalina and San Clemente Islands may represent independent colonizations from this 6-island clade, displaying signatures of connectivity with each other and the mainland. The recovery of unnested island mouse clades divergent (0.98%–1.08%) from the central mainland *P. gambelii* clade is striking given their relatively short (~11,000 years) presumed evolutionary history on the Channel Islands based on archaeological evidence. We propose that mitochondrial genomes of most Channel Island deer mice may originate from a now-rare, ancient mainland *P. gambelii* haplogroup, which may have also colonized other California islands. Our results also validate the assignment of all subspecies to *P. gambelii* under the latest proposed taxonomy, though this species designation itself is an active area of research without consensus.

Resumen.—El complejo de especies *Peromyscus maniculatus* es un grupo diverso de América del Norte que comprende varios linajes de amplia distribución, así como formas endémicas insulares, incluidos los ratones ciervo de las Islas del Canal (Channel Islands). En este estudio se analizan secuencias completas del gen mitocondrial citocromo *b* de 75 ratones provenientes de las ocho Islas del Canal de California, con el objetivo de comprender mejor sus orígenes y analizar, por primera vez, la posición filogenética de los ratones ciervo insulares en un contexto más amplio del grupo de especies *P. maniculatus*. Recuperamos un clado, con buen soporte, de *P. gambelii* (Baird 1858) que incluye ratones de las Islas del Canal del Norte (Anacapa, Santa Cruz, Santa Rosa y San Miguel), así como de las islas Santa Bárbara y San Nicolás. Los patrones resultantes de estructura genética indican procesos biogeográficos naturales en las Islas del Canal del Norte y sugieren una posible translocación hacia la isla San Nicolás a través de las rutas comerciales de los Chumash. Es notable que las islas Santa Catalina y San Clemente podrían representar colonizaciones independientes a partir de este clado de seis islas, mostrando señales de conectividad entre sí y con el continente. La recuperación de clados de ratones insulares no anidados, divergentes entre un 0.98% y un 1.08% del clado continental central de *P. gambelii*, resulta sorprendente dada su supuesta reciente historia evolutiva (~11,000 años) en las Islas del Canal, según la evidencia arqueológica. Proponemos que los genomas mitocondriales de la mayoría de los ratones ciervo de las Islas del Canal podrían haberse originado a partir de un haplogrupo continental antiguo y actualmente escaso de *P. gambelii*, que también podría haber colonizado otras islas de California. Nuestros resultados también corroboran la asignación de todas las subespecies a *P. gambelii*, según la taxonomía más reciente propuesta, aunque esta clasificación sigue siendo un área de investigación activa y sin consenso.

*Corresponding author: BeckerM@si.edu

MAB orcid.org/0000-0003-2051-2911 AFK orcid.org/0000-0001-7792-0735 SCR orcid.org/0000-0002-4301-3579
JLO orcid.org/0000-0003-0768-7389 JEM orcid.org/0000-0002-4282-1072 CWE orcid.org/0000-0001-5912-6693

Peromyscus is the most abundant and speciose mammal genus in North America (Bedford and Hoekstra 2015), and the genus includes numerous insular endemic forms throughout the California islands. Channel Island deer mice comprise 8 subspecies within the large *Peromyscus maniculatus* species complex, each unique to a specific California Channel Island (Table 1). Composed of the sole nonhuman mammal found across all 8 Channel Islands, these populations exhibit significant morphological and genetic differentiation from mainland deer mice (Collins et al. 1979, Gill 1980, Ashley and Wills 1987, 1989, Pergams and Ashley 2002, Durst 2014, Orrock et al. 2021a). Archaeological evidence currently suggests that deer mice arrived on the Northern Channel Islands (NCI) around 11 kya (Shirazi et al. 2018), likely via unintentional translocations by Indigenous people (Walker 1980, Rick 2013). Early genetic studies, based both on allozyme patterns (Gill 1980) and mitochondrial restriction fragment length polymorphisms (RFLP), informed the hypothesis that the deer mouse colonization followed a general north-to-south pattern across the Channel Islands (Ashley and Wills 1987). Shared genotypes suggested that mice arrived on the NCI while these islands were connected to each other as a part of the "superisland" Santarosae. Further island-specific genetic studies such as those focusing on the conservation genetics of Anacapa (Pergams et al. 2000, Ozer et al. 2011) and exome-sequencing efforts on Santa Barbara and Santa Cruz Islands (Orrock et al. 2021a) have provided invaluable information for understanding these populations. However, recent genetic research has been limited in leveraging genetic information to clarify relationships within Channel Island *Peromyscus*, establishing relationships to mainland *Peromyscus* taxa, or inferring the colonization history of this group. For example, Durst (2014) found unique haplotypes and private microsatellite alleles on each island, but a plurality of samples shared a mitochondrial haplotype. Given the low sequence divergence between Channel Island and mainland deer mice (Ashley and Wills 1987), it is difficult to parse whether these results reflect a shared recent evolutionary history consistent with the archaeological record or reflect current or historical connectivity (Durst 2014).

In addition to important knowledge gaps that remain regarding relationships among island populations, our knowledge of evolutionary relationships between Channel Island mice and mainland taxa may also be incomplete. Studies have largely compared Channel Islands mice to local Southern California *P. gambelii gambelii* populations (Ashley and Wills 1987, Durst 2014) without a robust examination of other neighboring groups such as *P. g. coolidgei* in Baja California or California populations of wide-ranging *P. sonoriensis* (Gill 1980). Moreover, Channel Island mouse comparisons to mainland taxa have never extended beyond the California region, failing to consider the rest of the *P. maniculatus* species complex's vast range across North America, which is especially important given the recent suggestion of multiple species within *P. maniculatus* (Greenbaum et al. 2017, 2019, Bradley et al. 2019). While most taxa from California islands have been recently recognized as subspecies of *P. gambelii* (Baird 1858) based on geographic type locality (Bradley et al. 2019), no Channel Island specimens were examined or sequenced in this revision, leaving a critical gap in understanding the taxonomic status of the Channel Island deer mouse. The limited scope of these comparisons emphasizes the need for a more thorough examination of the Channel Island deer mouse and its relationships with various mainland populations within the *P. maniculatus* species complex.

Interrogating the taxonomy of the Channel Island deer mouse through a phylogeographic lens also provides useful insights into its evolutionary history, uncovering information about its closest mainland common ancestor(s) and potential source population(s). Accordingly, one goal of this study was to resolve a sister group to island mice and establish their closest mainland relatives. The importance of placing a lineage in its phylogenetic context is illustrated by similar mitochondrial analyses of the Channel Island fox (*Urocyon littoralis*) and mainland gray fox (*U. cinereoargenteus*): these studies demonstrated that gray fox populations geographically closest to the Channel Islands are not the closest genetically related populations as might have been expected. Instead the results inferred closer relationships between haplotypes from island foxes and Northern California than any mainland Southern California individuals, likely reflecting demographic turnover in Southern California (Hofman et al. 2015, Sacks et al. 2022). Santa Catalina Island shrews (*Sorex ornatus willetti*), by contrast, are found in a clade of Baja and Southern California samples, but they are highly

TABLE 1. Channel Island deer mouse subspecies names by island before and after proposed reassignment by Bradley et al. (2019).

Island	Former name (Musser and Carleton 2005)	Proposed name (Bradley et al. 2019)	Taxonomic authority
Anacapa Island (AI-E)	*Peromyscus maniculatus anacapae*	*Peromyscus gambelii anacapae*	von Bloeker 1942
Santa Catalina Island (CAT)	*P. m. catalinae*	*P. g. catalinae*	Elliot 1903
Santa Barbara Island (SBI)	*P. m. elusus*	*P. g. elusus*	Nelson and Goldman 1931
San Clemente Island (SCL)	*P. m. clementis*	*P. g. clementis*	Mearns 1896
Santa Cruz Island (SCZ)	*P. m. santacruzae*	*P. g. santacruzae*	Nelson and Goldman 1931
San Miguel Island (SMI)	*P. m. streatori*	*P. g. streatori*	Nelson and Goldman 1931
San Nicolas Island (SNI)	*P. m. exterus*	*P. g. exterus*	Nelson and Goldman 1931
Santa Rosa Island (SRI)	*P. m. sanctaerosae*	*P. g. sanctaerosae*	von Bloeker 1940

divergent from all surveyed mainland populations, consistent with long-term insular isolation concurrent to mainland northward expansion (Maldonado et al. 2001). Resolving deer mouse island–mainland relationships will not only provide evolutionary context for current island mouse populations but will also signify how mainland demographics have shifted in the thousands of years since deer mice arrived on the Channel Islands.

To reevaluate hypotheses regarding the origins of Channel Island deer mice and test their taxonomic assignment to *P. gambelii*, we adopted phylogenetic and phylogeographic approaches to position island mice within the broader *P. maniculatus* species complex. We generated mitochondrial cytochrome *b* gene sequence data from all Channel Island populations and geographically proximate mainland *P. gambelii* localities. We present results from a phylogenetic analysis of these samples paired with the taxonomically and geographically diverse dataset compiled by Bradley et al. (2019) from throughout the *P. maniculatus* species group, including multiple taxa and localities collected across California, to comprehensively test taxonomic hypotheses in the Channel Island deer mouse.

METHODS

Sampling

Novel samples were either collected directly in the field ($n = 71$) or derived from museum specimens ($n = 20$). Tail tips were collected during field surveys as detailed in Orrock et al. (2021b) and approved by University of Wisconson–Madison RARC Protocol L005041. Frozen tissue samples from vouchered specimens ($n = 13$) were requested from multiple natural history collections: the Field Museum (FMNH), Los Angeles County Natural History Museum (LACM), and Museum of Vertebrate Zoology (MVZ). The remaining museum-derived samples comprise whole claws excised from preserved study skins ($n = 7$) from LACM and the Santa Barbara Museum of Natural History (SBMNH) using sterile techniques (McDonough et al. 2018). The majority ($n = 75$) of these samples represent populations of *Peromyscus* from the 8 Channel Islands, while the rest ($n = 16$) were collected from mainland California (Los Angeles, Orange, San Diego, San Luis Obispo, Santa Barbara, and Ventura Counties and Baja California Norte) and are currently recognized as *P. gambelii* (Supplementary Material: sheets S1A–B). All novel sequences have been deposited in GenBank (PP746607–PP746697).

All other samples from the *P. maniculatus* species group ($n = 109$) comprise cytochrome *b* sequences on GenBank generated from several studies (Conroy and Cook 1999, Rinehart et al. 2005, Dragoo et al. 2006, Gering et al. 2009, MacDonald et al. 2009, Kalkvik et al. 2012, Cornejo-Latorre et al. 2017, Sawyer et al. 2017, Bradley et al. 2019) previously analyzed together by Bradley et al. (2019). The subset of samples selected from these studies includes representatives from each clade described by Bradley et al. (2019) throughout their ranges including all samples described as *P. gambelii* ($n = 45$) and *P. sonoriensis* samples collected in California ($n = 19$). These specimens and our novel samples are mapped by taxon and locality in Fig. 1. Additional selected samples from Bradley et al. (2019) include *P. keeni* ($n = 4$), *P. labecula* ($n = 7$), *P. maniculatus* (sensu stricto) ($n = 8$), *P. melanotis* ($n = 2$), *P. polionotus* ($n = 1$), *P. sejugis* ($n = 1$), *P. sonoriensis* outside of California ($n = 16$), and the undescribed Yukon species ($n = 1$). Additionally, we included their outgroups from the *P. leucopus* species group: *P. leucopus* ($n = 3$) and *P. gossypinus* ($n = 2$). Locality information,

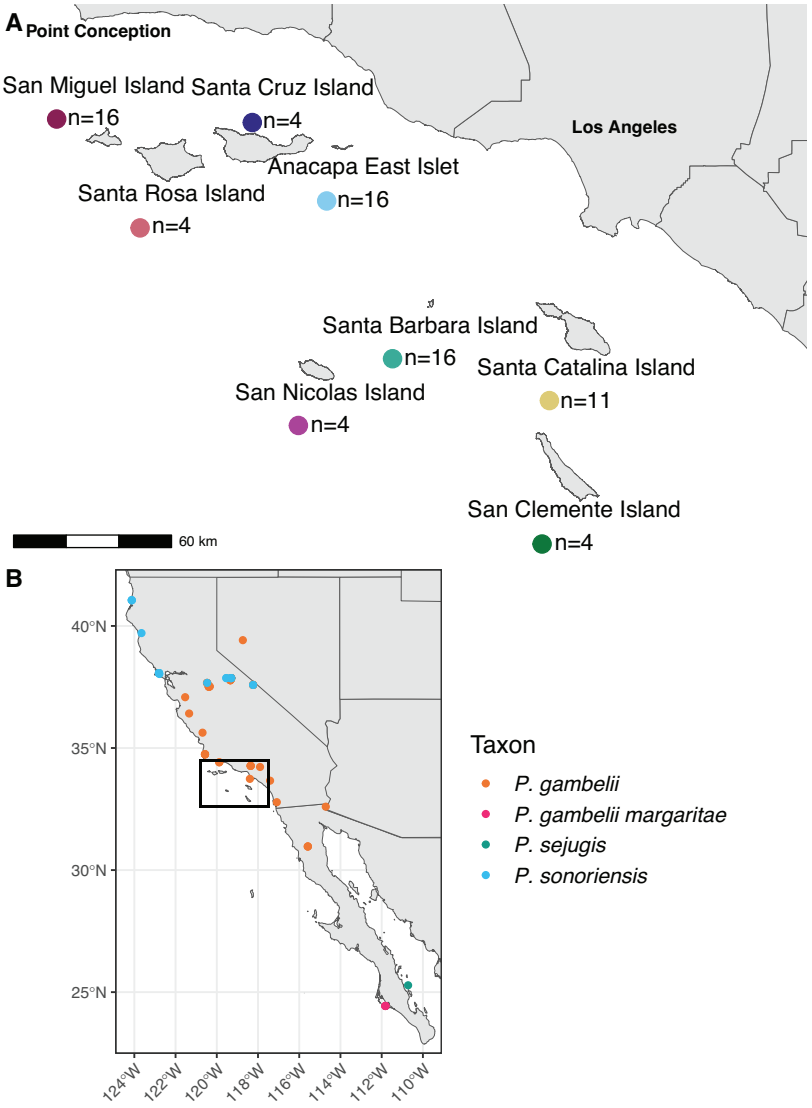

Fig. 1. ***A***, Novel sampling of deer mice across the Channel Islands. ***B***, Total sampling of mainland *Peromyscus gambelii*, California *P. sonoriensis*, and other California Island taxa *P. sejugis* and *P. gambelii margaritae*. The inset black box highlights the Channel Islands archipelago and regions shown in detail in panel *A*.

GenBank accession numbers, and voucher specimen institutional codes are available in Supplementary Material 1: sheet S1C.

Laboratory Methods and Sequencing

All cytochrome *b* sequences were computationally reconstructed from larger genomic datasets rather than targeted directly. Samples processed at Harvard University (n = 76; Supplementary Material 1: sheet S1B) were originally prepared for medium-high coverage whole genome sequencing (WGS) as part of a large-scale population genomic study as in Wooldridge et al. (2022). In brief, whole genomic DNA was extracted from tissue samples (tail tips and museum frozen tissue samples). Libraries were prepared using Illumina kits (Illumina, Inc., San Diego, CA) and sequenced (150 bp paired-end) on an Illumina NovaSeq S4 machine.

For samples processed at the Center for Conservation Genomics (CCG) at Smithsonian's National Zoo and Conservation Biology Institute

(n =15; Supplementary Material 1: sheet S1A), libraries were either prepared for genomic analysis with (1) low-coverage (~10×) WGS or (2) target capture methods yielding mitochondrial bycatch, following Castañeda-Rico et al. (2022). Supplementary Material 2 contains detailed laboratory methods for each sample type and technique employed. All libraries prepared at the CCG were pooled equimolarly and sequenced (150 bp paired-end) on an Illumina NovaSeq 6000 at the Clinical Genomics Center (Oklahoma Medical Research Foundation, Oklahoma City, OK).

Sequence Processing and Alignment

Harvard shotgun sequences were mapped to the *P. maniculatus bairdii* reference genome (GCF_003704035.1) using bwa mem v0.7.17 (Li and Durbin 2009). PCR and optical duplicate reads were flagged with Picard v2.27.1 (Broad Institute 2019) and not considered in any downstream analyses. Finally, variant and genotype calls across the mitogenome were performed with GATK v4.2.6.1 (Van der Auwera and O'Connor 2020).

Using this callset, for each sample, we used bcftools consensus v1.19 (Danecek et al. 2021) to apply its alternate alleles to the mitogenomic reference sequence, thereby reconstructing the haploid mitogenomic sequences. Per sample, sites with missing data and those with <20% average read depth across the mitogenome—inferred with samtools depth v1.19—were masked as "N," yet none were detected within the cytochrome *b* region. We delineated the cytochrome *b* region by aligning all reconstructed sequences together with the reference cytochrome *b* sequence (*P. maniculatus bairdii* NC_039921.1) using MAFFT v7.471 (Katoh and Standley 2013), and then we manually extracted the corresponding region in AliView v1.28 (Larsson 2014).

The raw data obtained for the samples prepared at the CCG were quality-checked with Fastqc v0.11.8 (Andrews 2010) using default parameters, and then trimmed with Trimgalore v0.6.4 and Cutadapt v2.4 (Martin 2011) with a quality cutoff -q 20. To assemble mitogenomes, sequence data was subsampled from trimmed whole-genome data files, between 5% and 15% of reads depending on file size. Target-captured libraries were not subsampled. Reads were mapped to the *P. maniculatus bairdii* reference mitogenome (NC_039921.1) in Geneious Prime v2020.1.2 (https://www.geneious.com) using the Geneious mapper with up to 5 iterations and default parameters. Bases with a coverage below 5 and sequencing ambiguities were assigned as missing data ("N"). Novel mitogenomes were aligned with MAFFT v7.407 (Katoh and Standley 2013) together with previously published mitogenomes including *P. maniculatus bairdii*, *P. boylii* (MZ433362.1), *P. californicus* (OP524493.1), *P. leucopus* (NC_037180.1), and *P. polionotus* (ON528117) (Castañeda-Rico et al. 2022). We extracted the entire cytochrome *b* gene from the complete mitogenome alignment in Geneious and re-aligned all Harvard and CCG novel sequences with the previously published cytochrome *b* sequence dataset (n =109). We also transferred annotations from each species-specific reference to rule out the presence of nuclear copies of mitochondrial genes (NUMTs) and translated all protein-coding genes to check for frame shifts or stop codons.

Phylogenetic Analyses

We analyzed the final cytochrome *b* alignment using Maximum Likelihood in IQTree v2.1.3 (Minh et al. 2020) and Bayesian Inference in MrBayes v3.2.7a (Ronquist and Huelsenbeck 2003) both with and without partitioning by codon. We used ModelFinder (Kalyaanamoorthy et al. 2017) as implemented in IQTree to infer optimal models of evolution for Maximum Likelihood analysis, using the TPM2+F+I+G4 model for the unpartitioned alignment and TN+F+G4, TIM2+F+I+G4, and HKY+F+I for each codon in the partitioned alignment, respectively. We ran PartitionFinder v2.1.1 (Guindon et al. 2010, Lanfear et al. 2012, 2017) to search for models available in MrBayes with a greedy search and corrected Akaike information criterion for model selection, choosing HKY+I+G for the unpartitioned alignment, GTR+I+G for the first 2 codons of the partitioned alignment, and HKY+I+G for the third codon. MrBayes ran for 20 million generations with a burn-in of 25%, a sample frequency of 1000, and 4 Monte-Carlo Markov Chains. Posterior probabilities and final topologies result from 50% majority-rule consensus trees, with a probability of >0.95 indicating support. Maximum Likelihood support scores are based on 1000 Ultrafast bootstraps (Hoang et al. 2018), with a score of >95 indicating support. Only unique haplotypes were analyzed, and all trees were rooted with *P. californicus*,

P. boylii, and *P. truei* as outgroups. These analyses were conducted on the Smithsonian High Performance Cluster (SI/HPC; Smithsonian Institution 2024).

Genetic Diversity and Distance

Using only sequences without missing data (Ns), we calculated basic genetic diversity metrics of Channel Island deer mice ($n = 74$), other California island taxa (*P. sejugis*, Isla Santa Cruz [$n = 1$], and *P. gambelii margaritae*, Isla Santa Margarita [$n = 4$]), and across mainland *P. gambelii* ($n = 53$). We used DnaSP v6.12 (Rozas et al. 2017) and Arlequin v3.5.2.2 (Excoffier and Lischer 2010) to estimate haplotype diversity (*Hd*), parsimony informative sites, nucleotide diversity (π), and Watterson's estimator (θ_S) within geographic populations and clades identified by phylogenetic analysis. Following Bradley et al. (2019), we also calculated genetic distance between these clades in Arlequin using Kimura's 2-parameter model of evolution (Kimura 1980).

Lastly, we constructed a median-joining haplotype network (Bandelt et al. 1995, 1999) in PopART (Leigh and Bryant 2015) of sequences assigned to *P. gambelii*. Only sequences 1143–1144 bp long without missing data were included to maximize the genetic data used in this analysis: Channel Islands populations ($n = 74$; all but 1 CAT sample), *P. gambelii margaritae* ($n = 4$), and mainland *P. gambelii* ($n = 18$) from Los Angeles, Orange, San Luis Obispo, Santa Barbara, and Ventura Counties, California; Churchill County, Nevada; and Baja California Norte. A detailed inventory of which sequences were used in each analysis is available in Supplementary Material 3.

RESULTS

Cytochrome *b* Alignment and Genetic Diversity

All novel cytochrome *b* sequences were 1144 bp long, with no ambiguities from any shotgun-sequenced samples. However, there were some missing data (2.9%–22.4%) in bycaught samples ($n = 4$) captured for UCEs (Supplementary Material 4). Previously published sequences varied in length (437–1205 bp), resulting in a total final alignment length of 1221 bp.

Unique cytochrome *b* haplotypes were recovered for each of the Channel Islands, and no haplotypes were shared among islands or between island and mainland samples. Of the 3 historical island samples, the haplotypes sequenced from SMI and SBI specimens (collected in 1939) were also present in mouse samples collected in 2015. The historical CAT specimen collected in 1949 seemingly represents a unique haplotype, though missing data (9.4%) makes it difficult to quantify how closely related this specimen is to mainland or other CAT samples. Despite uneven sample sizes, all islands contained multiple cytochrome *b* haplotypes except for Anacapa's East Islet. Catalina harbored the highest genetic diversity among island populations by all metrics, even when the haplotype with missing data was removed (Table 2).

Phylogenetic Analysis

Overall topologies from both Maximum Likelihood and Bayesian trees (Figs. 2, 3) recapitulate the findings of Bradley et al. (2019), with interclade relationships similarly unresolved. These unsupported nodes include the relationships between *P. labecula*, *P. maniculatus*, *P. sonoriensis*, and *P. polionotus*, as well as the placement of the clade including *P. keeni* and a proposed species from the Yukon that has yet to be formally described (Bradley et al. 2019), labeled in all trees as "Yukon clade." All Channel Island samples group within or as sister to a primary *P. gambelii* clade and/or *P. gambelii* sequences. Trees constructed with both methods, with or without partitions, generally recovered the same topologies (although the above unresolved relationships appear to differ).

All samples from AI-E, SCZ, SMI, and SRI (the Northern Channel Islands) as well as SBI and SNI form a well-supported clade in all trees (Figs. 2, 3; Supplementary Materials 5, 6). In maximum likelihood trees (Fig. 3), this well-supported clade resolves as sister to a *P. gambelii* sample collected in 1995 at Vandenberg Air Force Base (now Space Force Base), Santa Barbara County, California (MSB:Mamm:87492; Dragoo et al. 2006). This haplotype is closer to the 6-island haplogroup than other mainland sequences in the cytochrome *b* haplotype network (Fig. 4) and shows a 1.33% divergence from the main *P. gambelii* clade (Table 3). This divergence from the rest of *P. gambelii* and the 3 other Vandenberg sequences appears consistent with phylogenies presented by previous authors (Dragoo et al. 2006, Bradley et al. 2019), although this outlier is not explicitly addressed. Another divergent (0.96%) *P. gambelii* haplo-

TABLE 2. Genetic diversity of geographic populations within Channel Island deer mice, mainland *Peromyscus gambelii*, and Isla Santa Margarita, Baja California Sur, subspecies *P. gambelii margaritae*. Only sequences without missing data were included in these analyses.

Statistics	Mainland *P. gambelii* ($n = 53$)	AI-E ($n = 16$)	CAT ($n = 10$)	SBI (n=16)	SCL ($n = 4$)	SCZ ($n = 4$)	SMI ($n = 16$)	SNI ($n = 4$)	SRI ($n = 4$)	*P. gambelii margaritae* ($n = 4$)
Unique haplotypes	47	1	5	3	2	2	2	2	2	3
Haplotype diversity (*Hd*)	0.993	0.000	0.756	0.575	0.500	0.667	0.400	0.667	0.667	0.833
Hd standard deviation	0.006	0.000	0.130	0.080	0.265	0.204	0.114	0.204	0.204	0.222
Total bp	1178	1144	1144	1144	1144	1144	1144	1144	1144	1143
Parsimony-informative sites	34	0	2	1	0	1	2	2	1	1
Nucleotide diversity $\pi \times 10^3$	7.74	0.00	5.74	0.547	0.437	0.583	0.700	1.17	0.583	1.90
π standard deviation	4.01	0.00	3.35	0.507	0.542	0.654	0.597	1.07	0.654	1.57
Watterson estimator θ_S	25.121	0.000	10.605	0.603	0.545	0.545	0.603	1.091	0.545	2.182
θ_S standard deviation	7.163	0.000	4.614	0.452	0.545	0.545	0.452	0.876	0.545	1.490

type from a specimen collected from Yosemite National Park is recovered as sister to the main *P. gambelii* clade and *P. sejugis*, though this relationship is unresolved and polytomic (Figs. 2, 3). While the phylogenetic position and support of a clade including *P. gambelii margaritae*, *P. sejugis*, and mainland *P. gambelii* are consistent with trees presented by Bradley et al. (2019), the addition of more related sequences reveals a *Peromyscus gambelii* complex of uncertain relationships between these taxa and Channel Island deer mice. Genetic distance between clades within the *Peromyscus gambelii* complex is between 0.82% and 1.33% (Table 3). These values are lower than genetic distance between typical deer mouse species, which are 2% to 5% (Bradley and Baker 2001, Bradley et al. 2019). Nonetheless, these between-clade divergences are greater than all estimated values of within-clade genetic distance.

Within the 6-island clade, there is limited genetic structure, and relationships between or within islands are largely unresolved with very short branch lengths (Fig. 3). Nonetheless, SBI and SRI were recovered as monophyletic. SNI may be paraphyletic with respect to SBI, but this relationship is only supported in ML trees. The remaining Channel Islands, CAT and SCL, are present in 2 clades. Four of the CAT haplotypes make up their own clade, supported in Bayesian but not ML trees (Fig. 2). Conversely, the other CAT ($n = 2$) and SCL ($n = 2$) haplotypes are within the largely unresolved mainland *P. gambelii* clade. SCL samples are monophyletic, while 1 CAT haplotype is sister to the SCL group in ML trees. While the historical CAT haplotype forms an unsupported relationship with this group in the partitioned ML tree, this sequence is found in the *P. gambelii* polytomy in other trees.

Novel samples identified as *P. gambelii* all clustered within the central *P. gambelii* polytomy. However, 2 samples obtained from museum specimens, LACM 044994 and SBMNH 4250, were likely misidentified. The LACM 044994 cytochrome *b* sequence is highly supported as sister to the *P. boylii* reference, while SBMNH 4250 is sister to this clade. Additional BLAST searches confirmed that LACM 044994 is a member of *P. boylii*, while SBMNH 4250 is a member of *P. truei*. Accordingly, these sequences are now labeled with their corrected identifications on all trees.

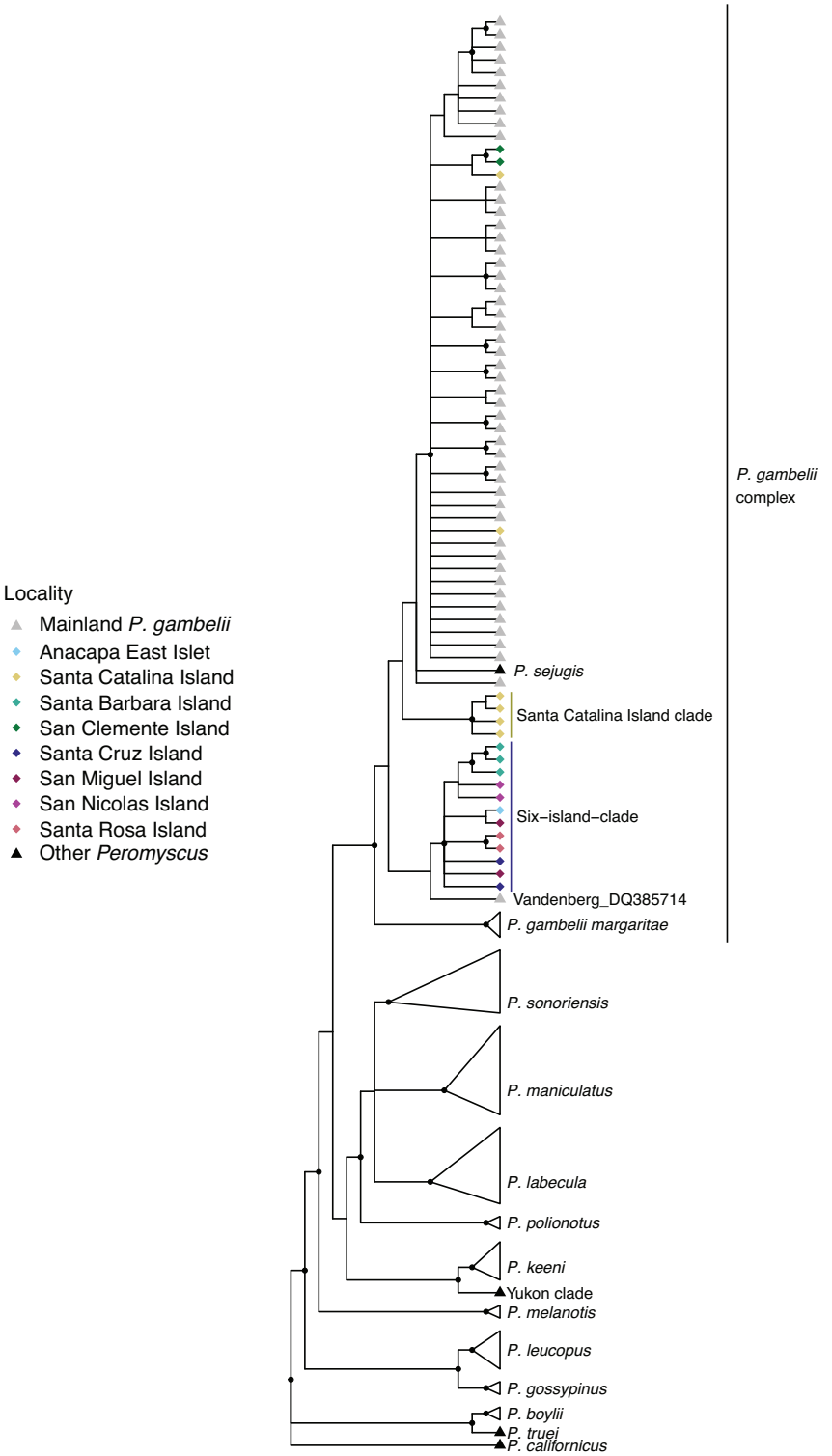

Fig. 2. Bayesian Inference (MrBayes) 50% majority-rule consensus tree with partitions. Nodes with black dots indicate high support with posterior probabilities >0.95.

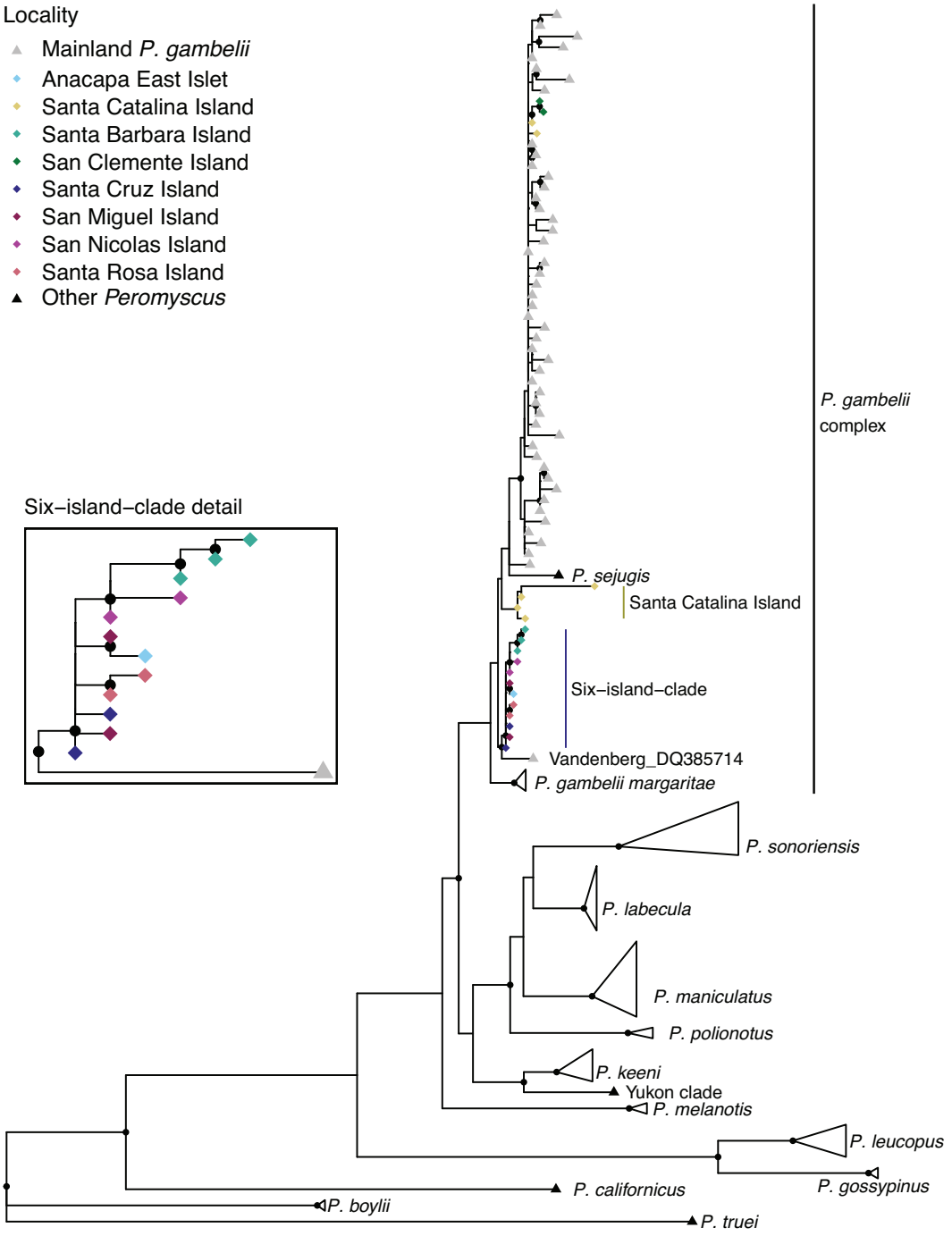

Fig. 3. Maximum Likelihood (IQTree) 50% majority-rule consensus tree with partitions. Nodes with black dots indicate high Ultrafast bootstrap support >95. Inset shows 6-island-clade branching patterns in more detail and most closely related haplotype, which is also labeled in the larger trees by its locality (Vandenberg Space Force Base, Santa Barbara County, California) and GenBank accession number.

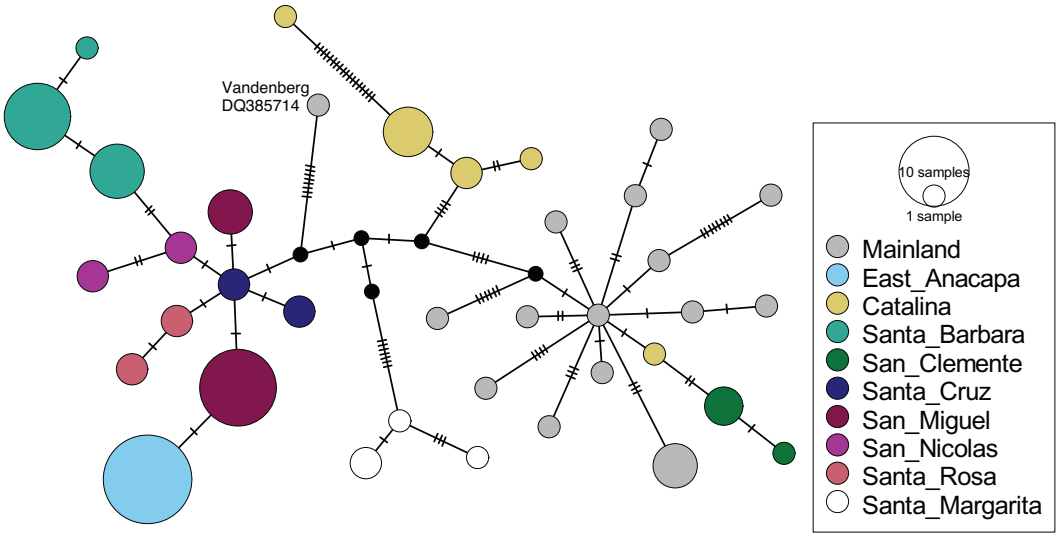

Fig. 4. Median-joining network of complete cytochrome *b* haplotypes (1143–1144 bp) assigned to *P. gambelii*, including the Channel Islands, mainland localities, and Isla Santa Margarita, Baja California Sur. Black nodes represent inferred missing haplotypes. The mainland haplotype most closely related to island haplotypes is labeled by its locality (Vandenberg Space Force Base, Santa Barbara County, California) and GenBank accession number (DQ385714).

DISCUSSION

This study is the first to test the phylogenetic placement of Channel Island deer mice within the *Peromyscus maniculatus* species group and provides additional insight into the genetic structure and origins of island mice. Contrary to our expectations given the recent expansion of Channel Island deer mice, most island mice are not nested within the large mainland clade or do not demonstrate clear relationships with source population(s). Instead, we recover a well-supported clade of haplotypes from 6 islands: the Northern Channel Islands (Anacapa, Santa Cruz, Santa Rosa, San Miguel), Santa Barbara Island, and San Nicolas Island (Figs. 3, 4). We also detect a clade from Santa Catalina Island, although this clade is not well supported in all trees. However, 2 additional samples from Santa Catalina Island and both San Clemente haplotypes are nested within the mainland *P. gambelii* polytomy. Relationships within *P. gambelii*, including these 3 clades and the insular subspecies from Baja California Sur, *P. g. margaritae* Osgood 1909, and with the insular species *P. sejugis* Burt 1932, remain largely unresolved, forming a tangled *P. gambelii* complex within this already taxonomically fraught group.

Genetic Structure and Insights into Channel Island Deer Mouse Colonization

The lack of genetic structure within mainland *P. gambelii* and the divergence observed in the 6-island and Catalina-only clades present challenges in inferring the source population(s) of Channel Island deer mice. Nonetheless, our mitochondrial DNA analysis suggests that there have been at least 2 colonizations of the Channel Islands by *P. gambelii*: (1) at minimum 1 colonization which gave rise to the Catalina and 6-island clades and (2) at least 1 introduction to San Clemente that may be related to secondary contact on Santa Catalina Island. The haplotypes from this second group are only 1–4 bp divergent from the closest related mainland haplotype(s) (Fig. 4). Therefore, it is conceivable that further sampling and genetic data could reveal shared haplotypes or source populations.

On Santa Catalina Island, we find strong evidence of secondary gene flow, with 4 haplotypes recovered in a clade while the other 2 haplotypes resolved within the *P. gambelii* polytomy. The small sample size on San Clemente Island ($n = 4$) makes it unclear whether the mainland-associated haplotypes are the only lineage present on this island, or whether a second haplogroup was just not recovered by this study. Ashley and Wills (1987) also found evidence of secondary

TABLE 3. Genetic distances between clades identified within the *Peromyscus gambelii* complex. Gray cells on the diagonal represent within-clade genetic distance, which is not applicable to clades containing only one sequence. Only sequences without missing data were included in these analyses.

	P. gambelii polytomy ($n = 56$)	Six-island clade ($n = 60$)	Catalina clade ($n = 9$)	*P. gambelii margaritae* ($n = 4$)	*P. sejugis* ($n = 1$)	DQ385714 Vandenberg ($n = 1$)	EF666164 Yosemite ($n = 1$)
P. gambelii polytomy	0.57%						
Six-island clade	0.98%	0.21%					
Catalina clade	1.08%	0.82%	0.36%				
P. gambelii margaritae	1.15%	0.89%	1.21%	0.15%			
P. sejugis	1.06%	0.97%	0.98%	1.17%	—		
DQ385714 (Vandenberg)	1.33%	0.79%	1.19%	1.32%	1.01%	—	
EF666164 (Yosemite)	0.96%	0.80%	0.97%	0.88%	0.88%	1.23%	—

contact on Catalina but hypothesized a direct colonization of San Clemente from the mainland because they too did not detect a second, more divergent San Clemente lineage. We infer a relationship between the mainland-associated Catalina and San Clemente haplotypes (Figs. 3, 4), suggesting connectivity between these 2 islands and to the mainland. We did not conduct divergence dating due to the low amount of variation in this dataset (Fig. 4) and because these analyses can be inflated both (1) in cases of recent divergence due to a relatively high substitution rate (Ho et al. 2005, 2007) and (2) when based on a small number of loci, especially from mitochondrial DNA (Zheng et al. 2011). Therefore, we cannot determine whether these mainland-nested samples were a product of ancient, historical (i.e., during the ranching period), or contemporary connectivity. Nonetheless, detection of connectivity between Santa Catalina and San Clemente Islands aligns with patterns observed in other southern Channel Islands organisms likely facilitated by Gabrielino/Tongva trade routes (Rick et al. 2005). Further analyses with additional genetic loci and, ideally, fossil data as employed by Hofman et al. (2015) for the island fox will be essential for elucidating the timing of these introductions and the structure of these lineages on Catalina.

Within the 6-island clade recovered in our phylogenetic analyses, the relationships between populations generally follow established biogeographical patterns on the Northern Channel Islands, while likely reflecting ancient human activity in their connectivity to Santa Barbara and San Nicolas Islands. Santa Barbara Island and East Anacapa Islet, both of which are very small islands, were monophyletic and monomorphic, respectively. The recovery of a single Anacapa haplotype is consistent with prior analysis of the cytochrome *c* oxidase subunit II gene, which found a single haplotype in 1400 mice across all Anacapa islets (Ozer et al. 2011). Multiple northern populations (Santa Cruz, San Miguel) were not recovered as monophyletic, but no shared haplotypes between islands were recovered with our limited sample sizes. While interisland migration cannot be completely ruled out, morphological data suggest that this phenomenon is unlikely (Pergams and Ashley 1999), and this pattern is congruent with incomplete lineage sorting after the breakup of Santarosae. Archaeological evidence places the appearance of island mice after human arrival but before

rising sea levels completely separated the Northern Channel Islands from each other ~9 kya (Shirazi et al. 2018). This timeframe suggests that matrilines could still partially reflect the genetic structure of this larger ancient population. Interestingly, this clade also includes Santa Barbara and San Nicolas Islands. Differentiating between signatures of anthropogenic versus natural dispersal on Santa Barbara Island is challenging, but San Nicolas is the most remote of the Channel Islands, situated 80 km south of the Northern Channel Islands. Nevertheless, San Nicolas haplotypes are largely undifferentiated from the northern island populations, suggesting a comparatively recent expansion more consistent with translocation rather than a natural rafting event (Ashley and Wills 1987). Furthermore, the Chumash maintained trade networks between San Nicolas and the northern islands, providing a mechanism for this expansion (Hudson et al. 1978). It is worth noting that San Nicolas Island foxes are more closely related to foxes on the other southern islands than to those on the northern islands (Hofman et al. 2015), despite also likely being translocated by Indigenous people. This difference in genetic structure could be related to their different modes of translocation: deer mice were likely unintentionally translocated, perhaps stowed away in food supplies (Walker 1980), while island foxes were probably purposefully brought to the southern islands (Collins 1991a, 1991b). Therefore, it is reasonable that island mouse phylogeography more closely recapitulates different aspects of historical trade routes than island foxes. Nonetheless, further sampling is needed to interrogate this pattern and determine whether any haplotypes from the other southern islands are also present on San Nicolas.

Relationships to Mainland Deer Mice and Implications

The near-complete lineage sorting of the 6-island clade and the Catalina clade with a small amount of data (~1144 bp) is striking among Channel Island mammals. For example, the island fox demonstrates very little divergence from mainland California gray foxes at cytochrome *b*, with at least 1 shared haplotype (Hofman et al. 2015). Another rodent on the Channel Islands, the western harvest mouse *Reithrodontomys megalotis*, meanwhile shows minimal mitochondrial and morphological divergence with mainland populations (Ashley 1989, Collins and George 1990). Nonetheless, genetic divergence between mainland *P. gambelii* and recovered Channel Island deer mouse clades is dwarfed by animals whose arrival on the Channel Islands predates human occupation (Maldonado et al. 2001, McCormack et al. 2011, Salerno et al. 2023). The recovery of island mouse clades outside of mainland *P. gambelii* rather than nested within the mainland clade, co-incident with the presence of 2 rare divergent mainland haplotypes, may be better explained by the loss or rarity of intermediate mainland haplotypes that gave rise to the island mouse, as opposed to inference of a substantially earlier date of initial colonization based on divergence and substitution rate alone (Ashley and Wills 1987).

The 6-island clade is sister to a haplotype from a mouse originally collected on Vandenberg Air Force Base in 1995 (MSB:Mamm:87492; Vandenberg_DQ385714; Figs. 2–4). Assuming no contamination or sequencing artifacts in this highly divergent haplotype, this locality is not a straightforward island mouse source population. Dragoo et al. (2006) sequenced 4 other specimens collected at Vandenberg at the same time, and their haplotypes were all recovered in the unstructured mainland *gambelii* polytomy, so this is likely a rare haplotype. Furthermore, the relative lack of phylogenetic structure throughout the range of *P. gambelii*, including in peripheral localities in Arizona and Nevada, suggests that this particular haplotype is not likely representative of structure driven by recent biogeography. We recovered another divergent haplotype derived from a *gambelii* specimen collected in Yosemite, which is sister to the mainland polytomy and Baja California's Isla Santa Cruz species *P. sejugis*. These singular haplotypes are between 0.88% and 1.33% genetically distant to each other, the mainland *P. gambelii* polytomy, and both island mouse clades, while the other *P. gambelii* sequences ($n = 43$) show little differentiation (Table 3). We suggest that mitochondrial lineages of Channel Island deer mice originated from a divergent group of *P. gambelii* that is now extirpated or rare on the mainland. The divergent Vandenberg sequence may have stemmed from this rare lineage, though more parsimonious explanations should be ruled out. Nonetheless, even discounting the Vandenberg haplotype, the complete lineage sorting and genetic distance between island mouse and mainland haplogroups is significant,

with multiple inferred "missing haplotypes" central to our median-joining network that could represent the links between these divergent groups.

While we did not date the divergence between haplogroups, a study by Sacks et al. (2022) dated mitogenome haplotype divergence in the island fox and found a similar gap in haplogroups at odds with the timing of known fox colonization 10–13 kya (Rick et al. 2009). They explained this discordance with a hypothesized extinction of an ancestral mainland population in Southern California shortly after the initial colonization of *Urocyon* to the northern Channel Islands, followed by eventual replacement by other clades (Sacks et al. 2022). This hypothesis is corroborated by massive extinction and turnover events throughout Southern California contemporaneous to the arrival and spread of mice and foxes on the Channel Islands. Analysis of the fossil record and climatic data in the Los Angeles Basin uncovered the local extinction of 7 species of megafauna by 12.9 kya, coinciding with dramatic changes in fire regimes, and more broadly, the "transition from a postglacial megafaunal woodland to a human-mediated chaparral ecosystem" (O'Keefe et al. 2023). Small mammals like *Peromyscus* were possibly also affected by this massive and rapid change in habitat on the Southern California mainland. Since deer mice readily evolve into ecotypes across their range (Osgood 1909), a woodland-adapted clade could have been supplanted by a more scrub-adapted clade in the kind of turnover hypothesized by Sacks et al. (2022). While much of this is speculative, subfossils and ancient DNA from island and mainland specimens could greatly clarify these complex biogeographic dynamics and help answer key related questions about the timing of colonization. Additionally, further phylogeographic study of *P. gambelii* on the mainland and other California islands may reveal how rare these divergent matrilines are while also assessing how divergent their nuclear genomes are from other *P. gambelii* populations.

Taxonomy of the Channel Island Deer Mouse

Phylogenetic analyses of cytochrome *b* sequences from Channel Island deer mice and various samples throughout the *Peromyscus maniculatus* species group consistently support the placement of all island mouse subspecies within the species *P. gambelii* (Baird 1858). In our Bayesian and Maximum Likelihood phylogenetic trees, every island mouse haplotype demonstrated the closest relationships with mainland *P. gambelii* sequences compared to any of the other clades identified by Bradley et al. (2019), except for the very closely related *P. sejugis*, which is nested within *P. gambelii* (Figs. 2, 3).

While our results support Channel Island deer mice as members of *P. gambelii* in the framework presented by Bradley et al. (2019), it is essential to acknowledge the complexity and provisional nature of these revisions in the absence of genome-wide nuclear data (Mammal Diversity Database 2024). The mitochondrial data utilized represent a single locus and gene tree, introducing the possibility of discordance with nuclear data and offering an incomplete picture of evolutionary history. The observed divergence between *P. gambelii* and California *P. sonoriensis* based on mitochondrial lineages contrasts with recent findings by Boria and Blois (2023), who conducted a phylogeographic analysis within the *Peromyscus maniculatus* species group using nuclear data from both species of mice from throughout California. Their results revealed a pattern indicative of isolation by distance and minimal genetic structure between taxa (Boria and Blois 2023), prompting questions regarding the validity of the species designations.

Determining whether *P. gambelii* constitutes a valid species extends far beyond the scope of this paper and remains an active area of research. Nonetheless, the taxonomic names assigned to Channel Island deer mice ultimately depend on the acceptance of a particular taxonomy of the broader *Peromyscus maniculatus* species complex.

CONCLUSIONS

Phylogenetic analyses of complete cytochrome *b* sequences of the Channel Island deer mouse reveal unique haplogroups in an unresolved *Peromyscus gambelii* complex. Our study reveals 1 well-supported clade of the Northern Channel Islands, Santa Barbara Island, and San Nicolas Island, demonstrating genetic structure consistent with both vicariance—the breakup of Santarosae and anthropogenic connectivity—and Chumash-facilitated translocation to remote San Nicolas Island. Santa Catalina Island may possibly represent an independent colonization from this clade, while also displaying signatures

of secondary contact with the mainland or San Clemente Island or both. San Clemente Island haplotypes are unique and monophyletic but show low levels of divergence from mainland *P. gambelii*. While the timing of these colonizations could not be reliably estimated with a single 1144-bp locus, resolving the chronology of these events is a priority for future research. Channel Island deer mouse cytochrome *b* sequences also contextualize rare divergent haplotypes in mainland *P. gambelii* detected by prior research (Bradley et al. 2019). The California island taxa of deer mice—including most Channel Island deer mice, *P. sejugis* on Isla Santa Cruz, and *P. g. margaritae* on Isla Santa Margarita in Baja California—may descend from an ancient matriline of *P. gambelii* that is extremely rare on the mainland today. In addition to these populations' morphological distinction and crucial role in contemporary island ecosystems, their divergent ancestry should warrant their special consideration as evolutionarily significant units within the *Peromyscus maniculatus* species group despite their presumed recent history on the islands and human-assisted expansion. Further genomic analysis of *Peromyscus* on California islands, paired with phylogeographic research into these cryptic lineages on the mainland, may provide a powerful window into understanding the complex and dynamic biogeography of Southern California faunal transitions from the Pleistocene to the Holocene.

Supplementary Material

Seven online-only supplementary files accompany this article (https://scholarsarchive.byu.edu/wnan/vol85/iss2/16).

Supplementary Material 1. Sample metadata for CCG samples, Harvard samples, and previously published sequences.

Supplementary Material 2. Detailed laboratory methods for samples prepared for genomic analysis at the Center for Conservation Genomics (CCG).

Supplementary Material 3. List of total samples used in each set of analyses.

Supplementary Material 4. Raw and percent missing data for novel cytochrome *b* sequences.

Supplementary Material 5. Bayesian Inference (MrBayes) 50% majority-rule consensus tree without partitions.

Supplementary Material 6. Maximum Likelihood (IQTree) 50% majority-rule consensus tree without partitions.

Supplementary Material 7. Genetic diversity by clade in *Peromyscus gambelii* complex identified in phylogenetic analyses.

Acknowledgments

We appreciate the outstanding logistical support provided by A. Little and other staff at the U.S. National Park Service Channel Islands, the U.S. Navy (M. Booker, M. Ruane), and Catalina Island Conservancy. We thank D. Cabrera, J. Chandler, B. Connolly, C. Drost, and staff at Institute for Wildlife Studies for specimen collection. Work on San Clemente Island was supported by ongoing natural resource projects funded by U.S. Navy Commander, Pacific Fleet. Thanks to K. and S. Robson (LACM), K. Fahy (SBMNH), C. Conroy (MVZ), and A. Ferguson (FMNH) for museum samples. Further thanks to the LACM for a Student Collections Study Award which enabled collection of museum specimens for this study. This work is supported by NSF DEB-1439550, DEB-2042211, the CCG, the American Society of Mammalogists Grants-in-Aid and Horner Award, the Society of Systematic Biologists Graduate Student Research Award, an American Wildlife Conservation Foundation Grant, and a Cosmos Scholar Grant. This project is supported in part by federal funding from the Latino Initiatives Pool, administered by the National Museum of the American Latino. This funding supports the UCSB-Smithsonian Scholars Program and C. Carrasco's internship. Thanks to Ma. Castellanos, C. Soto Balderas, and Me. Castellanos for support of UCSB-Smithsonian Scholars. MAB is also supported by an SMSC Fellowship funded by the Jacquemin Family Foundation. Thanks to C. Hofman and T. Rick for feedback, support, and initial insights into this research. Thanks to CCG members for advice and support of this work including N. McInerney and L. Parker for laboratory training, and M. Chua and S. Lyons for comments on the manuscript.

Literature Cited

Andrews, S. 2010. FastQC: a quality control tool for high throughput sequence data. Babraham Bioinformatics, Cambridge, United Kingdom.

Ashley, M.V. 1989. Absence of differentiation in mitochondrial DNA of island and mainland harvest mice, *Reithrodontomys megalotis*. Journal of Mammalogy 70: 383–386.

Ashley, M.V., and C. Wills. 1987. Analysis of mitochondrial DNA polymorphisms among Channel Island deer mice. Evolution 41:854–863.

ASHLEY, M.V., AND C. WILLS. 1989. Mitochondrial-DNA and allozyme divergence patterns are correlated among island deer mice. Evolution 43:646–650.

BAIRD, S.F. 1858. General Report upon the Zoology of the Several Pacific Railroad Routes. Mammals. 1 vol. 4to. Washington, 1857, Annals and Magazine of Natural History 1:5, 369–373. https://doi.org/10.1080/00222935808696935

BANDELT, H.-J., P. FORSTER, AND A. RÖHL. 1999. Median-joining networks for inferring intraspecific phylogenies. Molecular Biology and Evolution 16:37–48.

BANDELT, H.-J., P. FORSTER, B.C. SYKES, AND M.B. RICHARDS. 1995. Mitochondrial portraits of human populations using median networks. Genetics 141:743–753.

BEDFORD, N.L., AND H.E. HOEKSTRA. 2015. *Peromyscus* mice as a model for studying natural variation. eLife 4: e06813.

BORIA, R.A., AND J.L. BLOIS. 2023. Phylogeography within the *Peromyscus maniculatus* species group: understanding past distribution of genetic diversity and areas of refugia in western North America. Molecular Phylogenetics and Evolution 180:107701.

BRADLEY, R.D., AND R.J. BAKER. 2001. A test of the genetic species concept: cytochrome-b sequences and mammals. Journal of Mammalogy 82:960–973.

BRADLEY, R.D., J.Q. FRANCIS, R.N. PLATT II, T.J. SONIAT, D. ALVAREZ, AND L.L LINDSEY. 2019. Mitochondrial DNA sequence data indicate evidence for multiple species within *Peromyscus maniculatus*. Special Publications, Museum of Texas Tech University, TX. 68 pp.

BROAD INSTITUTE. 2019. Picard tools [software]. Version 2.27.1. Broad Institute, Cambridge, MA. https://broadinstitute.github.io/picard/

BURT, W.H. 1932. Descriptions of heretofore unknown mammals from islands in the Gulf of California, Mexico. Transactions of the San Diego Society of Natural History 7:161–185.

CASTAÑEDA-RICO, S., C.W. EDWARDS, M.T.R HAWKINS, AND J.E. MALDONADO. 2022. Museomics and the holotype of a critically endangered cricetid rodent provide key evidence of an undescribed genus. Frontiers in Ecology and Evolution 10:930356.

COLLINS, P.W. 1991a. Interaction between island foxes (*Urocyon littoralis*) and Indians on islands off the coast of southern California: I. Morphologic and archaeological evidence of human assisted dispersal. Journal of Ethnobiology 11:51–81.

COLLINS, P.W. 1991b. Interaction between island foxes (*Urocyon littoralis*) and Native Americans on islands off the coast of southern California: II. Ethnographic, archaeological, and historical evidence. Journal of Ethnobiology 11:205–229.

COLLINS, P.W., AND S.B. GEORGE. 1990. Systematics and taxonomy of island and mainland populations of western harvest mice (*Reithrodontomys megalotis*) in southern California. Contributions in Science (Natural History Museum, Los Angeles County, CA) 420:1–26.

COLLINS, P.W., J. STORRER, AND K. RINDLAUB. 1979. XI. Vertebrate zoology: biology of the deer mouse. Pages 11.1–11.74 *in* D.M. Power, editor, A natural resources study of the Channel Islands National Park, California. Final Technical Report to the U.S. National Park Service, Washington, DC.

CONROY, C.J., AND J.A. COOK. 1999. MtDNA evidence for repeated pulses of speciation within arvicoline and murid rodents. Journal of Mammalian Evolution 6: 221–245.

CORNEJO-LATORRE, C., P. CORTÉS-CALVA, AND S.T. ÁLVAREZ-CASTAÑEDA. 2017. The evolutionary history of the subgenus *Haplomylomys* (Cricetidae: *Peromyscus*). Journal of Mammalogy 98:1627–1640.

DANECEK, P., J.K. BONFIELD, J. LIDDLE, J. MARSHALL, V. OHAN, M.O. POLLARD, A. WHITWHAM, T. KEANE, S.A. MCCARTHY, R.M. DAVIES, ET AL. 2021. Twelve years of SAMtools and BCFtools. GigaScience 10:giab008.

DRAGOO, J.W., J.A. LACKEY, K.E. MOORE, E.P. LESSA, J.A. COOK, AND T.L. YATES. 2006. Phylogeography of the deer mouse (*Peromyscus maniculatus*) provides a predictive framework for research on hantaviruses. Journal of General Virology 87:1997–2003.

DURST, P.A. 2014. Ecological factors and historical biogeography influence the evolutionary divergence of insular rodents. Doctoral dissertation, Department of Biology, Duke University, Ann Arbor, MI. 119 pp.

ELLIOT, D.G. 1903. Descriptions of apparently new species and subspecies of mammals from California, Oregon, the Kenai Peninsula, Alaska, and lower California, Mexico. Field Columbian Museum, Chicago, IL. 173 pp.

EXCOFFIER, L., AND H.E.L. LISCHER. 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.

GERING, E.J., J.C. OPAZO, AND J.F. STORZ. 2009. Molecular evolution of cytochrome b in high- and low-altitude deer mice (genus *Peromyscus*). Heredity 102:226–235.

GILL, A.E. 1980. Evolutionary genetics of California Islands *Peromyscus*. Pages 719–743 *in* D.M. Power, editor, The California Islands: proceedings of a multidisciplinary symposium. University of California, Los Angeles, CA.

GREENBAUM, I.F., S.E. CHIRHART, M.L. WALKER, AND R.L. HONEYCUTT. 2017. Molecular phylogenetics of western deer mice (*Peromyscus*): taxonomic and biogeographic implications. Southwestern Naturalist 62:129–137.

GREENBAUM, I.F., R. HONEYCUTT, AND S. CHIRHART. 2019. Taxonomy and phylogenetics of the *Peromyscus maniculatus* species group. Pages 559–575 *in* R.D. Bradley, H.H. Genoways, D.J. Schmidly, and L.C. Bradley, editors, From field to laboratory: a memorial volume in honor of Robert J. Baker. Museum of Texas Tech University, Lubbock, TX.

GUINDON, S., J.-F. DUFAYARD, V. LEFORT, M. ANISIMOVA, W. HORDIJK, AND O. GASCUEL. 2010. New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. Systematic Biology 59:307–321.

HO, S.Y.W., M.J. PHILLIPS, A. COOPER, AND A.J. DRUMMOND. 2005. Time dependency of molecular rate estimates and systematic overestimation of recent divergence times. Molecular Biology and Evolution 22:1561–1568.

HO, S.Y.W., B. SHAPIRO, M.J. PHILLIPS, A. COOPER, AND A.J. DRUMMOND. 2007. Evidence for time dependency of molecular rate estimates. Systematic Biology 56: 515–522.

HOANG, D.T., O. CHERNOMOR, A. VON HAESELER, B.Q. MINH, AND L.S. VINH. 2018. UFBoot2: improving the ultrafast bootstrap approximation. Molecular Biology and Evolution 35:518–522.

HOFMAN, C.A., T.C. RICK, M.T.R. HAWKINS, C.W. FUNK, K. RALLS, C.L. BOSER, P.W. COLLINS, T. COONAN, J.L. KING, S.A. MORRISON, ET AL. 2015. Mitochondrial genomes suggest rapid evolution of dwarf California Channel Islands foxes (*Urocyon littoralis*). PLOS ONE 10:e0118240.

Hudson, T., J. Timbrook, and M. Rempe, editors. 1978. Tomol: Chumash watercraft as described in the ethnographic notes of John P. Harrington. Ballena Press Anthropological Papers No. 9, Ballena Press and Santa Barbara Museum of Natural History.

Kalkvik, H.M., I.J. Stout, T.J. Doonan, and C.L. Parkinson. 2012. Investigating niche and lineage diversification in widely distributed taxa: phylogeography and ecological niche modeling of the *Peromyscus maniculatus* species group. Ecography 35:54–64.

Kalyaanamoorthy, S., B.Q. Minh, T.K.F. Wong, A. von Haeseler, and L.S. Jermiin. 2017. ModelFinder: fast model selection for accurate phylogenetic estimates. Nature Methods 14:587–589.

Katoh, K., and D.M. Standley. 2013. MAFFT multiple sequence alignment software. Version 7. Improvements in performance and usability. Molecular Biology and Evolution 30:772–780.

Kimura, M. 1980. A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. Journal of Molecular Evolution 16:111–120.

Lanfear, R., B. Calcott, S.Y.W. Ho, and S. Guindon. 2012. PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. Molecular Biology and Evolution 29: 1695–1701.

Lanfear, R., P.B. Frandsen, A.M. Wright, T. Senfeld, and B. Calcott. 2017. PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. Molecular Biology and Evolution 34:772–773.

Larsson, A. 2014. AliView: a fast and lightweight alignment viewer and editor for large datasets. Bioinformatics 30: 3276–3278.

Leigh, J.W., and D. Bryant. 2015. popart: Full-feature software for haplotype network construction. Methods in Ecology and Evolution 6:1110–1116.

Li, H., and R. Durbin. 2009. Fast and accurate short read alignment with Burrows–Wheeler transform. Bioinformatics 25:1754–1760.

MacDonald, S.O., E. Waltari, R.A. Nofchissey, Y.E. Sawyer, G.D. Ebel, and J.A. Cook. 2009. First records of deermice (*Peromyscus maniculatus*) in the Copper River basin, southcentral Alaska. Northwestern Naturalist 90:243–247.

Maldonado, J.E., C. Vilà, and R.K. Wayne. 2001. Tripartite genetic subdivisions in the ornate shrew (*Sorex ornatus*). Molecular Ecology 10:127–147.

Mammal Diversity Database. 2024. Mammal diversity database [dataset]. Version v1.12. Zenodo, Genève, Switzerland. https://doi.org/10.5281/ZENODO.10463715

Martin, M. 2011. Cutadapt removes adapter sequences from high-throughput sequencing reads. EMBnet.Journal 17: 10–12.

McCormack, J.E., J. Heled, K.S. Delaney, A.T. Peterson, and L.L. Knowles. 2011. Calibrating divergence times on species trees versus gene trees: implications for speciation history of *Aphelocoma* jays: divergence dating on species trees. Evolution: International Journal of Organic Evolution 65:184–202.

McDonough, M.M., L.D. Parker, N. Rotzel McInerney, M.G. Campana, and J.E. Maldonado. 2018. Performance of commonly requested destructive museum samples for mammalian genomic studies. Journal of Mammalogy 99:789–802.

Mearns, E.A. 1896. Preliminary diagnoses of new mammals from the Mexican border of the United States. Proceedings of the United States National Museum 18: 443–447.

Minh, B.Q., H.A. Schmidt, O. Chernomor, D. Schrempf, M.D. Woodhams, A. von Haeseler, and R. Lanfear. 2020. IQ-TREE 2: new models and efficient methods for phylogenetic inference in the genomic era. Molecular Biology and Evolution 37:1530–1534.

Musser, G.G., and M.D. Carleton. 2005. Superfamily Muroidea. Pages 894–1531 *in* D.E. Wilson and D.M. Reeder, editors, Mammal species of the world: a taxonomic and geographic reference. Johns Hopkins University Press, Baltimore, MD.

Nelson, E.W., and E.A. Goldman. 1931. Six new white-footed mice (*Peromyscus maniculatus* group), from islands off the Pacific Coast. Journal of the Washington Academy of Sciences 21:530–535.

O'Keefe, F.R., R.E. Dunn, E.M. Weitzel, M.R. Waters, L.N. Martinez, W.J. Binder, J.R. Southon, J.E. Cohen, J.A. Meachen, L.R.G. DeSantis, et al. 2023. Pre–Younger Dryas megafaunal extirpation at Rancho La Brea linked to fire-driven state shift. Science 381:eabo3594.

Orrock, J.L., L. Abueg, S. Gammie, and J. Munshi South. 2021a. Exome sequencing of deer mice on two California Channel Islands identifies potential adaptation to strongly contrasting ecological conditions. Ecology and Evolution 11:17191–17201.

Orrock, J.L., B.M. Connolly, P.W. Guiden, J.L. Chandler, G.M. Bron, C.A. Drost, and D.K. Garcelon. 2021b. Sin Nombre Virus prevalence from 2014–2017 in wild deer mice, *Peromyscus maniculatus*, on five of the California Channel Islands. Zoonoses and Public Health 68:849–853.

Osgood, W.H. 1909. Revision of the mice of the American genus *Peromyscus*. North American Fauna 28:1–285.

Ozer, F., H. Gellerman, and M.V. Ashley. 2011. Genetic impacts of Anacapa deer mice reintroductions following rat eradication. Molecular Ecology 20:3525–3539.

Pergams, O.R.W., and M.V. Ashley. 1999. Rapid morphological change in Channel Island deer mice. Evolution 53:1573–1581.

Pergams, O.R.W., and M.V. Ashley. 2002. California Island deer mice: genetics, morphometrics, and evolution. Pages 278–288 *in* D.R. Browne, K.L. Mitchell, and H.W. Chaney, editors, Proceedings of the Fifth California Islands Symposium. Santa Barbara Museum of Natural History, Santa Barbara, CA.

Pergams, O.R.W., R.C. Lacy, and M.V. Ashley. 2000. Conservation and management of Anacapa Island deer mice. Conservation Biology 14:819–832.

Rick, T.C. 2013. Hunter-gatherers, endemic island mammals, and the historical ecology of California's Channel Islands. Pages 41–64 *in* V.D. Thompson and J.C. Waggoner, editors, The archaeology and historical ecology of small scale economies. University Press of Florida, Gainesville, FL.

Rick, T.C., J.M. Erlandson, R.L. Vellanoweth, and T.J. Braje. 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., J.M. Erlandson, R.L. Vellanoweth, T.J. Braje, P.W. Collins, D.A. Guthrie, and T.W. Stafford. 2009. Origins and antiquity of the island fox (*Urocyon*

littoralis) on California's Channel Islands. Quaternary Research 71:93–98.

RINEHART, T.A., R.A. GRAHN, AND H.A. WICHMAN. 2005. SINE extinction preceded LINE extinction in sigmodontine rodents: implications for retrotranspositional dynamics and mechanisms. Cytogenetic and Genome Research 110:416–425.

RONQUIST, F., AND J.P. HUELSENBECK. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19:1572–1574.

ROZAS, J., A. FERRER-MATA, J.C. SÁNCHEZ-DELBARRIO, S. GUIRAO-RICO, P. LIBRADO, S.E. RAMOS-ONSINS, AND A. SÁNCHEZ-GRACIA. 2017. DnaSP 6: DNA sequence polymorphism analysis of large data sets. Molecular Biology and Evolution 34:3299–3302.

SACKS, B.N., M.J. STATHAM, L.E.K. SERIEYS, AND S.P.D. RILEY. 2022. Population genetics of California gray foxes clarify origins of the island fox. Genes 13:1859.

SALERNO, P.E., L.M. CHAN, G.B. PAULY, W.C. FUNK, AND J.M. ROBERTSON. 2023. Near-shore island lizard fauna shaped by a combination of human-mediated and natural dispersal. Journal of Biogeography 50:116–129.

SAWYER, Y.E., M.J. FLAMME, T.S. JUNG, S.O. MACDONALD, AND J.A. COOK. 2017. Diversification of deermice (Rodentia: genus *Peromyscus*) at their north western range limit: genetic consequences of refugial and island isolation. Journal of Biogeography 44:1572–1585.

SHIRAZI, S., T.C. RICK, J.M. ERLANDSON, AND C.A. HOFMAN. 2018. A tale of two mice: a trans-Holocene record of *Peromyscus nesodytes* and *Peromyscus maniculatus* at Daisy Cave, San Miguel Island, California. Holocene 28:827–833.

SMITHSONIAN INSTITUTION. 2024. Smithsonian: High Performance Computing Cluster. Smithsonian Institution, Washington, DC. https://doi.org/10.25572/SIHPC

VAN DER AUWERA, G.A., AND B.D. O'CONNOR. 2020. Genomics in the Cloud. O'Reilly Media Inc., Sebastopol, CA. https://www.oreilly.com/library/view/genomics-in-the/9781491975183/

VON BLOEKER, J.C. 1940. Contributions from the Los Angeles Museum – Channel Islands Biological Survey No. 11: a new race of white-footed mouse from Santa Rosa I. Bulletin of the Southern California Academy of Sciences 39:172–174.

VON BLOEKER, J.C. 1942. Contributions from the Los Angeles Museum – Channel Islands Biological Survey No. 22: a new subspecies of white-footed mouse from the Anacapa Islands, California. Bulletin of the Southern California Academy of Sciences 40:161–162.

WALKER, P.L. 1980. Archaeological evidence for the recent extinction of three terrestrial mammals on San Miguel Island. Pages 703–717 *in* D.M. Power, editor, The California Islands: proceedings of a multidisciplinary symposium. Santa Barbara Museum of Natural History, Santa Barbara, CA.

WOOLDRIDGE, T.B., A.F. KAUTT, J.-M. LASSANCE, S. MCFADDEN, V.S. DOMINGUES, R. MALLARINO, AND H.E. HOEKSTRA. 2022. An enhancer of agouti contributes to parallel evolution of cryptically colored beach mice. Proceedings of the National Academy of Sciences 119:e2202862119.

ZHENG, Y., R. PENG, M. KURO-O, AND X. ZENG. 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: 2521–2535.

Received 14 February 2024
Revised 28 May 2024
Accepted 6 June 2024
Published online 15 July 2025