Conservation and Management of Anacapa Island Deer Mice

OLIVER R. W. PERGAMS,* ROBERT C. LACY,† AND MARY V. ASHLEY*‡

*Department of Biological Sciences, 845 W. Taylor Street, University of Illinois at Chicago, Chicago, IL 60607–7060, U.S.A

†Department of Conservation Biology, Daniel F. and Ada L. Rice Center, Chicago Zoological Society, Brookfield, IL 60513, U.S.A.

Abstract: *We investigated the genetic and morphological status of an endemic subspecies of deer mice (*Peromyscus maniculatus anacapae*) on Anacapa Island of California through mitochondrial DNA (mtDNA) analysis, morphometric discriminant function analysis, and population viability analysis. We sought to assist the development of a management plan that may include captive breeding, reintroduction, or translocation of mice following eradication of introduced rats. The genetic and morphological data were used to investigate whether the subspecies or populations on each of the three islets of Anacapa represent evolutionarily significant units for conservation. The status of the East Anacapa population was of particular concern because deer mice have recently been caught there following more than 15 years of no records of deer mice. Sequences of the mtDNA cytochrome oxidase* c *subunit II gene (COII) indicated that the Anacapa subspecies had unique haplotypes not found on neighboring islands or the mainland and thus represents a distinct unit for conservation. Further, one of these haplotypes was shared among the islets, including most of the East Anacapa mice, suggesting that the East Anacapa population had either recovered from a severe bottleneck or had been recolonized by* P. m. anacapae*, but that it was not derived from other subspecies. Discriminant function analysis of morphological data also supported classification of the East Anacapa mice as* P. m. anacapae*. The mitochondrial mtDNA sequence data yielded estimates of two to seven migrants per generation among the Anacapa islets, suggesting a functioning metapopulation. Incorporating these data and information available on the life history and demographics of deer mice, we used a novel type of population viability analysis to develop a captive breeding and reintroduction plan for Anacapa deer mice should they be eradicated along with the rats. A sine wave was incorporated into the population viability analysis to simulate population size cyclicity. Our study provides baseline information needed for developing a comprehensive conservation and management plan for a threatened island endemic.*

Conservación y Manejo del Ratón *Peromyscus maniculatus anacapae* de la Isla Anacapa

Resumen: *Investigamos el estado genético y morfológico del ratón* Peromyscus maniculatus anacapae *de la isla Anacapa en California mediante un análisis del ADN mitocondrial, un análisis de función discriminante de los datos morfométricos y un análisis de viabilidad poblacional. Pretendimos colaborar con el desarrollo de un plan de manejo que podría incluir la reproducción en cautiverio, la reintroducción o el desplazamiento de ratones después de la erradicación de ratas introducidas. Los datos genéticos y morfológicos fueron utilizados para investigar si las subespecies o las poblaciones en cada una de las tres isletas de Anacapa representan unidades evolutivas significativas para la conservación. El estado de la población de Anacapa del Este fue de interés particular debido a la captura reciente de ratones, después de 15 años sin registros de esta especie. Las secuencias del gen citocromo oxidasa* c *subunidad II del ADNmt (COII) indicaron que la subespecie de Anacapa tiene haplotipos únicos, que no se encuentran en las islas vecinas ni en tierra firme y, por lo tanto, representa una unidad única para la conservación. Más aún, uno de estos haplotipos fue compartido entre las isletas, incluyendo la mayoría de los ratones de Anacapa del Este, lo que sugiere que*

‡ *Address correspondence to M. V. Ashley, email ashley@uic.edu*
Paper submitted November 6, 1998; revised manuscript accepted September 14, 1999.

la isla ha sido recolonizada por P. m. anacapae *o que la población de Anacapa del Este se ha recuperado de un cuello de botella severo pero que no ha derivado de otras subespecies. El análisis de función discriminante de los datos morfométricos también respalda la clasificación de los ratones de Anacapa del Este como* P. m. Anacapae. *Los datos de secuencias del ADNmt proveen estimaciones de 2 a 7 migrantes por generación entre las isletas Anacapa, lo que sugiere la presencia de una metapoblación en funcionamiento. Con la incorporación de estos datos y la información disponible sobre los antecedentes biológicos y la demografía del ratón, se utilizó un nuevo tipo de análisis de viabilidad poblacional para desarrollar un plan de reproducción en cautiverio y de reintroducción del ratón de Anacapa en caso de que los ratones sean exterminados junto con las ratas. Se incorporó una función seno al análisis de viabilidad poblacional para simular los ciclos del tamaño poblacional. Nuestro estudio provee la información básica necesaria para desarrollar un plan de conservación y de manejo integral para una especie endémica insular amenazada.*

Introduction

The eight California Channel Islands (Fig. 1), including Anacapa, are each home to an endemic subspecies of deer mouse, *Peromyscus maniculatus*. The land vertebrate fauna of the Channel Islands is depauperate, and deer mice are the only land mammal species endemic to all eight islands. Deer mouse populations reach high densities on several of the islands, probably because there are few predators, and may exhibit cyclicity in population size, as do voles and lemmings (Drost & Fellers 1991). In a study of morphological divergence between deer mice on the Channel Islands and their closest mainland relatives, Gill (1980) examined morphological traits and found that five of the island subspecies could be discriminated from one another and from mainland mice with 98% accuracy. Gill (1976, 1980) also examined variation at 30 allozyme loci and found that heterozygosity was slightly reduced in island subspecies and that genetic distances were small between the island and mainland subspecies. Ashley and Wills (1987) used mitochondrial DNA (mtDNA) restriction-fragment-length polymorphisms (RFLPs) to study Channel Island and California mainland *P. maniculatus*. They found that all of the island samples have haplotypes not found on the mainland and that five of the islands, including Anacapa, have unique haplotypes.

Anacapa Island is the most northeastern of the Channel Islands, lying approximately 20 km from the nearest mainland point (Fig. 1). Anacapa, the other three northern Channel Islands (Santa Cruz, Santa Rosa, and San Miguel), and Santa Barbara Island comprise Channel Islands National Park, established in 1978. Anacapa is an 8-km-long chain of three separate east-to-west-trending islets referred to as East, Middle, and West Islands. All three islets are rugged and steep.

Although *P. m. anacapae* has been shown to be distinct in morphology (Gill 1980; Pergams & Ashley, 1999), allozyme variation (Gill 1976, 1980), and mtDNA (Ashley & Wills 1987), it is not known whether deer mice from the different islets are genetically distinct. Further, the history and current status of East Anacapa deer mice are uncertain. Deer mice on East Anacapa Island had been thought to be extinct since 1981–1982 (G. Austin, personal communication) and greatly reduced in numbers since 1966 (Collins et al. 1979). Deer mice were again seen on East Anacapa in 1997, but it is not known whether deer mice recovered on East Anacapa from a severely bottlenecked population or whether mice have recolonized East Anacapa from elsewhere.

The native flora and fauna of Anacapa are threatened by the introduction and proliferation of black rats (*Rattus rattus*). Rats are thought to have invaded Anacapa via boat, possibly as a result of a shipwreck in 1853 (Collins et al. 1979; Doran 1980). Rats may threaten *P. m. anacapae* through resource competition and predation on their young and may have been a factor in the decline of deer mice on East Anacapa. Rats also prey on seabird eggs and young (Collins et al. 1979) and are considered a threat to native species. Although it may be possible to specifically target rodents for eradication, it is probably impossible to poison rats without poisoning deer mice. A rat eradication project, currently being planned by the Channel Islands National Park, may therefore include plans for the capture, captive breeding, and reintroduction of deer mice during and following the eradication program. An alternative plan under consideration is translocation of mice among the islets. That is, the poisoning would proceed sequentially, with mice from one islet being used to "restock" an islet that had undergone rodent eradication.

Our goal was to provide a detailed characterization of the current genetic and morphological status of *P. m. anacapae* on all three islets. This would accomplish three objectives: (1) to provide information on the connectivity of the Anacapa islet populations for management purposes; (2) to evaluate the status of East Anacapa deer mice; and (3) to provide baseline data for

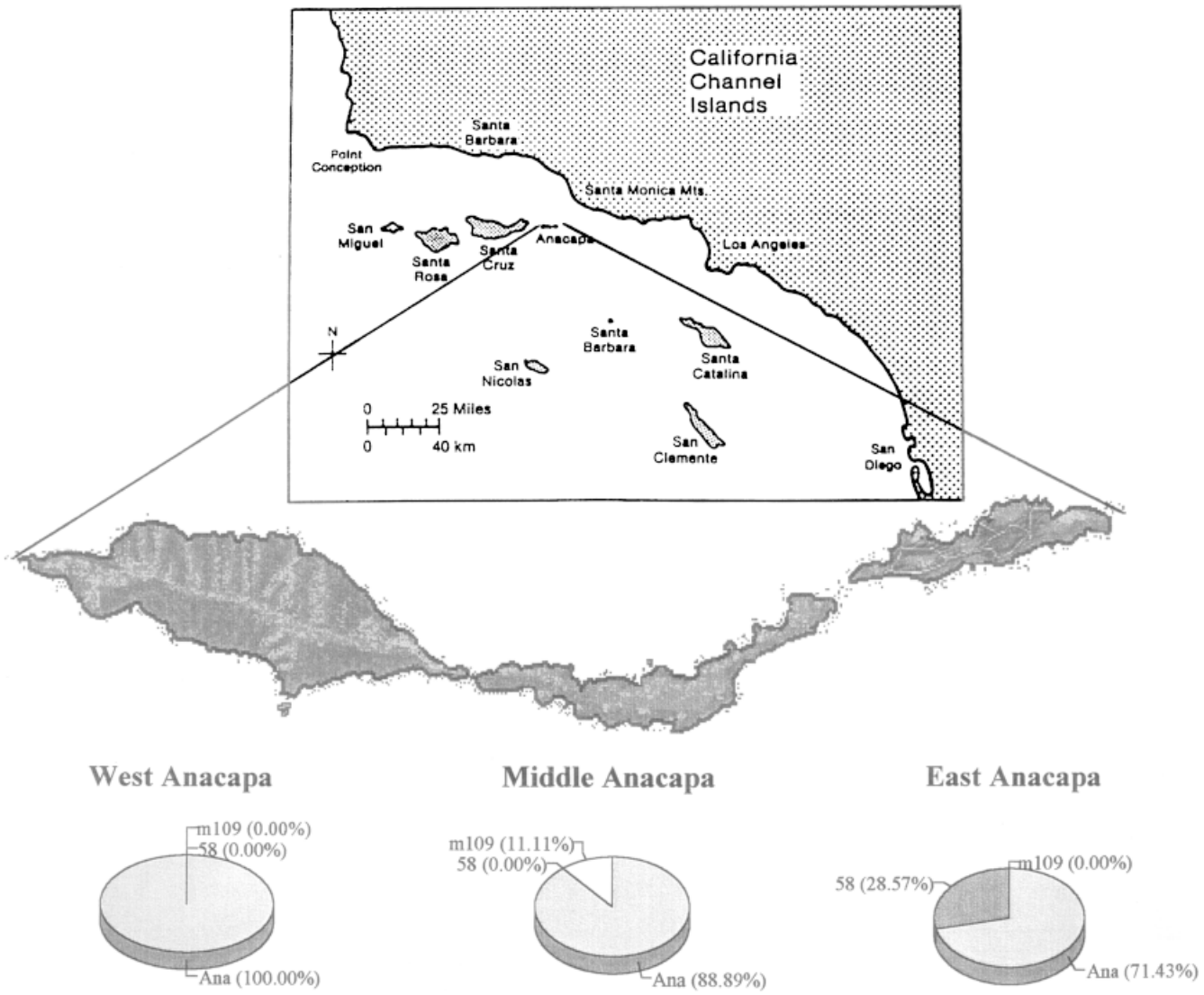

Figure 1. Map of the California Channel Islands with an expanded view of the Anacapas. Pie charts represent distributions of COII mtDNA haplotypes found in P. maniculatus *spp. on each islet.*

comparisons with "post-eradication" deer mice in the future. We obtained genetic data by sequencing the mitochondrial cytochrome oxidase *c* subunit II (COII) gene from Anacapa deer mice and other island and mainland deer mice. We obtained morphological information through discriminant function analysis of 16 cranial and body measurements of museum specimens, including those from the original subspecies description.

We also included a unique application of population viability analysis (PVA) for use in "planning" a deer mouse population bottleneck should rat eradication be conducted. The PVA was conducted with VORTEX (Lacy 1993; Miller & Lacy 1999), a species- and habitat-specific simulation that models demographic events (mate selection, birth, sex determination, and death), catastrophic events, and environmental variation and genetic variation. The value of PVA models in general and VORTEX in particular is in developing species- and habitat-specific "what if" analyses when considering only one or a few variables at a time. Such sensitivity testing can reveal the level of a variable needed to achieve a certain probability of population persistence or other measure of performance or the relative vulnerability of population dynamics to incremental shifts in a factor. These assessments can then be used to set recovery goals or management actions and to identify threatening factors and variables needing further study (Burgman et al. 1993; McCarthy et al. 1995). The "what if" variable we considered for Anacapa deer mice is initial population size, that is, the number of mice that must be reintroduced and/or translocated in order to reestablish the populations after extirpation of rats.

The ecology and life history of *Peromyscus*, including *P. maniculatus*, has been extensively studied, and relatively accurate parameters can be input for many demo-

graphic characteristics. Cyclicity of population size was modeled into the PVA as a sine wave imposed on the carrying capacity (upper limit of population size). The results of our genetic and discriminant analyses guided our PVA and management recommendations. Through use of various PVA scenarios, the feasibility and cost of a plan can be weighed against varying probabilities of population persistence and can be estimated prior to implementation, before deer mice are trapped or poisoned. The success of the plan can be ascertained in future studies by monitoring demographic, ecological, morphological, and genetic parameters and comparing these with prebottleneck conditions. In this way, Anacapa Island deer mice provide a rare opportunity to assess the effect of population bottlenecks, captive breeding and reintroduction, and/or translocation.

Methods

Mitochondrial DNA

Sequences of COII were obtained for 34 specimens (Table 1). The mice were collected during two time periods, 1983–1985 (n = 13) and 1996–1997 (n = 21). The mice from 1983–1985 had been examined previously for mtDNA RFLPs (Ashley 1986; Ashley & Wills 1987, 1989). Six island locations (West Anacapa Island, Middle Anacapa Island, East Anacapa Island, Santa Cruz Island, Santa Barbara Island, and Santa Rosa Island) and three coastal California mainland locations (La Jolla, Las Flores Ranch, and Los Alamos) were sampled.

Samples consisted either of purified mtDNA isolated by differential centrifugation (those from 1983–1985; Table 1; Ashley & Wills 1987) or of total genomic DNA (1996–1997) isolated from alcohol-preserved heart or liver tissue by standard phenol-chloroform extraction. The entire COII gene (684 bp) was amplified via the polymerase chain reaction (PCR) with primers designed from $tRNA^{Asp}$ and $tRNA^{Lys}$ genes that flank COII in the mammalian mitochondrial genome (Adkins & Honeycutt 1994). Five other primers were also designed for amplification and/or sequencing, including three external primers, Mus-Ser1 (AAAGGAAGGAATCGAACCC), Mus-Ser2 (AAAGGAAGGAATCGAACC), and Mus-Lys (AACGCTCTTAGCTTCATAGTG), and two internal primers, Per-IntF (CCCAAGAAGTTGAAACAATTGAAC) and Per-IntB (TCTAGTAGGCGTAGTTCTCCTGG). The PCR amplifications were performed in 50 μL reaction volumes that included 0.2 μM of each primer, 0.2 μM of dNTPs, 1 unit Taq polymerase, reaction buffer, and approximately 2 ng of DNA. Amplification proceeded for 32 to 40 cycles of 94° C for 1 minute, 50–51° C for 1 minute, and 72° C for 2 minutes. Five microliters of PCR reaction product were electrophoresed in 1% agarose gels and stained with ethidium bromide for visualization. We removed excess primers and dNTPs from the remaining PCR product using the QIAquick PCR Purification Kit (Qiagen). We sequenced the PCR products either manually using the Thermo Sequenase Radiolabeled (^{33}P) Terminator Cycle Sequencing Kit (Amersham Life Science) or on an automated sequencer (ABI 373A) using the ABI PRISM Dye Terminator Cycle Sequencing Ready Reaction Kit. We analyzed sequences using MacVector 4.0 and AssemblyLIGN Sequence Analysis Software (IBI).

We examined levels of mitochondrial variation using indices of nucleotide diversity (π) and average number of nucleotide differences (k, Tajima 1983). Calculation of π follows equations 10.5 or 10.6 of Nei (1987). Calculation of k follows equation A3 of Tajima (1983). We used the computer program DnaSP 2.9 (Rozas & Rozas 1997, 1998) to perform these and the Nm calculations.

Gene flow, Nm, was estimated from sequence data, an approach that estimates migration averaged over the period of evolutionary time in which the nucleotide substitutions took place. These methods need to be viewed with caution because they are based on premises (such as constant migration rates and population sizes) that are often violated. We therefore conducted a sensitivity analysis of migration rates in our PVA, described below. Gene flow was calculated following Hudson et al. (1992), Lynch and Crease (1990), and Nei (1982). Nei's (1982) equation 2 gave the most conservative (lowest) estimates, and therefore we used it:

$$\pi_s = \frac{\sum_{i=1}^{s} w_i \pi_i}{\sum_{i=1}^{s} w_i},$$

where $Nm = \pi_s$, the average of nucleotide diversities between subpopulations, and w_i and π_i are the relative size and the nucleotide diversity of the ith subpopulation. Because we were using mtDNA, a maternally inherited genome, estimates are of female migration only. Male dispersal distance is greater than female in all subspecies of *P. maniculatus* studied (Howard 1949; Dice & Howard 1951; Blair 1958), so our estimates of female Nm are likely underestimates of total migration rates.

Discriminant Function Analysis

Prior to discriminant function analysis (DFA), the specimens were resolved to the species level through the use of taxonomic keys (Ashley & Pergams 1997). Given the apparent absence of deer mice from East Anacapa for several years, it was possible that recent specimens were not *P. m. anacapae* but rather the result of colonization from elsewhere. The goal of our DFA was therefore to assess whether specimens from East Anacapa were *P. m. anacapae*. Because we had previously found

Table 1. Specimen numbers, species or subspecies, collection location and date, and COII haplotype information for mice sequenced in this study.

Specimen	*Species/subspecies*	*Location*	*Date*	*Haplotype*
1	*P. m. anacapae*	West Anacapa	October 1996	Ana
2	*P. m. anacapae*	West Anacapa	October 1996	Ana
11	*P. m. anacapae*	West Anacapa	October 1996	Ana
14	*P. m. anacapae*	West Anacapa	October 1996	Ana
23	*P. m. anacapae*	West Anacapa	October 1996	Ana
26	*P. m. anacapae*	West Anacapa	October 1996	Ana
30	*P. m. anacapae*	West Anacapa	October 1996	Ana
35	*P. m. anacapae*	West Anacapa	October 1996	Ana
37	*P. m. anacapae*	West Anacapa	October 1996	Ana
38	*P. m. anacapae*	West Anacapa	October 1996	Ana
51	*P. m. anacapae*	Middle Anacapa	December 1996	Ana
52	*P. m. anacapae*	Middle Anacapa	December 1996	Ana
53	*P. m. anacapae*	Middle Anacapa	December 1996	Ana
55	*P. m. anacapae*	West Anacapa	December 1996	Ana
56[a]	*P. m. anacapae*	East Anacapa	July 1997	Ana
57	*P. m. anacapae*	East Anacapa	July 1997	Ana
58[b]	*P. m. anacapae*	East Anacapa	July 1997	58
59	*P. m. anacapae*	East Anacapa	July 1997	58
60	*P. m. anacapae*	East Anacapa	September 1997	Ana
61	*P. m. anacapae*	East Anacapa	September 1997	Ana
62[c]	*P. m. anacapae*	East Anacapa	September 1997	Ana
m20	*P. m. santacruzae*	Santa Cruz Island	September 1983	unique
m79	*P. m. elusus*	Santa Bartbara Island	December 1983	unique
m109	*P. m. anacapae*	Middle Anacapa	May 1983	m109
m110	*P. m. anacapae*	Middle Anacapa	May 1983	Ana
m116	*P. m. anacapae*	Middle Anacapa	May 1983	Ana
m141	*P. m. gambelii*	mainland (La Jolla)	October 1984	unique
m195	*P. m. santarosae*	Santa Rosa Island	February 1985	unique
m198	*P. eremicus*	Del Mar	February 1985	unique
m214	*P. m. anacapae*	Middle Anacapa	March 1985	Ana
m215	*P. m. anacapae*	Middle Anacapa	March 1985	Ana
m219	*P. m. anacapae*	Middle Anacapa	March 1985	Ana
m233	*P. m. gambelii*	mainland (Las Flores ranch)	May 1985	unique
m240	*P. m. gambelii*	manland (Los Alamos)	May 1985	unique

[a] *Species and subspecies of specimen 56–62 inferred in this study.*
[b] *Specimen was a juvenile and was not used for morphometrics.*
[c] *Specimen had missing head and was not used for morphometrics or taxonomic keys.*

that significant morphological change in Channel Island deer mice had occurred over the last century (Pergams & Ashley, 1999), we used only mice collected since 1955. We examined specimens from the following locations: Anacapa (*P. m. anacapae*), Santa Barbara Island (*P. m. elusus*), Santa Cruz Island (*P. m. santacruzae*), and the California coastal mainland (*P. m. gambelii*). These locations were chosen because they were considered possible, although unlikely, sources for colonists to East Anacapa. Santa Cruz is the closest island in any direction, lying 7 km west of Anacapa. The National Park Service transfers equipment from Santa Barbara to Anacapa, and mice could perhaps stow away (G. Austin, personal communication). The mainland is 20 km from Anacapa, and there is regular but limited boat traffic.

We measured 91 mice determined to be adults by pelage color and tooth wear (Layne 1968; Hinesley 1979; Rich et al. 1996). Our sample included 5 East Anacapa mice (56–57, 59–61), 35 *P. m. anacapae* (15 from West Anacapa, 20 from Middle Anacapa), 21 *P. m. elusus*, 17 *P. m. santacruzae*, and 13 mainland *P. m. gambelii* skulls and skins from the Santa Barbara Natural History Museum, the Natural History Museum of Los Angeles County, and the Field Museum in Chicago. Twelve cranial measurements were taken (following the methods described by Hooper (1952), Fisler (1965), and Collins and George (1990) unless otherwise indicated): intermeatus width (IW), length of nasals (LN), length of palate plus incisor (LPI, measured as the greatest distance from the anterior edge of the alveoli of the incisors to the mesopterygoid fossa), breadth of rostrum (BR), alimentary toothrow (AL), length of incisive foramen (LIF), nasal width (NW, the narrowest width of the nasals and premaxilla dorsally and directly anterior to the infraorbital foramen), zygomatic breadth (ZB), interorbital breadth (IB), depth of braincase (DBC), breadth of braincase (BB), and breadth of zygomatic plate (BZP). All cranial measurements were taken with a digital caliper to the

nearest 0.01 mm by O.R.W.P. Cranial measurement error was estimated and was found to be small, <2% of the variation between mice (Pergams & Ashley, 1999). The four standard external measurements were taken from museum tags: total length (TOT), tail length (TAIL), hind foot length (HIND), and ear length (EAR). Ear length was not available for one *P. m. elusus*, so it was removed from the data set.

The program SYSTAT (SPSS 1997*a*) was used for all statistical analysis. Normality of data was determined by visual inspection of normal probability plots, following the method of Afifi and Clark (1996). We plotted 85% ellipses of concentration as group scatterplot matrices and we visually inspected plots to determine if covariances were approximately equal (SPSS 1997*b*). To evaluate sexual dimorphism, we performed two-sample *t* tests on each subspecies. Results of *t* tests were considered significant at the 95% confidence level. Discriminant analyses were performed with the default tolerance of 0.001. Tolerance refers to the matrix inversion tolerance limit, below which a variable is excluded from the classification function. Correct classification rates are jackknifed values. Wilk's λ was transformed to an approximate *F* statistic for comparison with the *F* distribution, and an associated *p* value was calculated.

Discriminant function analysis used the "weight" function in SYSTAT's data handling component to assign a weighting of 0 to mice from East Anacapa and 1 to the rest, the individuals of known subspecies. A complete discriminant function was derived only from the museum specimens but was then applied to the East Anacapa specimens.

Population Viability Analysis

VORTEX (Lacy 1998) was used for all PVA. VORTEX is an individual based simulation, in which the fate of each animal is tracked as it experiences demographic events (aspects of reproduction, mortality, and dispersal) in each discrete time step ("year"). Users specify mean probabilities of occurrence of each demographic event and the extent of annual fluctuation (expressed as SDs) in the rates as a result of environmental variation. In addition, catastrophic events in the simulation model may cause reductions in survival and reproduction, and the user specifies the probability of occurrence of any catastrophes and the severity of their effects. Carrying capacity of the habitat is modeled as a ceiling population size. When the carrying capacity is exceeded, VORTEX applies an additional risk of mortality to each individual, such that the population size will on average return to the carrying capacity.

Demographic rates can be specified as functions of density, time, genetic diversity, sex, age, and other characteristics of the population and individuals. In each year of the simulation, VORTEX determines the demographic rates for that year by sampling from the distribution with the specified mean and SD and then reduces rates for that year if a catastrophe is deemed to have occurred. Stochastic events—catastrophes, inclusion in the pool of mates for a year, mate selection, litter size, sex determination, survival, dispersal—are determined to have occurred if a random number drawn from a uniform 0–1 distribution is less than the probability of occurrence of the event.

VORTEX also models genetic processes of random drift and the effects of inbreeding. Loss of variation due to genetic drift is simulated by monitoring the random transmission through the generations of alleles at a hypothetical neutral genetic locus. Effects of inbreeding are modeled by simulating one to five genetic loci that can carry recessive lethal alleles and/or by specifying that survival is a declining function of the inbreeding coefficient. For further details about the VORTEX model, (see Lacy 1993, 2000; Miller and Lacy 1999).

Through VORTEX, we sought to determine the number of mice previously removed from an islet for translocation and/or captive breeding which would need to be released to ensure successful reestablishment of the deer mouse population following eradication of rats. We did this by varying the parameter "initial population size" in a sensitivity analysis calculating the probability of population persistence for 102 years. VORTEX models population dynamics in discrete annual time steps and requires demographic rates on an annual basis. Therefore, we let 3 real weeks = 1 VORTEX "year." For example, 100 real years = 52/3 × 100, or 1733.33 VORTEX years. We rounded up to 1768 VORTEX years, or 102 real years, for the duration of our simulations. A 3-week interval is a logical time step for modeling *Peromyscus* because this is about the length of gestation, the weaning age, the interbirth interval, and half the mean age of first estrus (Millar 1989). Other VORTEX PVA input and sources are presented in the Appendix.

We had to determine whether and how to incorporate cyclicity of population size in our PVA. To determine if cycles similar to those reported for Santa Barbara deer mice (Drost & Fellers 1991) exist on Anacapa, we extrapolated population size on Middle Anacapa from National Park Service sampling grids for five years, 1993–1997 (Schwemm 1995; Austin 1996*a*, 1996*b*; G. Austin, personal communication). No more than 2 years of data were available for the other islets. Density per hectare was multiplied by islet area to yield estimates of population size. The traps were placed in each type of habitat and in the same locations each year, so estimates should reflect the relative size of the population from year to year, although the actual size estimates may be imprecise.

To model cyclicity of population size into VORTEX as a sine wave, we used the nonlinear regression analysis in

SYSTAT (SPSS 1997*a*) to regress Middle Anacapa data onto the function:

$$N = a + b\sin\left[\frac{(V+d)2\pi}{60.666}\right]$$

where N is population size, a is the mean population size across years, b is the amplitude of the variation, d is included to allow the sine wave to best align with the data chronologically, and V is VORTEX years. The value 60.666 was used to force the length of the wave to be 60.666 VORTEX years, or 3.5 real years. This was the approximate observed length of the population-size cycle in both Santa Barbara and Middle Anacapa. The resulting parameters were $a = 9105.4$, $b = 4499.3$, and $d = 351.91$, with the regression explaining 80% of the variance in the population-size estimates.

When calculating sine wave parameters for East and West Anacapa, we used the same value for d because we assumed that weather patterns will cause considerable synchronicity of population cycles among the three islets. This is a conservative approach; if the populations vary independently, then the metapopulation would be more stable than projected in our model. We also assumed that the carrying capacity (K) of the other islets was directly related to their relative land area. Middle Anacapa is 62.98 ha, West Anacapa is 181.82 ha, and East Anacapa is 45.31 ha. For East Anacapa, for example, a was then calculated with the ratio

$$\frac{9105.4}{a} = \frac{62.98}{45.31}.$$

Values of $a = 26286.8$ and $b = 12989.2$ were found for West Anacapa; $a = 6550.7$ and $b = 3237.0$ were found for East Anacapa. These functions were then input as K for each islet.

Some limitations of the VORTEX program necessitated adjustments to our analyses. VORTEX does not model inbreeding depression as a function of the inbreeding coefficient in populations over 6000 and does not model populations that exceed 62,000. The populations of individual islets cycled above 6000 during simulations, and the metapopulation size of all three islets sometimes cycled above 62,000. We made a programming change that allowed us to suspend breeding when $N \geq 62{,}000$ and to resume breeding when $N < 62{,}000$. This reflects the opinion of Drost and Fellers (1991) that females exercised breeding suppression at the peaks of cycles. Inbreeding depression was modeled with recessive lethal alleles only. This model of inbreeding depression allows selection to remove lethal alleles as inbred homozygous carriers die, thereby reducing the likelihood that inbred animals in future generations will die. Modeled populations rarely remained below a few hundred animals for more than a few generations, however, so inbreeding could not remove a substantial proportion of the lethal alleles.

Six different "initial population size" scenarios were modeled, with 100-iteration simulations of each scenario. Initial population sizes varied from 50 mice on each islet and 150 mice on all islets (50/150) to 700/2100. We chose these values for practical reasons; the lower value (50/150) was certainly a feasible number for captive breeding or translocation in terms of cost and logistics, whereas values above the 700/2100 level might exceed monetary or logistical constraints. These boundaries would allow us to determine whether the conservation plan we would propose would be feasible at all.

We used migration rates (m) between islets derived from estimates of Nm using the COII sequence analysis, generation time, and extrapolations of N from census data (see Appendix for details). This is a novel application of DNA sequence–based Nm estimates to a PVA. To test the sensitivity of the PVA to migration rate, we ran two additional simulations at the 333/1000 initial population size. In one simulation we halved the migration rates, and in the other simulation we doubled the migration rates. All other parameters were identical to those used for our other PVAs, as given in the Appendix. We then compared the results of these simulations to the 333/1000 initial population-size scenarios run with the original migration rates.

Results

Mitochondrial DNA

At least 606 bp of COII sequence were obtained for all specimens (Table 1), with 18 polymorphic sites (Table 2). Among the 27 specimens from Anacapa islets there were three haplotypes (Table 1; Fig. 1). Two of these, Ana and m109, had previously been identified through RFLP analysis (Ashley & Wills 1987). All but 2 specimens on East Anacapa and 1 on Middle Anacapa were the same haplotype, Ana (Table 1; Fig. 1). Two specimens from East Anacapa had a previously unknown haplotype that we designated 58. Among *P. maniculatus* subspecies π was 0.00714, or $<1\%$, and k was 4.0. Gene flow was estimated only for the Anacapa islets and was 7.27 individuals per generation between West and Middle Anacapa, 6.53 between Middle and East Anacapa, and 2.05 between West and East Anacapa.

Discriminant Function Analysis

The use of taxonomic keys resolved the East Anacapa specimens to the species level as *P. maniculatus* (Ashley & Pergams 1997). Mainland *P. m. gambelii* were markedly smaller than all island deer mice, and there was no overlap in the range of values measured for two traits (LPI and AL) between our specimens and *P. m. gambelii*. For another five traits (BR, ZB, BB, TOT, and

Table 2. Variable nucleotide positions in COII sequences of *P. maniculatus* spp.

Nucleotide position	38	84	117	150	267	273	303	308	327	334	432	435	442	480	546	552	596	621
Amino acid position	12	28	39	50	89	91	101	102	109	111	144	145	147	160	182	184	198	207
m20	C	G	A	G	A	T	T	C	A	G	A	C	T	T	T	T	T	A
58	C	A	A	G	A	T	T	A	A	G	A	C	C	T	T	T	T	A
m240	C	G	A	G	G	T	T	A	A	G	A	C	C	T	T	T	T	A
m141	C	G	A	A	G	T	T	A	A	C	A	C	C	T	T	T	T	A
Ana	C	G	A	G	A	T	T	A	A	G	G	C	C	T	T	C	T	A
m233	C	G	A	G	G	T	T	A	G	G	A	C	C	T	T	T	T	A
m109	C	G	A	G	A	C	C	A	A	G	A	A	C	C	T	T	T	G
m79	C	G	A	G	A	T	T	A	A	G	A	C	T	T	T	T	G	A
m195	T	G	G	G	A	T	T	A	A	G	A	C	C	T	C	T	T	A

TAIL), there was <10% overlap in values. We also measured Mahalanobis distances between the four subspecies. The distances between *P. m. anacapae*, *P. m. elusus*, and *P. m santacruzae* averaged 3.190, whereas the distances between *P. m. gambelii* and the three island subspecies were approximately twice as much, averaging 6.087. We therefore excluded *P. m. gambelii* as a source of East Anacapa stock and did not include it in further analyses.

The discriminant function classified 96% (69/72) of known specimens correctly. Of the three specimens incorrectly classified, two were *P. m. anacapae* classified as *P. m. santacruzae* and one was *P. m. santacruzae* classified as *P. m. elusus*. Table 3 shows classification functions, cumulative proportion of total dispersion, and Wilk's λ and the associated *F* statistic and probability. The probability associated with Wilk's λ was <0.00005, indicating highly significant differences among the subspecies. Complete DFA (Fig. 2) classified three East Anacapa specimens (57, 59, 60) to the subspecies level as *P. m. anacapae*. Specimen 59 had a new haplotype (58), and discriminant function analysis was the sole method used to classify it. Two specimens (56, 61) could not be classified but were determined not to be *P. m. santacruzae* or *P. m. elusus*, the most likely source of colonists other than Middle and West Anacapa.

Population Viability Analysis

Our extrapolation of Anacapa population sizes from National Park Service sampling grids on Middle Anacapa yielded estimates of population sizes of 709; 12,111;

Table 3. Classification functions, cumulative proportion of total dispersion (CPTD), and Wilk's λ with associated *F* statistic and *p* value[a] for discriminant analysis of three *P. maniculatus* subspecies.

Classification coefficients[b]	P. m. anacapae	P. m. elusus	P. m. santacruzae
Constant	−3005.268	−2932.265	−3018.292
IW	53.068	70.189	51.036
LN	31.034	28.780	30.840
LPI	−16.995	−2.279	−8.008
BR	90.559	68.716	81.786
AL	212.412	181.289	191.933
LIF	60.917	74.342	68.121
NW	183.717	181.922	179.387
ZB	42.023	34.271	37.747
IB	85.364	91.038	91.666
DBC	142.213	138.398	140.713
BB	151.085	162.864	162.168
BZP	−57.049	−71.768	−67.112
TOT	−0.809	−0.954	−1.033
TAIL	3.917	3.005	3.640
HIND	9.899	8.693	9.510
EAR	−14.180	−13.504	−13.417
CPTD = 0.876			
Wilk's λ = 0.078, *F* = 8.675, $p < 0.00005$			

[a] *The CPTD represent the proportion (maximum = 1) of variability between groups that the first canonical variable captures. The higher the value, the more between-group variability is being captured. Wilk's λ tests the equality of group means for the variables. The lower the value (minimum = 0), the less the group means are equal and the more the function is discriminating. Wilk's λ was transformed to an approximate* F *statistic for comparison with the* F *distribution, and an associated* p *was calculated.*

[b] *Measurements described in the text.*

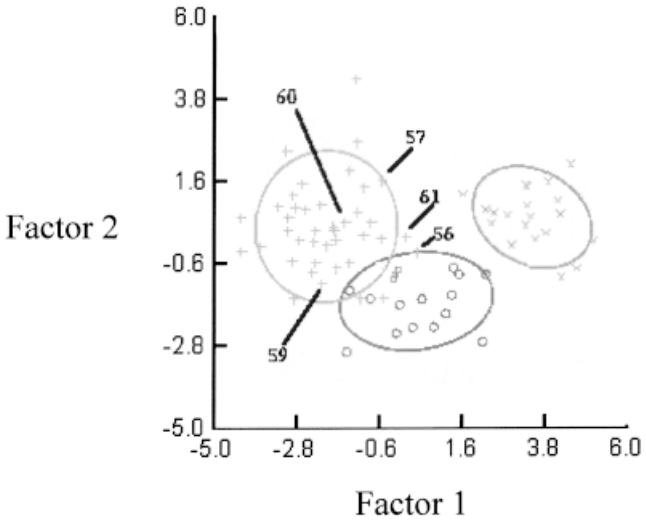

Figure 2. Canonical scores plot from discriminant function analysis of three deer mouse subspecies: P. m. anacapae *(+),* P. m. elusus *(x), and* P. m. santacruzae *(o). The axes are the first two canonical variables, and the points are the canonical variable scores. The canonical scores of the unknown specimens from East Anacapa are indicated by their specimen numbers. The confidence ellipses are centered on the centroid of each group.*

9,888; 14,895; and 2835 for years 1993–1997, respectively. These values suggest a 3- to 4-year cycle similar to that found among Santa Barbara deer mice (Drost & Fellers 1991), although one wave does not necessarily make a cycle. Because cyclicity of population size increases a population's extinction risk, we included it in our PVA to avoid underestimating the risk of failure of the reestablishment program.

All reintroduced populations grew quickly, and by year 12 population sizes ranged from 7358 in the 50/150 scenario to 10,520 in the 700/2100 scenario (Table 4). Final population sizes were similar for all scenarios (Table 4). The probability of the metapopulation going extinct within 102 years was 0% in each scenario except 50/150, for which probability of metapopulation extinction was 1% (Table 4). At least one subpopulation went extinct in all scenarios except 700/2100. The total number of subpopulations going extinct during the 100 iterations of each simulation ranged from 116 in the 50/150 scenario to 0 in the 700/2100 scenario, and in all but three cases recolonizations occurred to reestablish populations (the three exceptions were all in the 50/150 scenario). The mean time to first extinction was usually short and approximately equal (3–4 years) in the 50/150, 100/300, and 200/600 scenarios, suggesting that local extinctions often occurred within the first few years before the smaller populations grew to sufficient size. Heterozygosity values (Table 4) represent the ratio of $H(t)/H(0)$, the loss relative to starting levels. Observed heterozygosity (H_o) was approximately equal to expected heterozygosity (H_e) in each simulation, so only a composite H is reported. Heterozygosity ranged from 75% of the initial level in the 50/150 scenario to 88% in the 500/1000 scenario and remained approximately unchanged in the 700/2100 population-size simulation. The sensitivity analysis conducted on the 333/1000 scenario indicated that altering migration rates had relatively minor effects (Table 5). Even when migration rates were halved, all subpopulations were recolonized.

Discussion

The Anacapa Island deer mice presented an opportunity to apply several methods of population and conservation biology to specific management questions for an endemic island mammal, including the following: Is *P. m. anacapae* an evolutionarily significant unit (ESU) for conservation? Are the separate populations on the three small islets of Anacapa each an ESU, or does gene flow among them warrant their treatment as a single unit for conservation? Are the mice currently on East Anacapa derived from *P. m. anacapae* stock or introduced from elsewhere? Can a management strategy be developed that would allow for the persistence of Anacapa deer mice during a massive rodent eradication project? Would strategies that are logistically and financially feasible have a high likelihood of success? To derive answers

Table 4. VORTEX ouput from six different initial population-size scenarios in *Peromyscus*, run for 102 years and 1000 iterations.*

Initial population	*Final population (year 12)*	*Mean* H ($H_e \approx H_o$)	*Metapopulation extinction probability*	*Mean time to first extinction (years)*	*Subpopulation extinctions*	*Subpopulation recolonizations*
50/150	6454 (7358)	0.77	0.01	3.1	116	113
100/300	5951 (8042)	0.80	0	3.2	85	85
200/600	6001 (8932)	0.84	0	3.8	42	42
333/1000	6112 (9853)	0.87	0	28.9	10	10
500/1500	6261 (10479)	0.88	0	10.3	1	1
700/2100	6147 (10520)	0.88	0	—	0	0

**Initial population size is considered for six scenarios of population size per islet/population size per metapopulation: 50 per islet/150 per metapopulation, and so forth.* H *represents* H(t)/H(0); H_e *is expected heterozygosity;* H_o *is observed heterozygosity.*

Table 5. Sensitivity analysis of *Peromyscus* migration rate of population viability analysis (PVA).*

Migration rate	*Final population (year 12)*	*Mean* H ($H_e \approx H_o$)	*Metapopulation extinction probability*	*Mean time to first extinction (years)*	*Subpopulation extinctions*	*Subpopulation recolonizations*
50% (0.000025–0.000075)	6185 (9012)	0.85	0	9.9	12	12
original (0.00005–0.00015)	6112 (9853)	0.87	0	28.9	10	10
200% (0.0001–0.0003)	6179 (10153)	0.90	0	4.7	3	3

**All simulations are run with the 333/1000 initial population size. All other parameters are identical to our other PVAs, as stated in Appendix.*

to these questions, we obtained and integrated data from genetics, morphometrics, and computer modeling. Because of the comprehensive nature of this investigation, it has relevance to conservation biology beyond the status of a single endemic subspecies.

Since Ryder (1986) introduced the ESU concept for guiding conservation and management, there has been much discussion but little agreement regarding the appropriate criteria for defining an ESU (e.g., Waples 1991; Dizon et al. 1992; Moritz 1994; Vogler & DeSalle 1994). In our view, *P. m. anacapae* warrants designation as an ESU because it is geographically discrete, historically isolated, and morphologically divergent (Fig. 2), and it contains unique mtDNA haplotypes. Morphologically, *P. m. anacapae* is well differentiated; the high classification rate of the discriminant function (96%) supports the original description of Anacapa deer mice as a distinct subspecies (von Bloeker 1941). Mitochondrial haplotypes unique to Anacapa, first identified by RFLP analysis on mice from Middle Anacapa (Ashley & Wills 1987, 1989), have been extended and refined with COII sequence data and mice from all three islets. Although the mtDNA haplotypes found on Anacapa do not form a monophyletic clade united by synapomorphic characters (Moritz 1994; Vogler & DeSalle 1994), the haplotypes are diagnostic for Anacapa and differ by at least two substitutions from other island and mainland subspecies (Table 2). Although the current study involved mice only from Santa Barbara Island, Santa Cruz Island, and three mainland locations, two of the three haplotypes we sequenced had previously been identified by RFLP analysis and were unique relative to a much larger sample of mice from all Channel Islands and several additional mainland locations (Ashley & Wills 1987).

The seven mice collected in 1997 from East Anacapa warranted careful investigation. Prior to 1997, no deer mice had been reported on East Anacapa for more than 15 years, and they were presumed to have been extirpated. The mice that we examined were trapped on East Anacapa as bycatch during rat trapping. Before the East Anacapa mice were included in a conservation and management plan, it was important to determine that these mice were not reintroductions from elsewhere but were indeed *P. m. anacapae*. Five of the seven mice had the Ana haplotype, providing genetic evidence for classification as *P. m. anacapae*. Two mice, 58 and 59, had a unique haplotype (58). Of the five East Anacapa mice that could be used for morphometrics, three were classified as *P. m. anacapae*, including 59, which supports the inclusion of haplotype 58 into the subspecies. We therefore conclude that East Anacapa deer mice are *P. m. anacapae* and either have recovered from a severe bottleneck on the islet or have been recolonized from Middle or West Anacapa. The bottleneck explanation may be more likely because the 58 haplotype has not been found on Middle or West Anacapa. In either case, East Anacapa deer mice should be included in the management plan for *P. m. anacapae*.

The conclusion that the three Anacapa islets comprise a single ESU for conservation guided our PVA. An important advantage of PVA for a well studied group is that many input parameters have been measured, and we searched the extensive literature on *Peromyscus* to use the most accurate data possible (Appendix). Although extrapolation and inference were necessary for some input parameters, our PVA represents the upper range of accuracy likely for a threatened species. Further refinements of the PVA input were made based on data generated in our study. The Ana haplotype was the most common haplotype in mice from East, Middle, and West Anacapa (24 of 27 = 89%; Fig. 1) and therefore supports the connectivity of the three Anacapa Islet populations.

Cyclicity of population size cyclicity for deer mice had been documented on another Channel Island, Santa Barbara (Drost & Fellers 1991). Santa Barbara shares many features with Anacapa, such as small size, lack of other terrestrial mammals, and high densities of deer mice, so we used census data from Middle Anacapa to look for evidence of cyclicity. Because population fluctuation was evident, we assumed that we had characterized a single wave of a cycle and that we should incorporate this cyclicity into the PVA because of the additional extinction risk it poses. We modeled six initial population sizes that spanned the range of both long-term persistence and logistical feasibility for either a captive breeding or a translocation scenario. Indeed, five of the six initial size scenarios showed a 100% probability of persistence of the Anacapa metapopulation (Table 4). Persistence of subpopulations resulted in recolonization of islands because in all scenarios but one (700/2100) at least one islet (subpopulation) extinction occurred. Therefore, the metapopulational structure is a critical component of

the management strategy. Subpopulation extinctions were reduced to three with initial population sizes 333/1000 and above. Heterozygosity declined in all scenarios, although in the 333/1000 scenario it stabilized at 87–88% of prebottleneck values. Mean time to first subpopulation extinction appeared to be less dependent on initial conditions in the 333/1000 scenario and above. Taken together, the PVA suggests that an initial population size of 333 animals per subpopulation and 1000 animals per metapopulation would likely persist with high probability and thus represents the minimum size we recommend for reintroduction.

The sequence data allowed us to estimate *Nm* of two to seven migrants per generation and guided us to model the islands as a metapopulation. Estimates of *Nm* from genetic data provide averages over evolutionary time, so they are inappropriate for estimating migration rates among populations that have been recently isolated, have recently lost a large portion of habitat and population size, or for which barriers to dispersal have changed with changes in the environment. In the case of dispersal among the Anacapa islets, however, it is likely that the frequency with which mice occasionally cross the narrow stretches of water has not changed markedly in recent times. VORTEX models migration as a stochastic event with constant probability, but successful dispersal among the islands may be more sporadic and clustered because of weather patterns or other facilitating factors. It is unlikely, however, that the distribution of migration would be characterized by bursts of a high number of migrants separated by long periods of no dispersal during which multiple subpopulations could go extinct before being recolonized. Given the low rates, the effect of migration in the model would be to permit occasional recolonization of extirpated local populations rather than strong genetic or demographic rescue of small populations.

Halving migration rates with the 333/1000 in initial population size resulted in no values equally or less desirable than those found in the 200/600 scenario run with the original migration rates, except that both simulations had zero metapopulation extinction probability (Table 5). We attribute this relative stability to the fact that the original migration rate inputs were already extremely low, so lowering them further had little effect. Doubling migration rates did have a minor effect. Mean *H* rose to 0.90, exceeding slightly the values obtained with the original migration rates. No other values from the simulation with higher migration rates were equally or more desirable than results from the original 500/1500 scenario, and both simulations had zero metapopulation extinction probability. In sum, our PVA was somewhat sensitive to migration rates, but not sensitive enough to change our PVA recommendations.

Our study did not directly address the issue of captive breeding versus translocation of deer mice, but some additional considerations apply. The metapopulation structure of deer mice on Anacapa, with two to seven migrants per generation, may likely hold for rats as well. A single islet that has undergone rodent eradication might quickly be recolonized by rats. Sequential eradication followed by translocation of deer mice therefore may be ineffective. Capture and captive breeding of 1000 deer mice, which we recommend, would be a large but feasible undertaking. Deer mice do well in captivity. Care should be taken to minimize selection for captive conditions and the number of generations in captivity should be as few as possible. This would minimize both the chance for captive selection occurring in the captive population and the effect of deer mice removal on the Anacapa terrestrial ecosystem.

Acknowledgments

We thank G. Austin, K. Faulkner, and the staff of Channel Islands National Park. We thank B. Tershy, D. Croll, and members of the Island Conservation and Ecology Group, Santa Cruz. We thank the Santa Barbara Natural History Museum, the Natural History Museum of Los Angeles County, and the Field Museum for the generous access they gave us to their collections. We thank J. Dubach and D. Nyberg for their comments. We thank B. Patterson, D. Mujumdar, J. Zhong, and the staff of the Statistics Laboratory at the University of Illinois at Chicago for their help with statistical analyses. We thank P. Collins, L. Heaney, and W. Stanley for their help with morphometrics. The manuscript was much improved by the comments of R. Waples and three anonymous reviewers. O.R.W.P. thanks his wife, V. Morrow, for her support. This work was funded by a contract with Channel Islands National Park and a subcontract with the Island Conservation and Ecology Group. This work is in partial fulfillment of the requirements of the degree of Master of Science at the University of Illinois at Chicago (to O.R.W.P.).

Literature Cited

Adkins, R. M., and R. L. Honeycutt. 1994. Evolution of the primate cytochrome *c* oxidase subunit II gene. Journal of Molecular Evolution **38:**215–231.

Afifi, A. A., and V. Clark. 1996. Computer-aided multivariate analysis. 3rd edition. Chapman and Hall, London.

Ashley, M. V. 1986. Analysis of mitochondrial DNA polymorphisms among Channel Island deer mice, *Peromyscus maniculatus*. Ph.D. dissertation. University of California, San Diego.

Ashley, M. V., and O. R. W. Pergams. 1997. An interim report on the taxonomic status of East Anacapa Island deer mice. Technical report. Channel Islands National Park, Ventura, California.

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.

Austin, G. A. 1996*a*. Terrestrial vertebrate monitoring, Channel Islands National Park, 1994 annual report. Technical report CHIS–96–03. U. S. National Park Service, Washington, D.C.

Austin, G. A. 1996*b*. Terrestrial vertebrate monitoring, Channel Islands National Park, 1995 annual report. Technical report CHIS–96–04. U. S. National Park Service, Washington, D.C.

Blair, W. F. 1940. A study of prairie deer mouse populations in southern Michigan. American Midlands Naturalist **24:**273–305.

Blair, W. F. 1942. Size of home range and notes on the life history of the woodland deer-mouse and eastern chipmunk in northern Michigan. Journal of Mammalogy **23:**27–36.

Blair, W. F. 1958. Effects of x-irradiation on a natural population of the deer mouse (*Peromyscus maniculatus*). Ecology **39:**113–118.

Brewer, B. A., R. C. Lacy, M. L. Foster, and G. Alaks. 1990. Inbreeding depression in insular and central populations of *Peromyscus* mice. Journal of Heredity **81:**257–266.

Burgman, M. A., S. Ferson, and H. R. Akçakaya. 1993. Risk assessment in conservation biology. Chapman and Hall, New York.

Catlett, R. H., and R. Z. Brown. 1961. Unusual abundance of *Peromyscus* at Gothic, Colorado. Journal of Mammalogy **42:**247–259.

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. Contribution in Science **420**. Natural History Museum of Los Angeles County, Los Angeles.

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. U.S. National Park Service, Washington, D.C.

Dice, L. R., and W. E. Howard. 1951. Distance of dispersal by prairie deer mice from birthplaces to breeding sites. Contribution 50. Laboratory of Vertebrate Zoology, University of Michigan, Ann Arbor.

Dizon, A. E., C. Lockyer, W. F. Perrin, D. P. DeMaster, and J. Sisson. 1992. Rethinking the stock concept: a phylogenetic approach. Conservation Biology **84:**7–15.

Doran, A. L. 1980. Pieces of eight Channel Islands: a bibliographic guide and source book. Arthur H. Clark Co., Glendale, California.

Drost, C. A., and G. M. Fellers. 1991. Density cycles in an island population of deer mice, *Peromyscus maniculatus*. Oikos **60:**351–364.

Fisler, G. F. 1965. Adaptations and speciation in harvest mice of the marshes of San Francisco Bay. Publications in Zoology **77**. University of California Publications in Zoology.

Gill, A. E. 1976. Genetic divergence of insular populations of deer mice. Biochemical Genetics **14:**835–848.

Gill, A. E. 1980. Evolutionary genetics of channel island deer mice. Pages 719–743 in D. M. Power, editor. The California Channel Islands: proceedings of a multidisciplinary symposium. Haagen Printing, Santa Barbara, California.

Hays, H. A. 1958. The distribution and movement of small mammals in central Oklahoma. Journal of Mammalogy **39:**235–244.

Hinesley, L. L. 1979. Systematics and distribution of two chromosome forms in the southern grasshopper mouse, genus *Onychomys*. Journal of Mammalogy **60:**117–128.

Hooper, E. T. 1952. A systematic review of the harvest mice (genus *Reithrodontomys*) of Latin America. Miscellaneous publications 77. Museum of Zoology, University of Michigan, Ann Arbor.

Howard, W. E. 1949. Dispersal, amount of inbreeding, and longevity in a local population of prairie deer mice on George Reserve, southern Michigan. Contribution 43. Laboratory of Vertebrate Biology, University of Michigan.

Hudson, R. R., M. Slatkin, and W. P. Maddison. 1992. Estimation of levels of gene flow from DNA sequence data. Genetics **132:**583–589.

Jiménez, J. A., K. A. Hughes, G. Alaks, L. Graham, and R. C. Lacy. 1994. An experimental study of inbreeding depression in a natural habitat. Science **266:**271–273.

Klein, H. G. 1960. Ecological relationships of *Peromyscus leucopus noveboracensis* and *P. maniculatus gracilis* in central New York. Ecological Monographs **30:**387–407.

Lacy, R. C. 1993. VORTEX-a model for use in population viability analysis. Wildlife Research **20:**45–65.

Lacy, R. C., G. Alaks, and A. Walsh. 1996. Hierarchical analysis of inbreeding depression in *Peromyscus polionotus*. Evolution **50:** 2187–2200.

Lacy, R. C. 1998. VORTEX-A stochastic simulation of the extinction process (computer program). Version 8.03. Chicago Zoological Society, Brookfield, Illinois. Available at http://www2.netcom.com/~rlacy/vortex.html.

Lacy, R. C. 2000. Structure of the VORTEX simulation model for population viability analysis. Ecological Bulletins: in press.

Layne, J. N. 1968. Ontogeny. Pages 148–253 in J. A. King, editor. Biology of *Peromyscus* (Rodentia). American Society of Mammalogists, Stillwater, Oklahoma.

Linduska, J. P. 1942. Winter rodent populations in field shocked corn. Journal of Wildlife Management **6:**353–363.

Lynch, M., and T. J. Crease. 1990. The analysis of population survey data on DNA sequence variation. Molecular Biology and Evolution **7:**377–394.

Manville, R. H. 1949. A study of small mammal populations in northern Michigan. Miscellaneous publication 73. Museum of Zoology, University of Michigan, Ann Arbor.

McCarthy, M. A., M. A. Burgman, and S. Ferson. 1995. Sensitivity analysis for models of population viability. Biological Conservation **73:** 93–100.

Mihok, S. 1979. Behavioral structure and demography of subarctic *Clethrionomys gapperi* and *Peromyscus maniculatus*. Canadian Journal of Zoology **57:**1520–1535.

Millar, J. S. 1989. Reproduction and development. Pages 169–232 in G. L. Kirkland Jr. and J. N. Layne, editors. Advances in the study of *Peromyscus* (Rodentia). Texas Technical University Press, Lubbock.

Miller, P. S., and R. C. Lacy. 1999. VORTEX. Version 8 users manual. A stochastic simulation of the simulation process. Conservation Breeding Specialist Group, World Conservation Union/Species Survival Commission, Apple Valley, Minnesota.

Moritz, C. 1994. Defining 'evolutionarily significant units' for conservation. Trends in Ecology and Evolution **9:**373–375.

Nei, M. 1982. Evolution of human races at the gene level. Pages 167–181 in B. Bonne-Tamir, T. Cohen, and R. M. Goodman editors. Human genetics, part A: the unfolding genome. Alan R. Liss, New York.

Nei, M. 1987. Molecular evolutionary genetics. Columbia University Press, New York.

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

Ralls, K., J. D. Ballou, and A. Templeton. 1988. Estimates of lethal equivalents and the cost of inbreeding in mammals. Conservation Biology **2(2):**185–193.

Rich, S. R., C. W. Kirkpatrick, J. L. Shippee, and K. L. Crowell. 1996. Morphological differentiation and identification of *Peromyscus leucopus* and *P. maniculatus* in northeastern North America. Journal of Mammalogy **77:**985–991.

Rozas, J., and R. Rozas. 1997. DnaSP v. 2.0: a novel software package for extensive molecular population genetics analysis. Computer Applications in Bioscience **13:**307–311.

Rozas, J., and R. Rozas. 1998. DnaSP-DNA Sequence Polymorphism (computer program). Version 2.9. Universitat de Barcelona, Barcelona. (Available at http://www.bio.ub.es/~julio/DnaSP.html.)

Ryder, O. 1986. Species conservation and systematics: the dilemma of subspecies. Trends in Ecology and Evolution **1:**9–10.

SPSS. 1997*a*. SYSTAT 7.0 for Windows (computer program). Chicago.

SPSS. 1997*b*. SYSTAT 7.0: statistics. SPSS, Chicago.

Schwemm, C. A. 1995. Terrestrial vertebrate monitoring, Channel Islands National Park, 1993 annual report. Technical report CHIS–94–02. National Park Service, Washington, D.C.

Sheppe, W. 1961. Systematic and ecological relations of *Peromyscus oreas* and *P. maniculatus*. Proceedings of the American Philosophical Society **105:**421–446.

Snyder, D. P. 1956. Survival rates, longevity, and population fluctuations in the white-footed mouse, *Peromyscus leucopus*, in southeastern Michigan. Miscellaneous publication 95. Museum of Zoology, University of Michigan, Ann Arbor.

Tajima, F. 1983. Evolutionary relationship of DNA sequences in finite populations. Genetics **105:**437–460.

Terman, C. R. 1968. Population dynamics. Pages 412–450 in J. A. King, editor. Biology of *Peromyscus* (Rodentia). Special publication 2. The American Society of Mammalogists, Stillwater, Oklahoma.

Vogler, A. P., and R. DeSalle. 1994. Diagnosing units for conservation. Conservation Biology **8:**354–363.

von Bloeker, J. C. 1941. A new subspecies of white-footed mouse from the Anacapa Islands, California. Bulletin of the Southern California Academy of Science **40:**161–162.

Waples, R. S. 1991. Pacific salmon, *Oncorhynchus* spp., and the definition of species under the Endangered Species Act. Marine Fisheries Review **53:**11–22.

Wolff, J. O. 1989. Social behavior. Pages 271–292 in G. L. Kirkland and J. N. Layne, editors. Advances in the study of *Peromyscus*. Texas Technical University Press, Lubbock.

Appendix

Input values used for the VORTEX PVA program.

3 REAL WEEKS = 1 VORTEX YEAR (V)

Simulations: 100.

Years (1768 VORTEX years = 102 real years): 1768.

Reporting interval (years) (104 VORTEX years = 6 real years): 104.

Definition of extinction (0 = only one gender left): 0.

Populations: 3.

Lower age for migration (Wolff 1989): 3.

Upper age for migration (Terman 1968; Collins et al. 1979): 17.

Migrating sex female, male, or both (Terman 1968): both.

Migration survival (%; migration rates, estimated from sequence data, provide numbers of successful migrants): 100.000000.

Minimum density for emigration (assuming that inter-island dispersal is a chance occurrence, not restricted to times when densities are high): 0.000000.

Migration from population 1 (West) to population 2 (Middle): 0.000048.

Migration from population 1 (West) to population 3 (East): 0.000062.

Migration from population 2 (Middle) to population 1 (West): 0.000048.

Migration from population 2 (Middle) to population 3 (East): 0.000147.

Migration from population 3 (East) to population 1 (West): 0.000062.

Migration from population 3 (East) to population 2 (Middle): 0.000147.

Figures were taken from this study and modified. For example, an *Nm* of 7.27 individuals per generation between West and Middle Anacapa was first halved to 3.635 to represent 3.635 going from West to Middle and 3.635 going from Middle to West. One generation = 84 days (Millar 1989) or 4 VORTEX years. The rate of 3.365 individuals per generation was converted to individuals per VORTEX year by dividing by 4 (0.90875 individuals per VORTEX year). Individuals per VORTEX year was converted to % of individuals per VORTEX year by dividing by the average number of individuals on each islet, extrapolated from census data. The average number on Middle Anacapa was (708 + 12111 + 9888 + 14895 + 2834)/5 = 8087; on West, (36,909 + 23,091)/2 ≈ 30,000 (Schwemm 1995; Austin 1996*a*,1996*b*; G. A. Austin, personal communication). The average number of individuals on both Middle and West Anacapa was (8087 + 30,000)/2 = 19,044. Individuals per VORTEX year divided by the average number of individuals on both Middle and West Anacapa equaled the migration rate, or 0.90875/19044 = 0.000048.

Inbreeding depression (see text)? Yes.

Lethal equivalents per diploid: 1.28. No data on inbreeding depression are available for these populations of mice. The value used is mean effect of inbreeding on overall reproductive success for three subspecies of *Peromyscus polionotus* measured in a large breeding study by Lacy et al. 1996. Similar values were reported for other populations of *Peromyscus*, including some island populations, by Brewer et al. (1990) and Jiménez et al. (1994) and as the median for rodent species in the survey of Ralls et al. (1988).

Percent of genetic load due to recessive lethals: 100.0.

Concordance of environmental variation (EV) between reproduction and survival? Yes.

Correlation of EV among populations: 0.500000.

Types of catastrophes (rats, storms): 2.

Monogamous, polygynous, or hermaphroditic (Wolff 1989): polygynous.

Female breeding age (Layne 1968): 4.

Male breeding age (Layne 1968): 3.

Maximum breeding age (Terman 1968): 17 years.

Sex ratio (Collins et al. [1979] for *P. m. anacapae*): 0.540000. It is not unusual for *P. maniculatus* to have male biased sex ratios at birth. The following are sex ratios recorded for other *P. maniculatus* spp. in natural populations, taken from Terman (1968): 0.47 (Catlett & Brown 1961), 0.59 (Hays 1958), 0.54 (Sheppe 1961), 0.51 (Blair 1940), 0.51 (Howard 1949), 0.50 (Linduska 1942), 0.55 (Blair 1942), 0.64 (Klein 1960), 0.56 (Manville 1949). The mean of these values is 0.54, the range 0.47–0.64.

Maximum litter size (Collins et al. 1979): 9.

Density dependent breeding? No.

(Input for population 1: West follows)

Percent females breeding: 49.000000. Regressed from population census data of Middle Anacapa (Schwemm 1995, Austin 1996*a*,1996*b*, G. A. Austin, personal communication) onto 5–85% range over 4 years (Drost & Fellers 1991) and then averaged, not corrected for demographic variation.

EV-breeding: 35.675000. Calculated as 1 SD from the mean of a 5–85% range over 4 years (Drost & Fellers 1991), not corrected for demographic variation.

Percent litter size 2: 3.0000000. Percent litter sizes are fitted to a normal distribution, with a mean litter size of 5.64 and a range of 2–9 (Collins et al. 1979).

Percent litter size 3: 6.0000000.

Percent litter size 4: 9.0000000.

Percent litter size 5: 21.000000.

Percent litter size 6: 29.000000.

Percent litter size 7: 19.000000.

Percent litter size 8: 8.0000000.

Percent litter size 9: 5.0000000.

FMort age 0 (Snyder 1956): 43.000000. We used data on survivorship by age, averaged over mice born in all seasons (spring/summer and fall) and over both genders. Visual extrapolation of this data utilizing the scatterplot-with-quadratic-smoother function of SYSTAT (SPSS 1997*a*) gave us these values. The extent of environmental variation in mortality is not known. We tested both low and relatively high values.

EV: 20.000000.

FMort age 1: 36.000000.

EV: 3.000000.

FMort age 2: 28.000000.

EV: 3.000000.

FMort age 3: 24.000000.

EV: 3.000000.

Adult FMort: 21.000000.

EV: 3.000000.

MMort age 0: 43.000000.

EV: 20.000000.

MMort age 1: 36.000000.

EV: 3.000000.

MMort age 2: 28.000000.

EV: 3.000000.

Adult MMort: 22.000000.

EV: 3.000000.

Local or global catastrophe? Global. Frequencies and effects of catastrophes unknown. We tested plausible low and high values. We assumed that storms would affect all three islets synchrounously (a "global" catastrophe) but that invasion by rats or other biotic catastrophes would affect the islets independently ("local" catastrophes).

Probability of catastrophe 1: 1.000000.

Severity, reproduction: 0.500000.

Severity, survival: 0.750000.

Local or global catastrophe? Local.

Probability of catastrophe 2: 1.000000.

Severity, reproduction: 0.500000.

Severity, survival: 0.750000.

All male breeders? No.

Litters per successful male: 2.500000. Mihok (1979) writes that a *P. maniculatus* family unit consists of two or three females (2.5) and one male. From this, VORTEX calculates percentage of males breeding, based on a Poisson distribution, as 26.6%.

Start at stable age distribution? Yes.

Initial population size: 200.

Function *K*:

$$K = 26285 + 12989 \sin\left[\frac{(V + 352)2\pi}{60.666}\right], \text{metaK} < 62{,}000.$$

EV—K: 0.0. We modeled fluctuations in carrying capacity as a sine wave (above) rather than as random variation across years.

Rates for breeding, mortality, and catastrophes for population 2, Middle Anacapa, are the same as those for population 1.

Initial population size for population 2, Middle Anacapa: 100.

Function *K*:

$$K = 9105 + 4499 \sin\left[\frac{(V + 352)2\pi}{60.666}\right], \text{metaK} < 62{,}000.$$

Rates for breeding, mortality, and catastrophes for population 3, East Anacapa, are the same as those for population 1.

Initial population size for population 3, East Anacapa: 100.

Function *K*:

$$K = 6550 + 3237 \sin\left[\frac{(V + 352)2\pi}{60.666}\right], \text{metaK} < 62{,}000.$$