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Authors: Caterino, Michael S., Chatzimanolis, Stylianos, and Richmond, Maxi Polihronakis

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ON THE ORIGINS OF THE INSECT FAUNA OF CALIFORNIA'S CHANNEL ISLANDS: A COMPARATIVE PHYLOGEOGRAPHIC STUDY OF ISLAND BEETLES

Michael S. Caterino[1,4], Stylianos Chatzimanolis[2], and Maxi Polihronakis Richmond[3]

ABSTRACT.—California's 8 Channel Islands host a large diversity of insects, the vast majority of which are shared with mainland southern California. The existence of a small number of recognized endemic species, however, suggest that, for some lineages, the islands are isolated enough to have permitted significant differentiation. Here we investigate the phylogeographic relationships of 4 beetle species (*Thinopinus pictus*, *Hadrotes crassus*, *Hypocaccus lucidulus*, and *Nyctoporis carinata*): all occurring on the mainland and on multiple (up to 6) Channel Islands. Sequences of the cytochrome oxidase I mitochondrial gene (and, for one species, an intron in the nuclear *guftagu* gene) are analyzed by Bayesian, haplotype network, and population genetic methods to examine relationships and gene flow among island and mainland populations. In no instances were all island populations resolved to be monophyletic, and northern (Santa Cruz, Santa Rosa, San Miguel) and southern (San Nicolas, San Clemente, Santa Catalina) island groups generally showed separate relationships to the mainland. Northern island populations of *Hy. lucidulus* were also found to be closely related to those on the southern island of San Nicolas. Populations on San Clemente and Santa Catalina islands did not show close relationships to each other or to San Nicolas Island populations in any species. San Clemente and especially San Nicolas islands hosted disproportionately high levels of diversity in all species examined. This study suggests that the Channel Islands do not function as a biogeographical unit and that several of the islands exhibit levels of diversity comparable to, or even exceeding, similarly sampled populations on the mainland. Thus, as an insular refuge from southern Californian development, the Channel Islands constitute a center of high conservation importance.

RESUMEN.—Las 8 Islas del Canal de California alojan una gran diversidad de insectos, la mayoría también habitan en la parte continental del sur de California. La existencia de un pequeño número de especies endémicas reconocidas, sin embargo, sugiere que, para algunos linajes, las islas son lo suficientemente aisladas como para haber permitido una diferenciación significativa. En este estudio investigamos las relaciones filogeográficas de 4 especies de escarabajos (*Thinopinus pictus*, *Hadrotes crassus*, *Hypocaccus lucidulus* y *Nyctoporis carinata*), que se están en el continente y en múltiples Islas del Canal (hasta 6). Las secuencias del gen mitocondrial citocromo oxidasa I (y, para una especie, un intrón en el gen nuclear *guftagu*) son analizados por un método Bayesiano, para construir una red de haplotipos, y los métodos de genética de poblaciones para examinar las relaciones y el flujo de genes entre las islas y las poblaciones de tierra firme. En ningún caso se determinó que las poblaciones de la islas fueran monofiléticas, y los grupos de islas del norte (Santa Cruz, Santa Rosa, San Miguel) y del sur (San Nicolás, San Clemente, Santa Catalina) en general, mostraron relaciones separadas con el continente. Las poblaciones de las Islas del norte de *Hy. lucidulus* también resultaron estar estrechamente relacionadas con las de la isla sureña de San Nicolás. Las poblaciones de San Clemente y las islas Santa Catalina no mostraron una estrecha relación entre sí o con las poblaciones de las islas de San Nicolás en ninguna especie. San Clemente y, sobre todo, las islas de San Nicolás tuvieron niveles desproporcionadamente altos de diversidad en todas las especies examinadas. Este estudio sugiere que las Islas del Canal no funcionan como una unidad biogeográfica, y que varias de las islas exhiben niveles de diversidad comparable, o incluso superiores, a las poblaciones muestreadas en el continente. Por lo tanto, como un refugio insular del desarrollo del sur de California, las Islas del Canal constituyen un centro de alta importancia para la conservación.

As with island systems around the globe, California's Channel Islands have attracted a great deal of scientific attention. Because islands serve as discrete natural laboratories, their evolutionary and biogeographic histories have been the subject of considerable study and have provided the foundation for key advances in modern biology—most obviously as Darwin's fundamental inspiration for the theory of natural selection (Darwin 1859, Losos and Ricklefs 2009), as well as a supporting source for Ernst Mayr's transformative ideas on the evolutionary process (Emerson 2008) and for general theories of

[1]Santa Barbara Museum of Natural History, 2559 Puesta del Sol Rd., Santa Barbara, CA 93105.
[2]Department of Biological and Environmental Sciences, University of Tennessee at Chattanooga, Dept. 2653, 615 McCallie Ave., Chattanooga, TN 37403.
[3]Division of Biological Sciences, University of California, San Diego, 9500 Gilman Drive #0116, La Jolla, CA 92093.
[4]Present address: Department of Agricultural and Environmental Sciences, Clemson University, Clemson, SC 29634. E-mail: mcateri@clemson.edu

diversity-area relationships (MacArthur and Wilson 1967).

Islands are often a natural laboratory in which to study the effects of serious anthropogenic disturbance (Gillespie and Roderick 2002). The California Channel Islands unfortunately share this attribute as well. These islands have a long history of human use, including some of the oldest occupied human settlements in the New World (>13,000 YBP; Reeder et al. 2008), intensive historic ranching, and ongoing recreational and military use. Invasive species—including plants, vertebrates, and invertebrates—have taken a substantial toll on the native species of all the islands (Powell 1994, Junak et al. 1995, Wetterer et al. 2000, Knowlton et al. 2007). Though recent efforts to remove invasive species and restore native habitats are alleviating some threats, the ability of the native systems to recover is uncertain. In addition to threats from invasive species, island populations may be at substantial risk from the effects of climate change because their isolation restricts their abilities to respond to shifts in habitat zones.

California's Channel Islands comprise 8 islands off the coast of southern California, ranging from 2.9 to 249 km^2 in size and from 20 to 98 km (Fig. 1) in distance from the mainland. Northern (Anacapa, Santa Cruz, Santa Rosa, San Miguel) and southern (San Nicolas, Santa Barbara, San Clemente, Santa Catalina) island groups are generally recognized. Although much of the geological history of the islands remains unclear, certain details are well established. Most significant is that none of the islands has had any direct mainland connection since their most recent complete emergence from the sea (Wenner and Johnson 1980). San Clemente, Santa Catalina, Santa Cruz, and Santa Rosa have had emergent land area since sometime in the Pliocene (2–5 MYBP), whereas San Nicolas, Santa Barbara, Anacapa, and San Miguel were most likely completely submerged at some point during glacial fluctuations in the earlier half of the past 500,000 years (Sorlien 1994, Dibblee and Ehrenspeck 2002). However, during the most recent glacial maximum (about 17,000–18,000 YBP; Vedder and Howell 1980), when sea levels were lowered by as much as 120 m, all 4 of the northern islands were joined into a single super-island (Santarosae), which was separated by as little as 6 km from the mainland to the immediate east (Wenner and Johnson 1980). Their connection might have persisted until as recent as 9000 YBP (Porcasi et al. 1999, Kennett et al. 2008). At this time, all other islands were larger and closer to each other as well as to the mainland. Thus, there has been increased opportunity for movement to and among islands in recent times.

California's Channel Islands are sufficiently isolated to host substantial numbers of endemic taxa. These include plants (Philbrick 1980, Junak et al. 1995), vertebrate animals (Knowlton et al. 2007), and invertebrates (Miller 1985, Rubinoff and Powell 2004). The origins of these endemic species have been varied, with some species representing ancient relicts (e.g., the island ironwood, *Lyonothamnus floribundus,* whose fossil record places it formerly at numerous locations in the mainland southwest) and others representing recent offshoots of extant mainland species (such as the island fox, *Urocyon littoralis,* a close relative of the gray fox, *Urocyon cinereoargenteus*).

Among insects, the level of endemicity on the Channel Islands is an open question. None of the 8 islands' insect faunas are well surveyed (nor, for that matter, is much of the adjacent mainland; Caterino 2006), and the poor state of taxonomy of many groups precludes confident assessment of true endemism. Nonetheless, a wide range of origins has been noted among insects, with some endemic *Lyonothamnus*-feeding Lepidoptera representing presumably old relicts (Powell 1994). Endemic Orthoptera mostly represent close relatives to mainland species in genera that tend to show local endemism (e.g., *Neduba* and *Cnemotettix;* Rentz and Weissman 1982, Weissman 1985), and this is also true for a recently described endemic beetle (*Actium vestigialis;* Caterino and Chandler 2010). Others are endemic only at the subspecies level, indicating even closer relationships to mainland forms (Miller 1985).

The biogeographic sources of few native island taxa have been extensively explored. In an analysis of the Lepidoptera faunas of the islands, Powell (1994) found that relationships to the mainland closely reflected overall habitat distribution, with the faunas of drier habitats on the islands closely resembling those of the mainland deserts to the southeast and taxa in more mesic parts of the islands resembling mainland faunas to the north. These similarities suggest no dominant source but rather

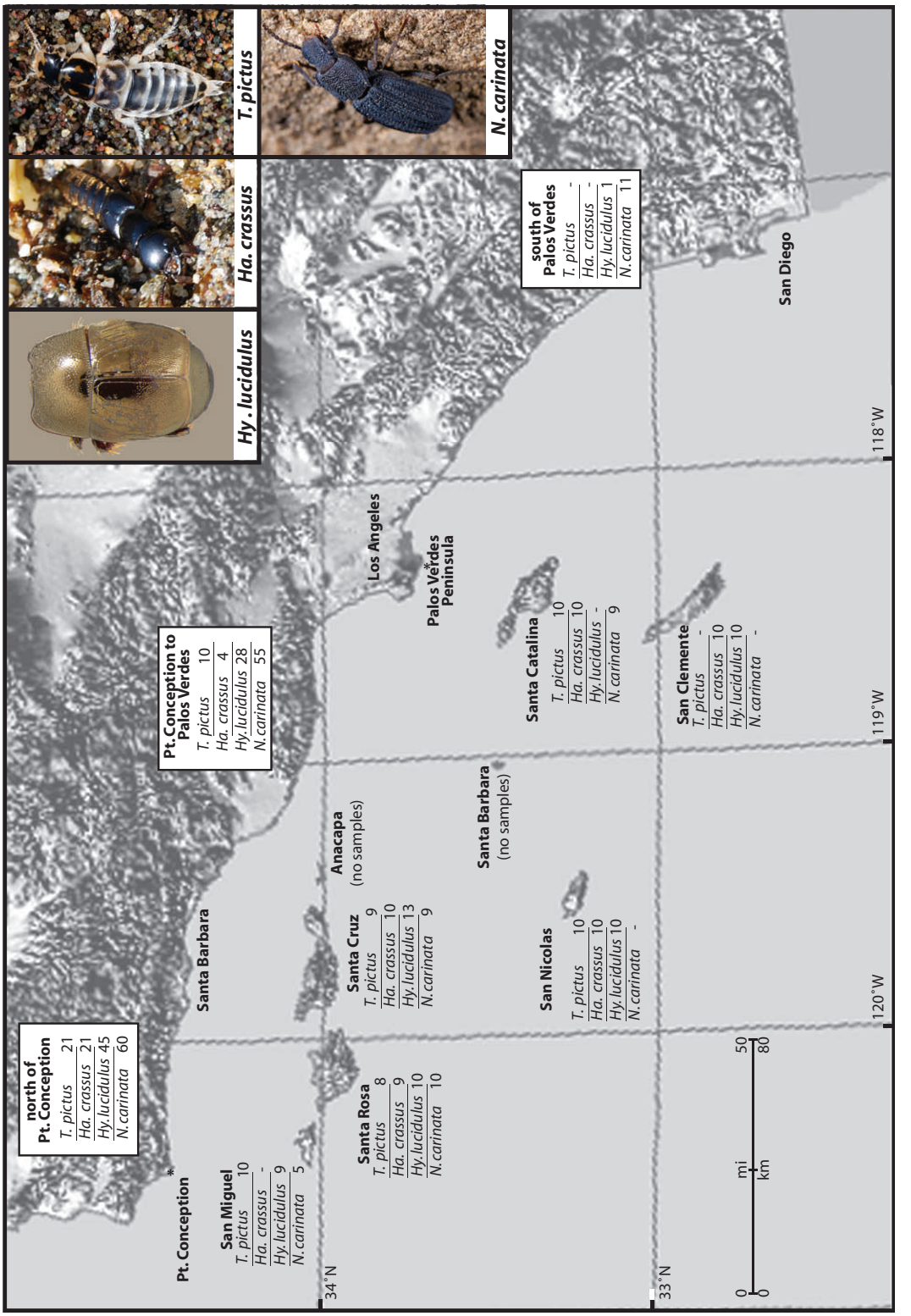

Fig. 1. Sampling of species by island and mainland region.

that Lepidoptera migrants have found their way to suitable habitats on the islands from multiple directions. In contrast, the vast majority of Orthoptera island populations and species find their conspecifics or near relatives in the immediately adjacent Santa Monica Mountains (Weissman 1985).

Besides the question of taxonomic endemicity, Channel Island insects "often vary slightly in color, sculpture, or size from conspecific mainland specimens" (Miller 1985). This variability suggests that some level of cryptic endemicity may be hidden by a conservative taxonomy. In a comparable case, the Island Scrub-Jay (*Aphelocoma insularis*), long considered a morphologically distinguishable subspecies of the widespread Western Scrub-Jay (*Aphelocoma californica*), has recently been shown to be highly divergent from any other western *Aphelocoma* (Delaney and Wayne 2005, Delaney et al. 2008). Although such work has been limited, studies on other taxa have generally shown significant divergence of island populations from mainland conspecifics and limited contact among populations on the different islands (Ramirez and Beckwitt 1995, Landry et al. 1999, Eggert et al. 2004, Rubinoff and Powell 2004, Wilson et al. 2009). In addition, many species present on the Channel Islands have reached there in very recent times, whether through natural means or through human transport (Powell 1994, Calderwood et al. 2002, Mahoney et al. 2003, Chatzimanolis and Caterino 2007a). It is likely that various insect species lie along this entire continuum, including deeply divergent endemics, occasional natural colonists, and recent anthropogenic introductions.

The beetles (Coleoptera) of the Channel Islands have received some previous attention (Miller 1985, Nagano 1985), and this insect order has been the focus of more intensive recent work through our California Beetle Project (Santa Barbara Museum of Natural History 2013). Of 225 beetle species previously recorded from the Channel Islands (Miller personal communication), 38 (17%) are considered to be endemic to one or more islands (Miller 1985). Our recent surveys, however, call these numbers into question: over 640 named species of beetles have now been recorded from the Channel Islands (Caterino et al. unpublished), in addition to dozens of additional morphospecies. Many of these morphospecies are in genera inclined toward local endemism on the mainland, and a sizeable proportion of these are likely to be undescribed endemics. More clearly understanding the origins of the insect fauna of the Channel Islands is critical to managing these potentially rare species and restoring island ecosystems.

In this paper, we analyze phylogeographic patterns among 4 beetle species, all of which occur on the Channel Islands and on the adjacent mainland: *Thinopinus pictus* LeConte, *Hadrotes crassus* (Mannerheim) (Staphylinidae), *Hypocaccus lucidulus* (LeConte) (Histeridae), and *Nyctoporis carinata* LeConte (Tenebrionidae). We previously studied the distribution of genetic diversity and phylogeographic relationships for *Hy. lucidulus* and *N. carinata* on the mainland (Chatzimanolis and Caterino 2008, Caterino and Chatzimanolis 2009, Polihronakis and Caterino 2010a). The other 2 are examined here for the first time. *Thinopinus pictus* and *Ha. crassus* are associated with beach wrack in intertidal zones; *Hy. lucidulus* is associated with coastal dunes; and *N. carinata* is found in inland, fully terrestrial habitats, where it is associated with fungus on dead wood. Of these 4, only *Hy. lucidulus* is capable of flight, permitting possible dispersal to and among islands by air. The other species would presumably be limited to dispersal by rafting, whether via beach wrack (e.g., Peck 1994) or extreme coastal flooding events (Wenner and Johnson 1980). There is also the possibility that any of the species might be anthropogenic introductions.

We use data from these species to address several questions of Channel Island biogeography concerning the origins, ages, and uniqueness of populations inhabiting the islands. Specifically, we examine phylogeographic relationships among haplotypes on the various islands and adjacent mainland and use phylogenetic trees to infer colonization frequency and sources for the islands. We use diversity statistics to compare the levels of intraspecific diversity found on the islands to that found in mainland populations. Finally, we use population genetic analyses to assess degree of isolation of populations among islands and between various subsets of the islands and the mainland. Together these analyses will help us address synthetic questions, such as whether the island populations represent endemic radiations and if not, how many colonizations

of the islands are necessary to explain the current distributions of each species; whether island populations have similar mainland sources, and what can be inferred from these about routes and means of colonization; whether there is evidence for ongoing contact between island and mainland populations; and whether island relationships reflect purported geological relationships. These results will provide a novel perspective on the assembly and conservation value of the insect fauna of this interesting group of islands.

METHODS

Sampling: Taxa and Areas

Focal species were selected based on broad distributions that included the mainland and enough islands to allow multiple comparisons, as well as abundance sufficient to obtain meaningful sample sizes. They also represent a diversity of habitats and life histories, permitting some exploration of relations between these factors and degree of phylogeographic structure. For most of these species our samples represent only a portion of their total distribution but most of the areas that might conceivably be related to island populations. The overall ranges of *Thinopinus pictus* and *Hadrotes crassus* extend from British Columbia, Canada, to northern Baja California, although the exact limits are poorly documented. The distribution of *Hypocaccus lucidulus* is somewhat more restricted, extending north only into Oregon and south into Baja California. Most of the range of *Nyctoporis carinata*, a species confined to California, is represented.

The samples used were gathered over several field trips. Most specimens were collected directly into 100% ethanol and stored at –70 °C. Where possible, we collected 10 individuals of each species from each island. Where specimens were available from multiple localities within an island, we selected a total of 10 samples with roughly equivalent numbers of samples from each sublocality and treated each island as a single population throughout. For studies on the California mainland, 10 individuals per species has been adequate to assess patterns of relationship and interregional diversity in several previous studies (Chatzimanolis and Caterino 2007b, 2008, Polihronakis and Caterino 2010a). The total number of samples of each species from each island is given in Table 1. DNA was extracted from each specimen using Qiagen's DNeasy tissue kit (Valencia, CA), with an identifiable voucher specimen mounted, labeled, and assigned a unique "California Beetle Project" catalog number. Full locality and voucher information are available online (http://www.sbcollections.org/cbp/cbpdatabase1.aspx). We used previously published data for several taxa and for most mainland samples. These sequences correspond to GenBank entries: EU179681–EU179712 for *Hypocaccus lucidulus* COI, EU037099–EU037189 and GU049332–GU049339 for *N. carinata* COI, and GU049270–GU049331 for *N. carinata* GFT. GenBank accession codes for all newly generated sequences are given in the appendix.

Sampling: Genes

For all 4 species, we generated sequences of the cytochrome oxidase subunit I (COI) gene. This well-studied mitochondrial protein coding gene has been used in a large number of phylogeographic and phylogenetic analyses, especially among insect and arthropod groups (Caterino et al. 2000). We analyzed a fragment approximately 826 bp long; most were amplified using primers C1-J-2183 and TL2-N-3014 (aka Jerry and Pat; Simon et al. 1994). In a few cases, other primers were necessary for successful amplification, but the resulting fragments were trimmed to this length. Though mitochondrial DNA is known to have some limitations for phylogeographic inference (e.g., rapid coalescence times, maternal lineage bias, and inability to detect hybridization; Irwin 2002, Zhang and Hewitt 2003), it has proven useful in establishing preliminary hypotheses of intraspecific phylogenetic histories. A previous study of *Nyctoporis carinata* (Polihronakis and Caterino 2010a) established the nuclear intron GFT (in the *guftagu* gene) as informative for population relationships, and we have added sequences of GFT for the island populations of this species as well. GFT haplotypes (alleles) were phased manually for individuals with one polymorphic site. Specimens with 2 or more polymorphic sites were phased using the program Phase v2.1 (Stephens et al. 2001, Stephens and Scheet 2005). Haplotype designations follow Polihronakis and Caterino (2010a). GFT primer sequences are available in Polihronakis and Caterino (2010a) or may be obtained from the authors.

TABLE 1. Sampling localities by region and/or island, with haplotype designations and numbers of individuals (in parentheses) exhibiting each haplotype.

Locality	Coordinates	*Hypocaccus lucidulus* Haplotypes	*Hadrotes crassus* Haplotypes	*Thinopinus pictus* Haplotypes	*Nyctoporis carinata*	
					COI Haplotypes	GFT Haplotypes
CA: Santa Barbara Co., Santa Cruz Island						
Santa Cruz Island					N33, N34	G04, G19
Christy Beach	34.0238°N, 119.8766°W	H9(2), H10(2), H11(6),H48, H49, H50	Hc2, Hc3	Tp5(4), Tp7(3), Tp20		
Johnson Canyon mouth	33.9705°N, 119.8400°W			Tp5		
Prisoners Harbor	34.0019°N, 119.7127°W		Hc2, Hc17, Hc18(6)			
Pelican Bay Trail	34.0222°N, 119.6906°W				N97, N98, N99, N100	G04, G19, G61, G62
Portezuela	34.0051°N, 119.7508°W				N112, N113	G04, G64
Lagunitas Secas	34.0320°N, 119.8033°W				N111	G19
CA: Santa Barbara Co., Santa Rosa Island						
Bee Canyon	33.9607°N, 120.2004°W	H35(3)		Tp5(4)		
Southeast Anchorage	33.9797°N, 119.9990°W	H10, H36		Tp5, Tp6, Tp7(2)		
Officers Beach	33.9094°N, 120.0936°W	H37(2), H38				
Arlington Canyon mouth	34.0053°N, 120.1762°W	H30(2)	Hc1, Hc11			
Cow Canyon mouth	34.0200°N, 120.1058°W		Hc9, Hc10, Hc18(5)			
Torrey pines grove	33.9828°N, 120.0220°W				N102	G19
Upper Cherry Canyon	33.9842°N, 120.0734°W				N104	—
Windmill Canyon	33.9850°N, 120.0764°W				N102, N105, N106	G04 (2), G19
Cherry Canyon	33.9979°N, 120.0614°W				N101	(G04, G19)
Lobo Canyon	34.0040°N, 120.0914°W				N104 (3)	G04(2), G19(2)
CA: Santa Barbara Co., San Miguel Island						
Simonton Cove	34.0628°N, 120.3735°W	H30(3), H58		Tp5(2), Tp22		
Cuyler Harbor	34.0460°N, 120.3515°W	H38(3), H51		Tp5(7)	N102	G04
Nidever Canyon	34.0418°N, 120.3534°W				N102, N114, N115	G04(2), G63
Willow Canyon	34.0380°N, 120.3169°W				N102	G04
CA: Los Angeles Co., Santa Catalina Island						
Little Harbor	33.3857°N, 118.4740°W		Hc1(7)	Tp14		
Ben Weston Beach	33.3680°N, 118.4812°W		Hc1	Tp15(9)		
South Two Harbors	33.3566°N, 118.4483°W		Hc1, Hc2			
Blackjack Road	33.3919°N, 118.4001°W				N107(2), N108(3)	G05(3), G65

TABLE 1. Continued.

Locality	Coordinates	*Hypocaccus lucidulus* Haplotypes	*Hadrotes crassus* Haplotypes	*Thinopinus pictus* Haplotypes	*Nyctoporis carinata*	
					COI Haplotypes	GFT Haplotypes
nr. Echo Lake	33.3974°N, 118.3946°W				N107, N108, N109, N110	G01, G05(2)
CA: Ventura Co., San Nicolas Island						
Thousand Springs	33.2836°N, 119.5300°W		Hc1(2), Hc2	Tp8(3), Tp9, Tp11, Tp12(2), Tp13		
Sissy Cove	33.2643°N, 119.4857°W		Hc1(7)	Tp8, Tp10		
Sandspit	33.2276°N, 119.4364°W	H41, H42(2), H43				
Southside dunes	33.2263°N, 119.5151°W	H9(2), H16, H39(2), H40				
CA: Los Angeles Co., San Clemente Island						
BUDS Beach	33.0282°N, 118.5875°W	H44(4)	Hc1, Hc2(2)			
Flasher Road dunes	33.0045°N, 118.5775°W	H45(3), H46(2), H47				
Graduation Beach	33.0303°N, 118.5789°W		Hc12(2), Hc13, Hc14			
West Cove	33.0165°N, 118.5958°W		Hc15(2), Hc16			
Northern Mainland						
Sonoma Co., Salmon Ceek	38.3503°N, 123.0666°W					
Monterey Co., Marina Beach	36.6986°N, 121.8095°W	H5(7), H6, H7, H8				
Monterey Co., Pfeiffer Beach	36.2384°N, 121.8162°W	H12(10)				
Monterey Co., UC Big Creek Reserve	36.0701°N, 121.6000°W		Hc1(8)			
San Luis Obispo Co., Arroyo de la Cruz	35.7097°N, 121.3107°W		Hc1(6), Hc2, Hc4(2), Hc5, Hc6, Hc7			
San Luis Obispo Co., Morro Strand	35.3850°N, 120.8645°W	H13, H14, H15, H16(2), H17, H18, H19, H20		Tp4		
San Luis Obispo Co., Montana de Oro	35.2935°N, 120.8788°W	H16, H17(2), H28, H29, H33	Hc2	Tp4(6), Tp14, Tp16(2), Tp17, Tp18, Tp19		
San Luis Obispo Co., Oceano Dunes	35.0383°N, 120.6309°W	H17, H25(7), H26, H27		Tp3(8), Tp21		

TABLE 1. Continued.

Locality	Coordinates	*Hypocaccus lucidulus* Haplotypes	*Hadrotes crassus* Haplotypes	*Thinopinus pictus* Haplotypes	*Nyctoporis carinata*	
					COI Haplotypes	GFT Haplotypes
Central Mainland						
Santa Barbara Co., Coal Oil Point Reserve	34.4133°N, 119.8833°W	H2(3), H4, H30(2)				
Santa Barbara Co., Coal Oil Point Reserve	34.4100°N, 119.8800°W	H1, H2, H3, H4		Tp1(9), Tp2		
Ventura Co., Ventura Harbor	34.2461°N, 119.2684°W	H2, H22, H23(2), H24				
Ventura Co., McGrath State Beach	34.2331°N, 119.2617°W	H2(2), H21, H22(2)				
Los Angeles Co., Dockweiler Bluff	33.9213°N, 118.4313°W	H2, H30, H31(2), H32(3)				
Los Angeles Co., El Segundo Beach	33.9172°N, 118.4289°W	H22				
Santa Barbara Co., El Capitan	34.4545°N, 120.0265°W		Hc2, Hc18			
Southern Mainland						
San Diego Co., Border Fields	33.5377°N, 117.1237°W	H34				

Analyses

Our most basic questions focused on the number of colonizations of the islands from the mainland, relying on a robust phylogeny of island and mainland haplotypes. All sequences for each species were filtered for unique haplotypes using Collapse (ver. 1.2; Posada 2006). Phylogenetic trees of unique haplotypes of all species were generated in MrBayes (ver. 3.1.2; Huelsenbeck and Ronquist 2001). Models were estimated using MrModelTest; the best model was selected as indicated by the Akaike information criterion (AIC). For all MrBayes runs, we ran 4,000,000 generations, with 4 chains, 3 of them heated with the temperature at 0.2, sampling every 1000 generations. The first 25% of the resulting trees were discarded as burn-in, and a majority-rule consensus was generated from the remainder, with consensus indices as posterior probabilities.

Trees were rooted with outgroups (with GenBank accession numbers) as follows: *T. pictus* rooted with the old world *Hadropinus fossor* Sharp (GU380341) and *Hadrotes crassus* (GU226635), both close relatives within the subtribe Staphylinina; *Ha. crassus* rooted with *Hadropinus fossor* and *T. pictus* (GU226619); *Hy. lucidulus* rooted with congener *Hy. bigemmeus* (LeConte) (GU380342 and GU380343); *N. carinata* rooted internally following the results of Polihronakis and Caterino (2010a) and lacking close relatives. Island colonizations were reconstructed on the complete rooted Bayesian topologies by using a binary character in parsimony (using MacClade v 4.06; Maddison and Maddison 2003), scoring each haplotype as present on the mainland or the islands or both (polymorphic). Given the low divergences among some haplotypes and the possibility of direct ancestor-descendant relationships among some, we also used TCS to generate parsimony network topologies (Clement et al. 2000) with all individuals (except outgroups) included.

The relative genetic diversities of island versus mainland populations were assessed using several measures of gene diversity and haplotype richness. Within each species we examined the contribution of each island population to total genetic diversity by using C statistics (Petit et al. 1998) calculated with the program Contrib (ver. 1.02; Petit 2006). These statistics use haplotype frequency data,

corrected via rarefaction, to assess relative diversity and differentiation of population samples. We report corrected allelic richness $r(N)$, where N is the minimum number of samples in any population, and C_T is the relative contribution of each population to total allelic richness. Where multiple mainland populations were available, they were grouped into the following categories: "northern" for north of Point Conception; "central" for Point Conception to Palos Verdes Peninsula; and "southern" for south of Palos Verdes. For inland populations (*N. carinata* only), these groups included "northern" for Sierra Nevada Mountains, Tehachapi Mountains, Santa Lucia Mountains, Northwest and Central Transverse Ranges, and Santa Ynez Mountains; "central" for Sierra Pelona, San Gabriel Mountains, and San Bernardino Mountains; and "southern" for San Jacinto Mountains. Finally, to assess level of sequence divergence (or phylogenetic distinctness), we calculated nucleotide diversity (π) for each population using Arlequin (ver. 3.1.1; Excoffier et al. 2005).

To examine phylogeographic structure among islands and between islands and the mainland, we conducted AMOVA analyses in Arlequin under 4 alternative models: a 2-group model (all island populations vs. all mainland populations); a 3-group model (northern islands/southern islands/mainland); a 4-group model (northern islands/mainland north of Pt. Conception/southern islands/mainland south of Pt. Conception); and an $n + 1$ model, separating all n islands occupied by each species plus the mainland. To detect and localize possible interisland and island–mainland connections, we calculated Phi_{ST} values (also in Arlequin) with all populations considered independent (including however many mainland populations were available). Interpopulation divergences were based on Tamura–Nei corrected distances.

RESULTS

Phylogenetic Patterns

NYCTOPORIS CARINATA.—In *Nyctoporis carinata,* the mitochondrial tree (Fig. 2) indicated a single colonization event for the northern islands (Fig. 3) and 2 separate colonizations for Santa Catalina Island. The 16 haplotypes occurring on the northern islands were interspersed, and individual populations did not appear to have been isolated long enough to achieve monophyly. Santa Cruz Island exhibited the greatest diversity, with 9 individuals each possessing a unique haplotype. Haplotypes on Santa Rosa and San Miguel showed much lower diversity. Those on San Miguel showed only direct relationships to ones present on Santa Rosa, reflecting their closer geographic proximity. The mainland origin for this lineage could not be specified very precisely. The closest mitochondrial haplotype occurs in the central portion of the mainland (specifically at Pine Mountain in the central Transverse Ranges), but these were separated by >10 changes and were not connected at the 95% confidence level in the haplotype network. The nuclear haplotype G04 is found on all the northern islands, as well as in northern and central mainland areas. Santa Cruz and Santa Rosa islands shared a unique GFT allele, with a closely related one restricted to San Miguel. Despite its much slower rate of evolution, the nuclear gene also indicates that the northern island lineage has been present long enough to have evolved multiple unique variants.

The Santa Catalina population of *N. carinata* represented 2 distinct colonizations from separate mainland lineages (Fig. 3), although both appear to have originated from the central region (specifically the San Gabriel Mountains), an area hosting a high diversity of both nuclear and mitochondrial lineages (see Polihronakis and Caterino 2010a). In the COI haplotype network, these 2 lineages were not connected at the 95% confidence level, although individuals exhibiting these haplotypes were intermingled at sampling sites on Santa Catalina. Three distinct nuclear haplotypes were present on Santa Catalina: one shared with northern and central mainland regions, one shared among all mainland regions, and one unique to the island.

HADROTES CRASSUS.—*Hadrotes crassus* exhibited 2 quite divergent clusters of mitochondrial haplotypes (Fig. 2), requiring 3 island colonizations (Fig. 3) total to explain their distribution on the Channel Islands. The largest cluster was dominated by a widespread haplotype (haplotype 1) present in the northern mainland region and all islands sampled (Santa Cruz and Santa Rosa, Santa Catalina, San Nicolas and San Clemente). Several similar haplotypes are found on Santa Cruz and Santa

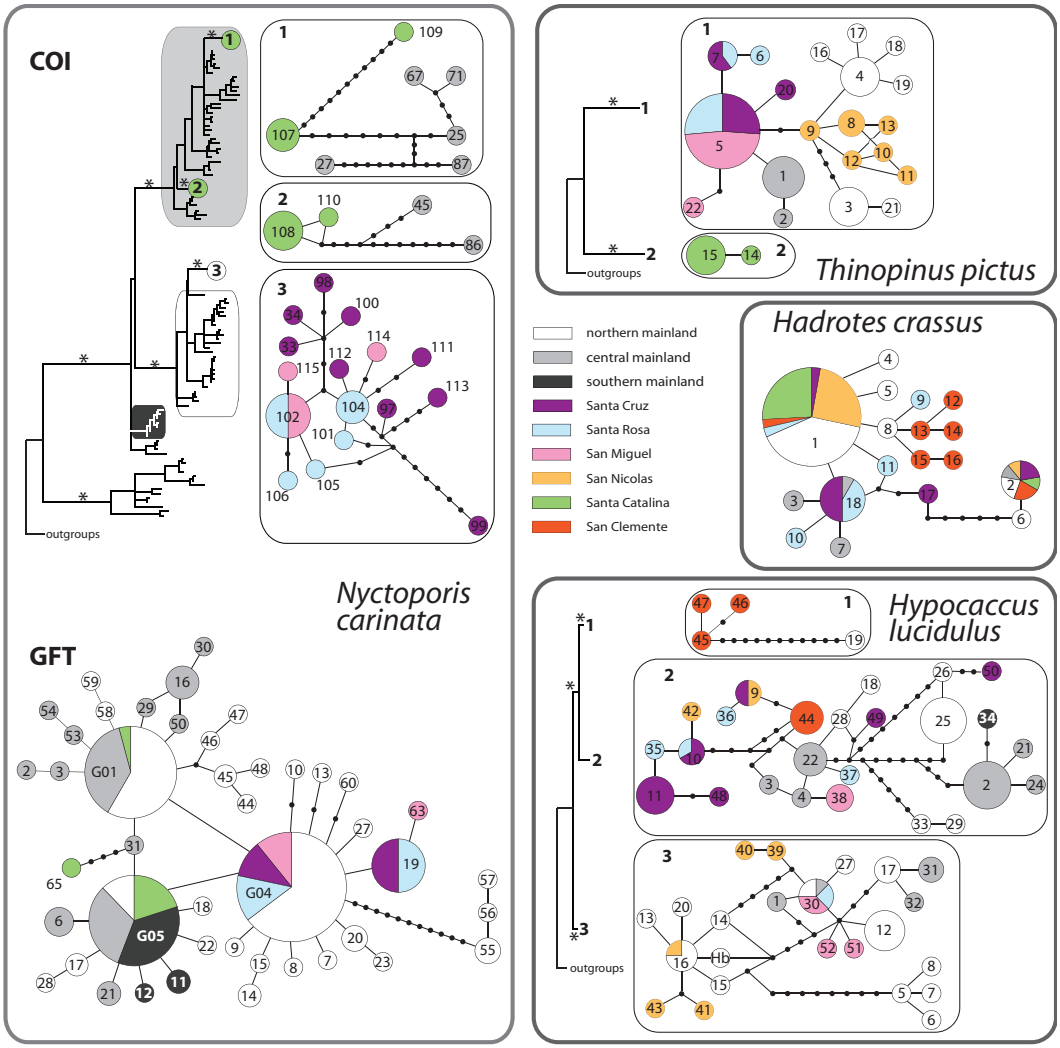

Fig. 2. Haplotype networks for all species, including networks for both COI and GFT for *Nyctoporis carinata.* Where multiple subnetworks for a gene/species could not be connected at the 95% confidence level, the relationships among them is indicated by an adjacent Bayesian phylogeny (rooted, although root not shown). In Bayesian trees, branch lengths are to the same scale among species but not between trees and networks (where changes are specifically indicated by small filled circles). Asterisks are shown for Bayesian branches relevant to island lineages that are supported at ≥95% posterior probability. Colors indicate localities of origin for individuals, with white and grays indicating mainland localities. Larger circles are proportional to numbers of individuals with each haplotype. Numbers within or next to circles correspond to haplotype numbers given in Table 1. Haplotype "Hb" in the *Hypocaccus lucidulus* network represents putative outgroup *Hypocaccus bigemmeus.*

Rosa islands, one of which is also present in the central mainland region (Santa Barbara County). A single haplotype from far north (haplotype 8, Sonoma County) on the mainland was found to be directly related to a highly diverse assemblage (5 haplotypes for 7 individuals) of haplotypes from San Clemente Island. A single Santa Rosa Island haplotype was also closely related to this northern one. Our sampling to the north was relatively sparse, however, so it remains to be seen whether this distant relationship might be bridged by intervening samples.

A second smaller cluster in *Ha. crassus* comprised 2 haplotypes: one (haplotype 2) was very widespread, again covering northern and

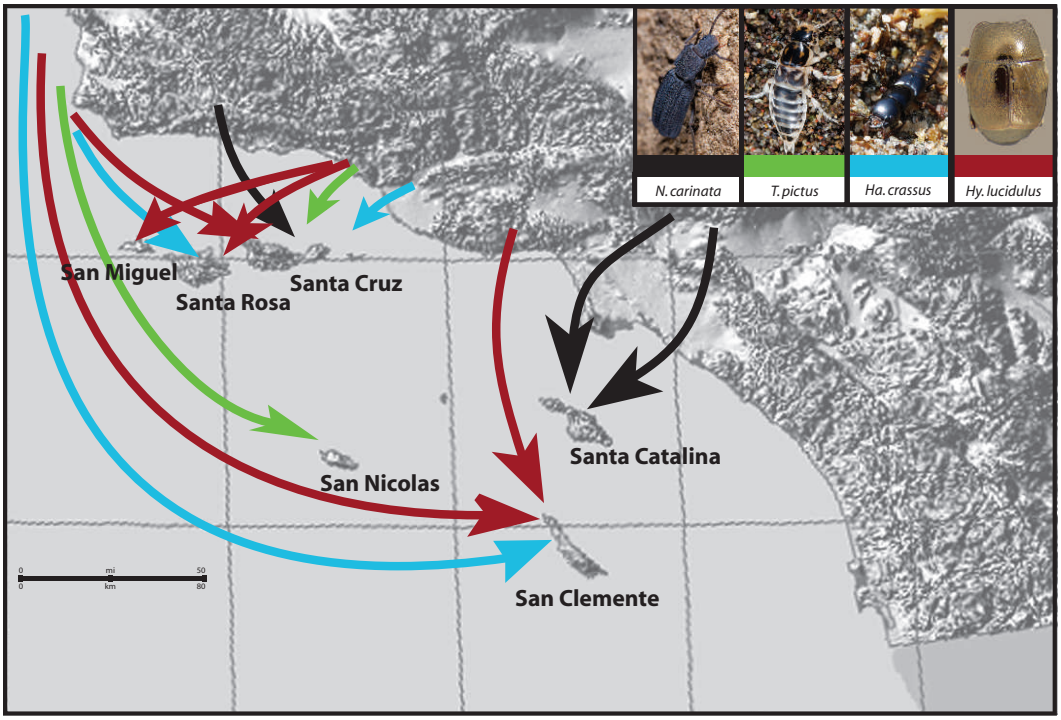

Fig. 3. Summary diagram showing hypothesized connections among islands and mainland for *Nyctoporis carinata, Thinopinus pictus, Hadrotes crassus,* and *Hypocaccus lucidulus.* Arrows represent reconstructed colonization events where mainland origin was unambiguous, as revealed by parsimony mapping on phylogenetic relationships among mtDNA haplotypes. Colored arrows are coded by species (see inset).

southern islands as well as central and northern mainland areas. These 2 divergent clusters were weakly linked by a single haplotype from Santa Cruz Island (haplotype 17), which was not closely related to anything else.

THINOPINUS PICTUS.—Most haplotypes of *Thinopinus pictus* were fairly closely related (Fig. 2), although the 2 haplotypes found on Santa Catalina Island were very divergent from anything else. The distribution of these haplotypes required at least 3 island colonizations (Fig. 3), though the source of the Santa Catalina population cannot be reconstructed. The 3 northern islands sampled mostly formed a tight cluster, with Santa Cruz and Santa Rosa islands sharing haplotypes 5 and 7, the former also found on San Miguel Island. Each northern island also hosted unique haplotypes. The closest mainland haplotypes to these northern islands were found in the central region, specifically along the Santa Barbara County coast. San Nicolas Island exhibited high diversity, with the 10 individuals exhibiting 6 closely interrelated haplotypes. The closest relatives to these are found exclusively in the northern mainland region, specifically in San Luis Obispo County.

HYPOCACCUS LUCIDULUS.—This species exhibited limited phylogeographic structure (Fig. 2), with at least 6 colonization events required to explain their distribution on the Channel Islands (Fig. 3). Haplotype diversity was very high (52 haplotypes for 126 individuals), and these were resolved into 3 well-supported lineages (resolved as 3 disconnected networks by TCS). However, despite well-supported relationships among haplotypes within these lineages, haplotype relationships showed little concordance with geography. One large lineage, dominated by haplotypes from north of Point Conception, was resolved as sister to the remaining two. This lineage included haplotypes from both northern (Santa Rosa and San Miguel) and southern (San Nicolas) islands, with the

TABLE 2. Results of Contrib analyses, with corrected allelic richness ($r[N]$), relative contribution of each population to total allelic richness (C_T), and nucleotide diversity (π). Multiple values for nucleotide diversity represent values for all populations lumped into northern and central mainland groups.

Species	Population	$r(N)$	C_T	π (%)
Hy. lucidulus	Mainland north	5.5	0.004	8.19, 13.3
	Mainland central	5.1	0.0	12.91, 11.6, 11.39
	Mainland south	N/A	N/A	0
	San Miguel Isl.	3.0	–0.005	9.611
	Santa Rosa Isl.	4.7	–0.005	10.13
	Santa Cruz Isl.	3.9	0.001	5.68
	San Nicolas Isl.	5.6	0.002	13.73
	San Clemente Isl.	2.9	0.004	12.11
Ha. crassus	Mainland north	1.2	–0.035	0, 0, 4.85
	Mainland central	3.0	0.051	6.5
	Santa Rosa Isl.	1.8	0.026	1.39
	Santa Cruz Isl.	1.5	0.016	4.27
	San Nicolas Isl.	0.4	–0.057	2.4
	San Clemente Isl.	2.6	0.055	5.87
	Santa Catalina Isl.	0.4	–0.057	2.4
T. pictus	Mainland north	3.4	0.033	3.12
	Mainland central	0.8	0.033	0.2
	San Miguel Isl.	0.8	–0.048	0.6
	Santa Rosa Isl.	2.0	–0.042	28.43
	Santa Cruz Isl.	1.0	–0.042	0.64
	San Nicolas Isl.	4.2	0.033	40.18
	Santa Catalina Isl.	0.8	0.033	10.2
N. carinata	Mainland north	3.8	0.003	4.51, 17.13, 17.12, 31.98, 36.07, 25.11, 4.60
	Mainland central	3.9	0.003	18.81, 16.38, 16.36
	Mainland south	3.5	0.004	17.24
	San Miguel Isl.	2.0	–0.009	2
	Santa Rosa Isl.	2.4	–0.009	1.91
	Santa Cruz Isl.	4.0	0.004	6.17
	Santa Catalina Isl.	2.1	0.004	17.19

central mainland sharing a haplotype with the northern islands. A small haplotype group was found predominantly on San Clemente Island (haplotypes 45–47), with a distant relative found in the northern parts of the mainland. The largest haplotype lineage included the majority of haplotypes from the central part of the mainland (Santa Barbara, Ventura, and Los Angeles counties), a smaller proportion from farther north on the mainland, the single southern mainland haplotype (from San Diego County), the majority of haplotypes found on the northern islands, and an additional common haplotype from San Clemente Island. Haplotype 10 in this cluster was found on Santa Cruz and Santa Rosa, with the closely related haplotype 42 on San Nicolas. Haplotype 9 was shared by Santa Cruz and San Nicolas islands, with the closely related haplotype 36 on Santa Rosa. Haplotype 44 from San Clemente Island was closest to a mainland haplotype found in the central region (the Los Angeles and Ventura county coasts, haplotype 22). The central mainland region is also directly related to single haplotypes from Santa Rosa (haplotype 37) and San Miguel (haplotype 38) islands. Finally, 2 unique haplotypes from Santa Cruz Island (haplotypes 49–50) were most closely related to isolated haplotypes occurring north of Point Conception on the mainland.

Diversity Patterns

Channel Islands populations of most species showed little indication of reduced genetic diversity compared to mainland populations that were sampled. Rather, diversity was high in nearly all species studied, by all measures (Table 2). San Nicolas Island especially emerged as hosting unusually high genetic diversity, exhibiting higher allelic richness (corrected by rarefaction for sampling unevenness) and nucleotide diversity than any other population, island or mainland, for both *Hypocaccus lucidulus* and *Thinopinus pictus.* In *Hadrotes crassus*, though the northern mainland populations led in these diversity measures, the San Clemente Island

TABLE 3. Phi_{ST} values for island–island population comparisons and island–mainland population comparisons. Asterisks indicate significant isolation between areas. Samples were not available for comparisons marked N/A. Mainland areas marked as "Montane" are noncoastal.

	Species	Santa Cruz	Santa Rosa	San Miguel	San Nicolas	San Clemente	Santa Catalina
Island–island comparisons							
Santa Rosa	*T. pictus*	0.033					
	N. carinata	0.117*					
	Ha. crassus	0.081					
	Hy. lucidulus	0.097					
San Miguel	*T. pictus*	0.170*	0.166*				
	N. carinata	0.120*	0.023				
	Hy. lucidulus	0.544*	0.240*				
San Nicolas	*T. pictus*	0.787*	0.725*	0.784*			
	Ha. crassus	0.130	0.108*	N/A			
	Hy. lucidulus	0.397*	0.154*	0.069			
San Clemente	*Ha. crassus*	0.138*	0.234*	N/A	0.135*		
	Hy. lucidulus	0.494*	0.318*	0.381*	0.294*		
Santa Catalina	*T. pictus*	0.996*	0.993*	0.996*	0.992*		
	N. carinata	0.707*	0.764*	0.707*	N/A	N/A	
	Ha. crassus	0.130	0.108*	N/A	–0.111	0.135	N/A
Mainland–island comparisons							
Sonoma/Northern	*Ha. crassus*	–0.094	0.265	N/A	–0.200	–0.725	–0.200
Big Sur/Northern	*N. carinata*	0.898*	0.938*	0.930*	N/A	N/A	0.752*
	Ha. crassus	0.316*	0.354*	N/A	–0.024	0.265*	–0.024
	Hy. lucidulus	0.657*	0.503*	0.309*	0.269*	0.505*	N/A
S.L.O./Central	*T. pictus*	0.561*	0.556*	0.557*	0.493*	N/A	0.978*
	N. carinata	0.614*	0.717*	0.635*	N/A	N/A	0.607*
	Ha. crassus	0.013	0.111	N/A	–0.024	0.054	–0.024
	Hy. lucidulus	0.403*	0.228*	0.125*	0.048	0.290*	
StaYnezMts/Central	*T. pictus*	0.735*	0.666*	0.712*	0.858*	N/A	0.998*
	N. carinata	0.422*	0.473*	0.404*	N/A	N/A	0.301*
	Ha. crassus	–0.163	0.114	N/A	0.145	0.043	0.145
	Hy. lucidulus	0.359*	0.119	0.152	0.153	0.323*	N/A
Ventura/Central	*Hy. lucidulus*	0.370*	0.187*	0.324*	0.240*	0.350*	N/A
LA/Central	*Hy. lucidulus*	0.588*	0.344*	0.067	0.126	0.379*	N/A
BorderField/Southern	*Hy. lucidulus*	0.663	0.431	0.553	0.388	0.479	N/A
SWSierra/Montane	*N. carinata*	0.724*	0.759*	0.693*	N/A	N/A	0.699*
Breck&Piute/Montane	*N. carinata*	0.941*	0.982*	0.983*	N/A	N/A	0.839*
Tehachapis/Montane	*N. carinata*	0.779*	0.808*	0.760*	N/A	N/A	0.719*
NW.Trv.Rg/Montane	*N. carinata*	0.504*	0.569*	0.523*	N/A	N/A	0.618*
Cen.Trv.Rg/Montane	*N. carinata*	0.883*	0.939*	0.929*	N/A	N/A	0.630*
SierraPelona/Montane	*N. carinata*	0.734*	0.798*	0.738*	N/A	N/A	0.366*
SanGabriels/Montane	*N. carinata*	0.712*	0.754*	0.715*	N/A	N/A	0.311*
SanBernardinos/Montane	*N. carinata*	0.728*	0.780*	0.733*	N/A	N/A	0.413*
SanJacintos/Montane	*N. carinata*	0.732*	0.780*	0.733*	N/A	N/A	0.557*

population ranked a close second. The San Clemente Island population also ranked second in nucleotide diversity for *Hy. lucidulus*, although both central and northern mainland populations showed higher allelic richness. In nucleotide diversity, Santa Rosa and Santa Catalina island populations of *T. pictus* ranked second and third, respectively, although the northern mainland population exceeded Santa Rosa in allelic richness. Of all these species, only in *N. carinata* did island populations show lower genetic diversity than most mainland populations.

Population Structure Among Island/Mainland Populations

The phylogeographic structuring among islands and species was predominantly high. Based on pairwise Phi_{ST} analyses (Table 3), we found significantly restricted gene flow among most islands in most species. The exceptions mostly involved pairs of northern islands. In *N. carinata*, though Santa Cruz and Santa Rosa Islands were significantly separated, Santa Rosa and San Miguel were not. In *Ha. crassus*, most significant comparisons involved Santa Rosa Island (especially in comparison

TABLE 4. Results of AMOVA analyses, with groups as defined in text. Asterisks indicate significance. Results are shown separately for the 2 markers examined for *Nyctoporis carinata.* Some tests were inapplicable to some species depending on sampling.

Species	Groups	Structure	Among-group variation (%)	Among-population variation (%)	Within-population variation (%)
Ha. crassus	2	Island/Mainland	–4.87	11.83*	93.05*
T. pictus	2	Island/Mainland	–23.9	118.63*	5.26*
Hy. lucidulus	2	Island/Mainland	6.43	26.36*	67.22*
N. carinata	2	Island/Mainland (mt)	8.87	59.56*	31.57*
		(gft)	1.39	53.94*	44.68
Ha. crassus	3	N.Isl./S.Isl./Mainland	0.53	8.7	90.77*
T. pictus	3	N.Isl./S.Isl./Mainland	10.25	85.08*	4.67*
Hy. lucidulus	3	N.Isl./S.Isl./Mainland	7.14	25.44*	67.42*
N. carinata	3	N.Isl./S.Isl./Mainland (mt)	11.56	57.37*	31.07*
		(gft)	–0.49	55.34*	45.15*
N. carinata	3	N.Isl. + N.Mainl./S.Isl + S.Mainl./SierraNev. (mt)	37.43*	33.49*	29.08*
		(gft)	39.69*	22.94*	37.37*
Ha. crassus	4	N.Isl./S.Isl./N.Mainl./S.Mainl.	2.11	7.41	90.48*
T. pictus	4	N.Isl./S.Isl./N.Mainl./S.Mainl.	–33.62	128.63*	4.99*
Hy. lucidulus	4	N.Isl./S.Isl./N.Mainl./S.Mainl.	8.71	23.11*	68.17*
Hy. lucidulus	4	N.Isl./Nic/Clem/Mainland	8.76	24.15*	67.09*
N. carinata	4	N.Isl./S.Isl./N.Mainl./S.Mainl. (mt)	12.11	55.68*	32.22*
		(gft)	0.81	54.97*	44.22*
Ha. crassus	5	N.Isl./Cat/Nic/Clem/Mainland	1.54	7.5	90.96*
N. carinata	5	N.Isl./S.Isl./N.Mainl./S.Mainl./SierraNev. (mt)	36.92*	32.05*	31.03*
		(gft)	31.92*	26.02*	42.06
Ha. crassus	6	$n + 1$	0.25	8.88	90.87*
T. pictus	6	$n + 1$	83.77	11.79*	4.45*
Hy. lucidulus	6	$n + 1$	8.05	24.44*	67.52*
N. carinata	5	$n + 1$ (mt)	–11.5	75.71*	35.8*
		(gft)	–28.27	74.21*	54.06*

with the southern islands), whereas Santa Cruz Island was not significantly isolated from several other islands, including most of the southern islands. Finally, in *Hy. lucidulus,* Santa Cruz and Santa Rosa Islands were not significantly separated, though all other interisland comparisons showed significant isolation.

Given the significant restriction in gene flow among most individual islands, it was interesting that some island-mainland population pairs were not significantly isolated according to Phi_{ST}. Some ongoing connectivity is indicated among mainland and insular populations in 2 of the 4 species. The lowest level of island isolation was found in *Ha. crassus,* with only extreme northern populations showing significant isolation from any Channel Island population. In *Hy. lucidulus,* Phi_{ST} indicated that central mainland (Santa Barbara County) populations were not significantly separated from those on the northern islands. Island populations of *N. carinata,* on the other hand, were all significantly isolated from any mainland population, as were those of *T. pictus.*

Very few of the 4 alternative groupings of islands or island-mainland populations tested indicated significant similarity according to AMOVA (Table 4). There was no significant among-group variation in any of the 2-group comparisons (mainland vs. island), and these values were <10% for all species. When the southern islands were separated in the 3-group comparisons, the among-group variation increased in all cases, although it remained small (<12%) relative to variation within and among populations in all species except *N. carinata.* The only significant among-group variation seen in *N. carinata* was in the 3-group scenario, which was likely driven by deep divergence among mainland populations, as reported in Polihronakis and Caterino (2010a). In general, among-group variation increased with greater partitioning among mainland populations, and few groupings of the island populations captured patterns of variation well.

DISCUSSION

Substantial work has been done on relationships of organisms on California's Channel Islands, much of it with the goal of determining the conservation status of particular islands' populations. In general, previous work has found many island populations to be highly divergent from each other and from mainland populations. In the current study, patterns of relationships are sufficiently varied to preclude inference of general patterns. None of the 4 widespread species examined here resolve island populations to be collectively monophyletic. All species require multiple colonization events to explain the distribution of haplotypes, from at least 2 or 3 colonizations in *Ha. crassus*, *T. pictus*, and *N. carinata* to at least 6 in *Hy. lucidulus*. In the latter case, there appear to have been back-colonizations to the mainland as well (or, less parsimoniously, several more island colonizations than this).

The only predictable and consistent pattern from previous work is the generally close relationship among populations on the northern islands of Anacapa, Santa Cruz, Santa Rosa, and San Miguel—expected on the basis of their Pleistocene unity as Santarosae. These islands share some endemic taxa (the tortricid moth *Argyrotaenia franciscana insulana:* Landry et al. 1999; the slender salamander *Batrachoseps pacificus:* Jockusch and Wake 2002) and exhibit close population relationships in more widespread species in a variety of taxa, including dune spiders (*Lutica:* Ramirez and Beckwitt 1995), deer mice (*Peromyscus maniculatus:* Ashley and Wills 1987, 1989), side-blotched lizard (*Uta stansburiana:* Mahoney et al. 2003), Loggerhead Shrike (*Lanius ludovicianus:* Eggert et al. 2004, Caballero and Ashley 2011), and marine eelgrass (*Zostera pacifica:* Coyer et al. 2008).

The species examined here largely support this pattern, most distinctly in *N. carinata* where the 3 northern islands sampled (Santa Cruz, Santa Rosa, San Miguel) form a strongly supported, divergent clade unrelated to populations on the one southern island sampled, Santa Catalina. These 3 northern islands also form a distinct cluster in *T. pictus*. In *Ha. crassus* and *Hy. lucidulus*, however, such relationships, though evident, are complicated by low levels of divergence or high migration rates or both. Furthermore, all northern islands have unique mitochondrial haplotypes in all species sampled. So if shared haplotypes are indicative of recent ancestry, there is also evidence that significant evolution has occurred since isolation. On the other hand, it is also possible that the super-island Santarosae exhibited within-island phylogeographic structure prior to separation into the modern islands. Similar isolation-by-distance patterns have been detected within islands, notably within the plant *Lithophragma maximum*, which is endemic to and highly variable within San Clemente Island (Furches et al. 2009). Clearly the presence of many taxa on the northern Channel Islands predates the most recent separation of these islands, and the sharing of haplotypes/alleles among them cannot be definitively attributed to either modern or historical connections.

The southern islands (Santa Catalina, San Clemente, and San Nicolas) show much lower phylogenetic coherence in the species studied here. Previous studies have suggested relationships between Santa Catalina and San Clemente islands, in particular eelgrass (Coyer et al. 2008), side-blotched lizards (Mahoney et al. 2003), Loggerhead Shrikes (Eggert et al. 2004), and one species of dune beetle (Chatzimanolis et al. 2010). The species examined here show little indication of southern island relationships.

San Nicolas Island shows a close relationship to one or more northern sources in a substantial number of taxa. Several previous studies have supported relationships to the northern islands for a variety of taxa, including tortricid Lepidoptera (Landry et al. 1999, Rubinoff and Powell 2004), deer mice (Ashley and Wills 1987, 1989), eelgrass (Coyer et al. 2008), dune spiders (Ramirez and Beckwitt 1995), and dune beetles (Chatzimanolis et al. 2010). Some *Hy. lucidulus* haplotypes show a similar San Nicholas–northern island relationship. In other cases, the San Nicolas Island populations appear most closely related to mainland populations well to the north of the Channel Islands. Even more disjunct relationships are shown in *T. pictus*, where San Nicolas haplotypes are most closely related to some from north of Point Conception. This pattern is also evident in *Hy. lucidulus*, where a haplotype is shared between San Nicolas Island and northern mainland (San Luis Obispo) populations. The most interesting aspect of these northern relationships for San Nicolas Island is that in most cases they appear to be very recent, involving very closely related or even

identical haplotypes. This finding seems to point to a direct colonization route in line with the California Current, which follows the coast southward to Point Conception, continuing directly southward past the western edge of San Miguel Island, then southeastward toward San Nicolas Island rather than continuing along the coastline. Where relationships to the northern islands are observed, they may owe something to a closer proximity of San Nicolas to the northern islands during depressed sea levels (–120 m) in the Late Pleistocene (between 10–20,000 YPB; Vedder and Howell 1980).

In general, relationships of the island populations to the mainland cannot be attributed to any consistent source. Shared haplotypes and close phylogenetic relationships between the mainland north of Point Conception and one or more of the islands predominate in the species examined here. However, it is difficult to separate this result from sampling bias in coastal species in more northerly mainland areas—coastal habitats that have unfortunately been severely degraded by human activities. Still, our sampling from the Santa Barbara and Ventura areas is relatively strong, and these mainland areas closest to the northern islands have not contributed to island populations as strongly as areas farther north. This difference is surprising not only because of modern proximity, but because of the very small Pleistocene gap (<6 km) between eastern Santarosae and the mainland directly to the east (Powell 1985, 1994). Furthermore, continued colonization avenues from these near-shore sources have been documented, particularly by direct rafting following seasonal coastal floods (Wenner and Johnson 1980). Where northern relationships have been noted, they have been considered a relictual link to a wetter past (Raven 1967, Powell 1994). Our results, especially where haplotypes are shared, show a much more recent, probably continuing, route for gene flow from northern populations (especially *Hy. lucidulus* and *Ha. crassus*).

Results of our own previous work involving Channel Islands beetles span much of the range reported here, even though until now these results have included only Santa Cruz Island samples. Several species have shown the high levels of island–mainland migration seen here in *Hy. lucidulus,* revealing multiple unrelated colonizations and source areas. These include *Cercyon fimbriatus,* an inhabitant of coastal wrack (Chatzimanolis and Caterino 2008); *Stictotarsus striatellus,* an inhabitant of freshwater streams and ponds (Short and Caterino 2009); and *Calathus ruficollis,* a widespread inhabitant of drier terrestrial environments (Chatzimanolis and Caterino 2007a). In the latter (a flightless species), we suspected anthropogenic introductions to account for at least some of the apparent island diversity. Other species previously examined have shown more-restricted patterns of genetic variation on and among islands. Island populations of the freshwater aquatic *Anacaena signaticollis* (Santa Cruz) and the terrestrial fungus-feeding *Phloeodes plicatus* (Santa Cruz, Santa Catalina) represent shallowly independent lineages (the latter separate on the 2 islands; Short and Caterino 2009, Polihronakis and Caterino 2010b). Santa Cruz and Santa Rosa Islands host a deeply divergent lineage of the litter-inhabiting weevil *Geodercodes latipennis* (Polihronakis et al. 2010). Thus the varied results of the present study are probably representative of a wide variety of species histories on the Channel Islands.

Many authors have sought explanations of phylogeographic structure in life history attributes, generally habitat association (Ribera and Vogler 2000, Marten et al. 2006, Abellán et al. 2009) or behavior (especially, in insects, the ability to fly; Smith and Farrell 2006). The underlying commonality in such explanations is dispersal propensity (Avise 1994). Our results do show some similarities with other studies of island and coastal taxa (especially Papadopoulou et al. 2009) in that the species most closely associated with coastal environments—*Ha. crassus, T. pictus* (both associated with intertidal wrack), and *Hy. lucidulus* (associated with coastal sand dune)—show lower levels of phylogeographic structure than the lone representative of more interior habitats, *N. carinata.* This pattern is presumably due to the highly dynamic nature of coastal habitats, which are subject to frequent short- and long-term disturbance (tidal and sea level fluctuations, respectively). Though this study was not designed to test the association of microhabitat and phylogeographic structure, previous work on the California mainland found generally similar patterns in these habitats (Chatzimanolis and Caterino 2008 vs. Caterino and Chatzimanolis 2009). Our results with respect to

flight capability also agree with these observations: the lone flying species represented here, *Hy. lucidulus,* does indeed show the largest number of island colonizations as well as the lowest interisland and island-mainland structuring. However, species within each of these categories often show extremely wide variance when multiple similar species are examined (results herein; Chatzimanolis and Caterino 2008, Caterino and Chatzimanolis 2009, Short and Caterino 2009), and it is apparent that any single ecological predictor provides only a rough expectation of population structure. Species-specific attributes and population size certainly play important roles as well.

Finally, high diversity was apparent on some islands, both in absolute terms given their areas and relative to mainland populations of similar extent (contra Frankham 1997). Our genetic contributions analyses reveal that several islands host exceptionally high levels of haplotype diversity, most notably San Clemente and San Nicolas. The latter is particularly remarkable if we accept its complete submergence in fairly recent time (<500,000 years). The levels of diversity found on San Nicolas in *T. pictus*, *Ha. crassus*, and *Hy. lucidulus* (as well as *Coelus pacificus;* Chatzimanolis et al. 2010) pose a challenge for this hypothesis. If its biota truly is that recent, the island has supported exceptional diversification over a short span of geological time. Some previous work on this subject has expressed concern with the potential loss of variability due to population depression during times of excessive grazing on the Channel Islands (Wallace and Helenurm 2009), but neither those results nor ours reveal unexpectedly low diversity in the islands. Rather, the opposite may be the case. (Furches et al. 2009, Wilson et al. 2009).

The finding of high levels of unique genetic diversity on California's Channel Islands suggests 2 important, nonexclusive explanations. First, it is quite possible that contemporary mainland populations are in fact more significantly depressed due to anthropogenic impacts. Mainland populations, especially in coastal species, have been extirpated in many areas due to a combination of beach grooming, recreational use, and invasive dune plants (Oppewall 1976, Powell 1981, Dugan et al. 2000, Connor et al. 2002). Indeed, it was impossible to find many of our focal species in historically suitable areas in Los Angeles and Orange counties. Obviously, there is no way to know what sort of diversity these areas once harbored. A previous study focused on mainland populations of one of these species did not reveal significant depression in highly impacted areas (Chatzimanolis and Caterino 2008), but island samples were not available to provide the contrast now observed. Second, it is possible that barriers to gene flow among islands helped prevent a significant amount of homogenization that might have occurred among better-connected mainland populations. Also, avoiding selective sweeps that continuous populations might experience and having genetic drift functioning on separate isolates might help maintain higher overall diversity, despite the seemingly inevitable tendency toward lower diversity within each island. Additional studies with greater density of within-island sampling will be necessary to begin to address these questions.

Despite many lingering and newfound mysteries, it is clear that, as a whole, California's Channel Islands host important levels of intraspecific diversity. Among the species examined here, there are several endemic lineages: most showing strong among-island diversification patterns and several exhibiting comparable or even greater diversity than conspecific (and similarly sampled) mainland populations. Given the patterns observed, it is clear that much of this diversity arose on the islands themselves. However, some of the islands' apparent diversity may also stand out as a result of declines in mainland populations in the southern part of the California Floristic Province. These and other potential explanations clearly justify further exploration, ideally with a multilocus approach to allow more detailed examination of biogeographic scenarios.

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LITERATURE CITED

ABELLÁN, P., A. MILLÁN, AND I. RIBERA. 2009. Parallel habitat-driven differences in the phylogeographic structure of two independent lineages of Mediterranean saline water beetles. Molecular Ecology 18: 3885–3902.

ASHLEY, M.V., AND C. WILLS. 1987. Analysis of mitochondrial DNA polymorphisms among Channel Island deer mice. Evolution 41:854–863.

_____. 1989. Mitochondrial DNA and allozyme divergence patterns are correlated among island deer mice. Evolution 43:646–650.

AVISE, J.C. 1994. Molecular markers, natural history, and evolution. Chapman and Hall, New York, NY.

CABALLERO, I.C., AND M.V. ASHLEY. 2011. Genetic analysis of the endemic island loggerhead shrike, *Lanius ludovicianus anthonyi.* Conservation Genetics 12: 1485–1493.

CALDERWOOD, J.A., A.M. WENNER, AND J.K. WETTERER. 2002. Argentine ants invade Santa Cruz Island, California. Pages 274–277 *in* D. Browne, K.L. Mitchell, and H.W. Chaney, editors, Proceedings of the Fifth California Islands Symposium, Santa Barbara, Santa Barbara Museum of Natural History. Santa Barbara, CA.

CATERINO, M.S. 2006. California beetle faunistics: 100 years after Fall. Coleopterists Bulletin. 60:167–191.

CATERINO, M.S., AND D.S. CHANDLER. 2010. A new species of *Actium* Casey (Staphylinidae: Pselaphinae) endemic to Santa Catalina Island, California. Coleopterists Bulletin 64:187–191.

CATERINO, M.S., AND S. CHATZIMANOLIS. 2009. Conservation genetics of three flightless beetle species in southern California. Conservation Genetics 10:203–216.

CATERINO, M.S., S. CHO, AND F.A.H. SPERLING. 2000. The current state of insect molecular systematics: a thriving Tower of Babel. Annual Review of Entomology 45: 1–54.

CHATZIMANOLIS, S., AND M.S. CATERINO. 2007a. Limited phylogeographic structure in the flightless ground beetle, *Calathus ruficollis*, in southern California. Diversity and Distributions 13:498–509.

_____. 2007b. Toward a better understanding of the "Transverse Range break": lineage diversification in southern California. Evolution 61:2127–2141.

_____. 2008. Phylogeography and conservation genetics of Californian coastal terrestrial communities: a comparative study using three beetles. Insect Conservation and Diversity 1:222–232.

CHATZIMANOLIS, S., L.A. NORRIS, AND M.S. CATERINO. 2010. Multi-island endemicity: phylogeography and conservation of *Coelus pacificus* (Coleoptera: Tenebrionidae) darkling beetles on the California Channel Islands. Annals of the Entomological Society of America 103:785–795.

CLEMENT, M., D. POSADA, AND K.A. CRANDALL. 2000. TCS: a computer program to estimate gene genealogies. Molecular Ecology 9:1657–1659.

CONNOR, E.F., J. HAFERNIK, J. LEVY, V.L. MOORE, AND J.K. RICKMAN. 2002. Insect conservation in an urban biodiversity hotspot, the San Francisco bay area. Journal of Insect Conservation 6:247–259.

COYER, J.A., K.A. MILLER, J.M. ENGLE, J. VELDSINK, A. CABELLO-PASINI, W.T. STAM, AND J.L. OLSEN. 2008. Eelgrass meadows in the California Channel Islands and adjacent coast reveal a mosaic of two species, evidence for introgression and variable clonality. Annals of Botany 101:73–87.

DARWIN, C. 1859. On the origin of species by the means of natural selection. John Murray, London.

DELANEY, K.S., AND R.K. WAYNE. 2005. Adaptive units for conservation: population distinction and historic extinctions in the Island Scrub-Jay. Conservation Biology 19:523–533.

DELANEY, K.S., S. ZAFAR, AND R.K. WAYNE. 2008. Genetic divergence and differentiation within the Western Scrub Jay (*Aphelocoma californica*). Auk 125:839–849.

DIBBLEE, T.W., AND H.E. EHRENSPECK. 2002. Geology of Santa Rosa Island, California. Pages 115–126 *in* D. Browne, K.L. Mitchell, and H.W. Chaney, editors, Proceedings of the Fifth California Islands Symposium, Santa Barbara, Santa Barbara Museum of Natural History.

DUGAN, J.E., D.M. HUBBARD, D.L. MARTIN, J.M. ENGLE, D.M. RICHARDS, G.E. DAVIS, K.D. LAFFERTY, AND R.F. AMBROSE. 2000. Macrofauna communities of exposed sandy beaches on the southern California mainland and channel islands. Pages 339–346 *in* D. Browne, K.L. Mitchell, and H.W. Chaney, editors, Proceedings of the Fifth California Islands Symposium, Santa Barbara, Santa Barbara Museum of Natural History.

EGGERT, L.S., N.I. MUNDY, AND D.S. WOODRUFF. 2004. Population structure of Loggerhead Shrikes in the California Channel Islands. Molecular Ecology 13: 2121–2133.

EMERSON, B.C. 2008. Speciation on islands: what are we learning? Biological Journal of the Linnean Society 95:47–52.

EXCOFFIER, L., G. LAVAL, AND S. SCHNEIDER. 2005. ARLEQUIN ver. 3.0: an integrated software package for population genetics data analysis. Evolutionary Bioinformatics 1:47–50.

FRANKHAM, R. 1997. Do island populations have less genetic variation than mainland populations? Heredity 78: 311–327.

FURCHES, M.S., L.E. WALLACE, AND K. HELENURM. 2009. High genetic divergence characterizes populations of the endemic plant *Lithphragma maximum* (Saxifragaceae) on San Clemente Island. Conservation Genetics 10:115–126.

GILLESPIE, R.G., AND G.K. RODERICK. 2002. Arthropods on islands: colonization, speciation, and conservation. Annual Review of Entomology 47:595–612.

HUELSENBECK, J.P., AND F. RONQUIST. 2001. MRBAYES: Bayesian inference of phylogenetic trees. Bioinformatics 17:754–755.

IRWIN D.E. 2002. Phylogeographic breaks without geographic barriers to gene flow. Evolution 56: 2383–2394.

JOCKUSCH, E.L., AND D.B. WAKE. 2002. Falling apart and merging: diversification of slender salamanders (Plethodontidae: *Batrachoseps*) in the American West. Biological Journal of the Linnean Society 76:361–391.

JUNAK, S., T. AYERS, R. SCOTT, D. WILKEN, AND D. YOUNG. 1995. A Flora of Santa Cruz Island. Santa Barbara Botanic Garden/CNPS, Santa Barbara.

KENNETT, D.J., J.P. KENNET, G.J. WEST, J.M. ERLANDSON, J.R. JOHNSON, I.L. HENDY, A. WEST, B.J. CULLETON, T.L. JONES, AND T.W. STAFFORD JR. 2008. Wildfire and abrupt ecosystem disruption on California's Northern Channel Islands at the Ållerød–Younger Dryas Boundary (13.0–12.9 ka). Quaternary Science Review 27:2528–2543.

KNOWLTON, J.L., C.J. DONLAN, G.W. ROEMER, A. SAMANIEGO-HERRERA, B.S. KEITT, B. WOOD, A. AGUIRRE-MUÑOZ, K.R. FAULKNER, AND B.R. TERSHY. 2007. Eradication of non-native mammals and the status of insular mammals on the California Channel Islands, USA, and Pacific Baja California Peninsula Islands, Mexico. Southwestern Naturalist 52:528–540.

LANDRY, B., J.A. POWELL, AND F.A.H. SPERLING. 1999. Systematics of the *Argyrotaenia franciscana* (Lepidoptera: Tortricidae) species group: evidence from mitochondrial DNA. Annals of the Entomological Society of America 92:40–46.

LOSOS, J.B., AND R.E. RICKLEFS. 2009. Adaptation and diversification on islands. Nature 457:830–836.

MACARTHUR, R.H., AND E.O. WILSON. 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ.

MADDISON, D.R., AND W.P. MADDISON. 2003. MacClade. Sinauer Associates, Sunderland, MA.

MAHONEY, M.J., D.S.M. PARKS, AND G.M. FELLERS. 2003. *Uta stansburiana* and *Elgaria multicarinata* on the California Channel Islands: natural dispersal or artificial introductions? Journal of Herpetology 37: 586–591.

MARTEN, A., M. BRANDLE, AND R. BRANDLE. 2006. Habitat type predicts genetic population differentiation in freshwater invertebrates. Molecular Ecology 15: 2643–2651.

MILLER, S.E. 1985. The California Channel Islands—past, present, and future: an entomological perspective Pages 3–28 *in* A.S. Menke and D.R. Miller, editors, Entomology of the California Channel Islands. Santa Barbara Museum of Natural History, Santa Barbara.

NAGANO, C.D. 1985. Distributional notes on the tiger beetles of the California Channel Islands. Pages 105–112 *in* A.S. Menke, and D.R. Miller, editors, Entomology of the California Channel Islands. Santa Barbara Museum of Natural History, Santa Barbara.

OPPEWALL, J.C. 1976. The saving of the El Segundo blue. Atala 3:25–28.

PAPADOPOULOU, A., I. ANASTASIOU, B. KESKIN, AND A.P. VOGLER. 2009. Comparative phylogeography of tenebrionid beetles in the Aegean Archipelago: the effect of dispersal ability and habitat preference. Molecular Ecology 18:2503–2517.

PECK, S.B. 1994. Diversity and zoogeography of the nonoceanic Crustacea of the Galapagos Islands, Ecuador (excluding terrestrial Isopoda). Canadian Journal of Zoology 72:54–69.

PETIT, R.J. 2006. Contrib, ver. 1.02. [Cited 1 February 2012]. Available from: http://www.pierroton.inra.fr/genetics/labo/Software/Contrib/

PETIT, R.J., A.E. MOUSADIK, AND O. PONS. 1998. Identifying populations for conservation on the basis of genetic markers. Conservation Biology 12:844–855.

PHILBRICK, R. 1980. Distribution and evolution of endemic plants of the California Islands. Pages 173–188 *in* D.M. Power, editor, The California Islands: proceedings of a multidisciplinary symposium, Santa Barbara, Santa Barbara Museum of Natural History.

POLIHRONAKIS, M., AND M.S. CATERINO. 2010a. Multilocus phylogeography of the flightless darkling beetle *Nyctoporis carinata* (Coleoptera: Tenebrionidae) in the California Floristic Province: deciphering an evolutionary mosaic. Biological Journal of the Linnean Society 99:424–444.

_____. 2010b. Contrasting patterns of phylogeographic relationships in sympatric sister species of ironclad beetles (Zopheridae: *Phloeodes* spp.) in California's Transverse Ranges. BMC Evolutionary Biology 10: 1–11.

POLIHRONAKIS, M., S. CHATZIMANOLIS, AND M.S. CATERINO. 2010. Elucidating the phylogeographic structure among a mosaic of unisexual and bisexual populations of the weevil *Geodercodes latipennis* (Coleoptera: Curculionidae) in the Transverse Ranges of southern California. Biological Journal of the Linnean Society 101:935–948.

PORCASI, P., J.F. PORCASI, AND C. O'NEILL. 1999. Early Holocene coastlines of the California Bight: the Channel Islands as first visited by humans. Pacific Coast Archaeological Society Quarterly 35:1–24.

POSADA, D. 2006. Collapse (ver. 1.2): describing haplotypes from sequence alignments. University of Vigo.

POWELL, J.A. 1981. Endangered habitats for insects: California coastal sand dunes. Atala 6:41–58.

POWELL, J.A. 1985. Faunal affinities of the Channel Islands Lepidoptera: a preliminary overview. Pages 69–94 *in* A.S. Menke and D.R. Miller, editors, Entomology of the California Channel Islands. Santa Barbara Museum of Natural History, Santa Barbara.

_____. 1994. Biogeography of Lepidoptera on the California Channel Islands. Pages 449–464 *in* W.L. Halvorson and G.J. Maender, editors, The Fourth Channel Islands Symposium: update on the status of resources, Santa Barbara, Santa Barbara Museum of Natural History.

RAMIREZ, M.G., AND R.D. BECKWITT. 1995. Phylogeny and historical biogeography of the spider genus *Lutica* (Araneae, Zodariidae). Journal of Arachnology 23: 177–193.

RAVEN, P. 1967. The floristics of the California Islands. Pages 57–67 *in* R. Philbrick, editor, Proceedings of the Symposium on the Biology of the California Islands, Santa Barbara, Santa Barbara Botanic Garden.

REEDER, L.A., T.C. RICK, AND J.M. ERLANDSON. 2008. Forty years later: what have we learned about the earliest human occupations of Santa Rosa Island, California? North American Archaeologist 29:37–64.

RENTZ, D.C.F., AND D.B. WEISSMAN. 1982. Faunal affinities, systematics, and bionomics of the Orthoptera of the California Channel Islands. University of California Publications in Entomology 94:1–240.

RIBERA, I., AND A.P. VOGLER. 2000. Habitat type as a determinant of species range sizes: the example of

lotic-lentic differences in aquatic Coleoptera. Biological Journal of the Linnean Society 71:33–52.

RUBINOFF, D., AND J.A. POWELL. 2004. Conservation of fragmented small populations: endemic species persistence on California's smallest channel island. Biodiversity and Conservation 13:2537–2550.

SANTA BARBARA MUSEUM OF NATURAL HISTORY. 2013. The California Beetle Project website. [Cited October 2013]. Available from: http://www.sbnature.org/collections/invert/entom/cbphomepage.php

SHORT, A.E.Z., AND M.S. CATERINO. 2009. On the validity of habitat as a predictor of genetic structure in aquatic systems: a comparative study using California water beetles. Molecular Ecology 18:403–414.

SIMON, C., F. FRATI, A. BECKENBACH, B. CRESPI, H. LIU, AND P. FLOOK. 1994. Evolution, weighting and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. Annals of the Entomological Society of America 87: 651–701.

SMITH, C.I., AND B.D. FARRELL. 2006. Evolutionary consequences of dispersal ability in cactus-feeding insects. Genetica 126:323–334.

SORLIEN, C.C. 1994. Faulting and uplift of the Northern Channel Islands, California. Pages 281–296 *in* W.L. Halvorson and G.J. Maender, editors, The Fourth Channel Islands Symposium: update on the status of resources, Santa Barbara, Santa Barbara Museum of Natural History.

STEPHENS, M., AND P. SCHEET. 2005. Accounting for decay of linkage disequilibrium in haplotype inference and missing data imputation. American Journal of Human Genetics 76:449–462.

STEPHENS, M., N.J. SMITH, AND P. DONNELY. 2001 A new statistical method for haplotype reconstruction from population data. American Journal of Human Genetics 68:978–989.

VEDDER, J.G., AND D.G. HOWELL. 1980. Topographic evolution of the southern California borderland during late Cenozoic time. Pages 7–32 *in* D.M. Power, editor, The California Islands: proceedings of a multidisciplinary symposium, Santa Barbara, Santa Barbara Museum of Natural History.

WALLACE, L.E., AND K. HELENURM. 2009. Has herbivory negatively impacted genetic variability in the flora of the California Channel Islands? Insights from *Crossosoma californicum.* International Journal of Plant Science 170:311–322.

WEISSMAN, D.B. 1985. Zoogeography of the Channel Island Orthoptera. Pages 61–68 *in* A.S. Menke and D.R. Miller, editors, Entomology of the California Channel Islands. Santa Barbara Museum of Natural History, Santa Barbara.

WENNER, A.M., AND D.L. JOHNSON. 1980. Land vertebrates on the California Channel Islands: sweepstakes or bridges? Pages 497–530 *in* D.M. Power, editor, The California Islands: proceedings of a multidisciplinary symposium, Santa Barbara, Santa Barbara Museum of Natural History.

WETTERER, J.K., P.S. WARD, A.L. WETTERER, J.T. LONGINO, J.C. TRAGER, AND S.E. MILLER. 2000. Ants of Santa Cruz Island, California. Bulletin of the Southern California Academy of Sciences 99:25–31.

WILSON, A., P. ARCESE, L.F. KELLER, C.L. PRUETT, K. WINKER, M.A. PATTEN, AND Y. CHAN. 2009. The contribution of island populations to in situ genetic conservation. Conservation Genetics 10:419–430.

ZHANG, D.X., AND G.M. HEWITT. 2003. Nuclear DNA analyses in genetic studies of populations: practice, problems and prospects. Molecular Ecology 12:563–584.

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APPENDIX. GenBank accession numbers for newly generated sequences, by haplotype.

Species	Haplotype	GenBank #
Hypocaccus lucidulus	h33	GU226593
	h34	GU226594
	h35	GU226595
	h36	GU226596
	h37	GU226597
	h38	GU226598
	h39	GU226599
	h40	GU226600
	h41	GU226601
	h42	GU226602
	h43	GU226603
	h44	GU226604
	h45	GU226605
	h46	GU226606
	h47	GU226607
	h48	GU226608
	h49	GU226609
	h50	GU226610
	h51	GU226611
	h52	GU226612
Hadrotes crassus	hc1	GU226635
	hc2	GU226636
	hc3	GU226637
	hc4	GU226638
	hc5	GU226639
	hc6	GU226640
	hc7	GU226641
	hc8	GU226642
	hc9	GU226643
	hc10	GU226644
	hc11	GU226645
	hc12	GU226646
	hc13	GU226647
	hc14	GU226648
	hc15	GU226649
	hc16	GU226650
	hc17	GU226651
	hc18	GU226652
Hadropinus fossor		GU380341
Hypocaccus bigemmeus		GU380342
		GU380343
Thinopinus pictus	tp1	GU226613
	tp2	GU226614
	tp3	GU226615
	tp4	GU226616
	tp5	GU226617
	tp6	GU226618
	tp7	GU226619
	tp8	GU226620
	tp9	GU226621
	tp10	GU226622
	tp11	GU226623
	tp12	GU226624
	tp13	GU226625
	tp14	GU226626
	tp15	GU226627
	tp16	GU226628
	tp17	GU226629
	tp18	GU226630
	tp19	GU226631
	tp20	GU226632
	tp21	GU226633
	tp22	GU226634
Nyctoporis carinata	**COI**	
	N101	GU230811
	N102	GU230812
	N104	GU230813
N105	GU230814	
	N106	GU230815
	N107	GU230816
	N108	GU230817
	N109	GU230818
	N110	GU230819
	N111	GU230820
	N112	GU230821
	N113	GU230822
	N114	GU230823
	N115	GU230824
Nyctoporis carinata	**GFT**	
	NcG63	GU230825
	NcG64	GU230826
	NcG65	GU230827