Identifying Evolutionarily Significant Units and Prioritizing Populations for Management on Islands

Authors: Robertson, Jeanne M., Langin, Kathryn M., Sillett, T. Scott, Morrison, Scott A., Ghalambor, Cameron K., et al.

Source: Monographs of the Western North American Naturalist, 7(1) : 397-411

Published By: Monte L. Bean Life Science Museum, Brigham Young University

URL: https://doi.org/10.3398/042.007.0130

Monographs of the Western North American Naturalist 7, © 2014, pp. 397–411

IDENTIFYING EVOLUTIONARILY SIGNIFICANT UNITS AND PRIORITIZING POPULATIONS FOR MANAGEMENT ON ISLANDS

Jeanne M. Robertson[1,2,3], Kathryn M. Langin[2], T. Scott Sillett[4],
Scott A. Morrison[5], Cameron K. Ghalambor[2], and W. Chris Funk[2]

ABSTRACT.—Islands host exceptionally high levels of endemism compared to mainland regions and are subject to disproportionately high rates of extinction and imperilment. Therefore, the protection and preservation of taxonomic units that are endemic to islands is a key component in mitigating the loss of global biodiversity. However, determining what is "endemic" on islands can be challenging. Conservation units are commonly delineated based on genetic divergence at neutral loci (e.g., genetic differentiation at microsatellite loci or reciprocal monophyly based on mitochondrial genes). Island populations of nonvolant species are expected to meet this criterion, regardless of adaptive differences, due to geographic isolation, founder effects, and small effective population sizes. We therefore argue that the delineation and management of island endemic populations should not be based on neutral genetic divergence and reciprocal monophyly alone. Instead, we recommend identifying island populations that have genetically based adaptations to their unique environments. A comprehensive framework specifically designed to delineate evolutionarily significant units (ESUs) on islands should be based on metrics of both neutral and adaptive genetic divergence. The California Channel Islands host several taxa considered to be endemic, and we highlight 2 case studies to illustrate how this framework can be applied. This approach can be applied broadly to continental islands and island archipelagos, enabling conservation practitioners to use an objective framework to prioritize units of biological diversity for management.

RESUMEN.—Las islas albergan niveles excepcionalmente altos de especies endémicas en comparación con las regiones continentales, y están sujetas a niveles desproporcionadamente altos de extinción y peligro. La protección y conservación de las unidades taxonómicas que son endémicas de las islas es, por lo tanto, un componente clave para mitigar la pérdida global de biodiversidad. Sin embargo, determinar qué es "endémico" en las islas puede ser un reto. Las unidades de conservación son comúnmente delineadas basándose en divergencias genéticas en lugares neutrales (por ejemplo, diferenciación genética en loci microsatelitales o monofilia recíproca basada en genes mitocondriales). Se espera que las poblaciones de las islas de especies que no pueden volar reúnan estos criterios, independientemente de diferencias de adaptación, debido al aislamiento geográfico, efectos de hundimiento y un tamaño de población efectivo pequeño. Por lo tanto, argumentamos que la delineación y el tratamiento de las poblaciones endémicas de la isla no deberían estar basados sólo en la divergencia genética neutral y en monofilia recíproca. En lugar de eso, nosotros apoyamos la identificación de poblaciones de la isla que tienen adaptaciones basadas genéticamente exclusivamente para su propio ambiente. Un marco comprensible específicamente diseñado para describir unidades evolutivamente importantes (UEIs) en las islas debería estar basado en ambas mediciones, tanto en la neutral como en la divergencia genética adaptativa. Las Islas del Canal de California albergan varios taxa que se consideran endémicos, y destacamos 2 casos prácticos para ilustrar como se puede aplicar esta estrategia. Este enfoque puede ser ampliamente aplicado a las islas continentales y a las islas del archipiélago, permitiendo a los profesionales de la conservación aplicar una estrategia objetiva para priorizar unidades de diversidad biológica para su manejo.

Islands host exceptionally high levels of endemism compared to mainland regions (Kier et al. 2009). Unfortunately, they are also subject to disproportionately high rates of extinction and local extirpation (Johnson and Statterfsfield 1990, Whittaker and Fernandez-Palacios 2008). Therefore, the protection and preservation of taxonomic units that are endemic to islands is a key component in mitigating the loss of global biodiversity. Endemic units include not only species-level divergence but also populations that are adaptively differentiated on islands. Distinct intraspecific units could be in the early stages of speciation and therefore represent incipient species-level biodiversity. Moreover, maintaining island populations adapted to different environmental conditions should maximize the potential of the populations to adapt to future environmental changes such as climate change. Therefore, it is critical to identify island

---

[1] Department of Biology, California State University Northridge, Northridge, CA 91330. E-mail: jeanne.robertson@csun.edu
[2] Department of Biology, Colorado State University, Fort Collins, CO 80523.
[3] Natural History Museum of Los Angeles County, Los Angeles, CA 90007.
[4] Migratory Bird Center, Smithsonian Conservation Biology Institute, National Zoological Park, Washington, DC 20013.
[5] The Nature Conservancy, San Francisco, CA 94105.

populations that represent unique lineages adapted to different environments.

Insular biota face myriad threats that make conservation management challenging. Populations restricted to islands are prone to demographic stochasticity and suffer from long-term reductions in census and effective population sizes, lower genetic and phenotypic diversity, and inbreeding depression (Frankham 1997, Woolfit and Bromham 2005). Their evolutionary history within the context of depauperate communities has also played a role in making them more susceptible to the introduction of new species—whether competitors, predators, or pathogens (Blondel 2000). These factors amplify the effects of anthropogenic stressors like habitat loss, invasive species, and climate change; and these effects in turn have necessitated the implementation of many intensive management programs on islands around the world (Wood 2000, Goldman et al. 2008, Gonzalez et al. 2008, Cruz et al. 2009, Morrison et al. 2011).

Many insular taxa exhibit high levels of genetic and phenotypic divergence from mainland populations or from other islands within the same archipelago, due in part to the unique suite of microevolutionary forces on islands that shape their trajectories (Barton 1996). Unless the island was once connected to the mainland, the initial colonization event usually involves a genetic bottleneck that limits the newly formed insular population to a subset of the genetic and phenotypic diversity of the source population (Frankham 1997). Novel populations are subject to a combination of selection pressures in their insular environment and pronounced genetic drift. The latter effect is stochastic in nature, but the former—selection—has been shown to operate deterministically for many traits, which are collectively referred to as the "insular syndrome" (Blondel 2000). Insular populations tend to have fewer competitors and predators, which can lead to directional selection for reduced predator defenses (Bowen and VanVuren 1997, Slikas et al. 2002), expanded niche space (Martin 1992), increased intraspecific competitive abilities (Robinson-Wolrath and Owens 2003), and a number of other morphological, demographic, and behavioral traits (Blondel 2000).

An important consideration in setting conservation priorities is the degree to which observed population divergence is adaptive versus the result of stochastic processes like founder effects (which are particularly pronounced on islands). Most island populations will show monophyly, or at least genetic differentiation (divergence in allele or haplotype frequencies) at neutral loci, due to founder effects and genetic drift. Hence, monophyly is not sufficient by itself to characterize the degree of endemism of an island population. We argue that degree of endemism—and so perhaps degree of conservation priority—should also require adaptive divergence from mainland or other island populations. Further, we propose a framework for categorizing divergence in island populations, and we discuss how to apply this framework using conservation management case studies from the California Channel Islands.

Evolutionarily Significant Units

Biodiversity conservation efforts traditionally focus on maintaining one or more minimum viable populations (MVP) of a focal taxon that, in theory, should persist on ecological time scales (Shaffer 1981). However, the past decade has seen an increased emphasis on conserving population-level genetic diversity and the processes that promote adaptive evolution within species (Crandall et al. 2000, Moritz 2002). Given the intensifying nature of ongoing threats to biological diversity, the latter strategy is aimed at enhancing the capacity of species to adapt to future environmental conditions and thus to increase the probability of persistence over evolutionary time scales. Conserving adaptive potential may be especially important for insular populations that have limited ability to move in response to environmental changes (e.g., shifts in climate) and instead must adapt in situ.

The term "evolutionarily significant unit" (ESU; sometimes also termed "evolutionary significant unit") was coined by Ryder (1986) to describe intraspecific taxonomic units worthy of conservation. The ESU concept is central to the development of population management strategies and the application of conservation legislation, particularly in determining "distinct population segments" (DPSs) as units of conservation for vertebrate species under the U.S. Endangered Species Act (Fay and Nammack 1996, Groom et al. 2005). The conservation genetics of Pacific salmon (*Oncorhynchus* spp.)

provided important empirical examples for application of an ESU to natural populations under the Endangered Species Act (Waples 1991, 1995, CDFG 2002). However, the criteria for delineating ESUs have varied considerably over time (Crandall et al. 2000), and the interpretation and application of ESUs and DPSs has historically spurred scientific and public debate (Waples 1998). Though Ryder's (1986) original definition focused on adaptive differentiation, an increase in the availability of genetic data facilitated a movement toward ESU definitions that focus solely on the presence of genetic differentiation or reciprocal monophyly at neutral loci (Moritz 2002, Zink 2004). Moritz (2002) asserts that the use of reciprocal monophyly provides an unambiguous definition of an ESU and preserves the genetic diversity of irreplaceable, isolated lineages. In contrast, Crandall et al. (2000) argue that the original ESU definition put forward by Ryder (1986) is more conservation relevant and that adaptive variation and "ecological exchangeability" (i.e., the degree to which populations are adapted to the same ecological niche and are thus exchangeable) must be considered, not just neutral genetic divergence and reciprocal monophyly (Shimizu 2008). Both viewpoints focus on the conservation of genetic diversity, as does the federal requirement of genetic or morphological distinction for delineating distinct population segments (Fay and Nammack 1996), but each differ in their emphasis on adaptive versus neutral regions of the genome and the type of data required to demonstrate that a population qualifies as an conservation unit. Fraser and Bernatchez (2001) argue that instead of debating the relative merits of each definition, we should recognize that both definitions have strengths and weaknesses and we should apply the appropriate definition(s) on a case-by-case basis. Island flora and fauna represent a special case for determining which ESU concept to apply.

We argue that the most useful ESU definition for island populations is one that incorporates both adaptive variation and measures of neutral genetic divergence. Compared to mainland and other insular populations, island populations often show pronounced divergence at neutral loci because of restricted gene flow across oceanic barriers and the strong effects of genetic drift in small isolated populations (Patirana et al. 2002). Exceptions to this phenomenon include highly mobile taxa that do not perceive oceans as a hard barrier to dispersal (Postma and van Noordwijk 2005). Insular terrestrial populations of most taxonomic groups tend to be sedentary and thus likely to show reciprocal monophyly at neutral loci (e.g., mtDNA), even if the time since divergence was relatively recent (Neigel and Avise 1986, Walker et al. 2006). This necessitates separate conservation units on each island or between island and mainland sites under the Moritz (1994) ESU definition.

The ESU definition is especially important for the conservation of insular populations because these populations are frequently subject to intensive, population-specific management actions (e.g., Coonan et al. 2010). We suggest that using neutral genetic divergence alone for delineating ESUs on islands is insufficient because the method may overestimate the evolutionary significance of any island population relative to other island and mainland populations. The method may also impede consideration of translocations as a management strategy aimed at facilitating demographic or genetic rescue for small insular populations. Conservation efforts on islands should focus on identifying units of insular endemism that are adaptively differentiated from other mainland or insular populations and that show marked genetic divergence.

Delineating ESUs on Islands

Effective management of insular populations requires an objective framework for identifying and prioritizing intraspecific conservation units (Pullin and Stewart 2006). To assess how others have defined ESUs on islands, we conducted an ISI Web of Knowledge literature search in March 2012 using the following terms: [islands AND (evolutionarily significant unit OR evolutionary significant unit OR distinct population segment)]. The search returned 71 articles, 39 of which were deemed relevant (Appendix). We included only empirical studies of island taxa at the population or subspecies level and excluded review articles, perspective pieces, empirical studies of marine or human populations, and studies conducted on island taxa that had been described as insular endemic species (rather than populations or subspecies relative to the mainland). We considered studies only when an island ESU was based on a comparison to a

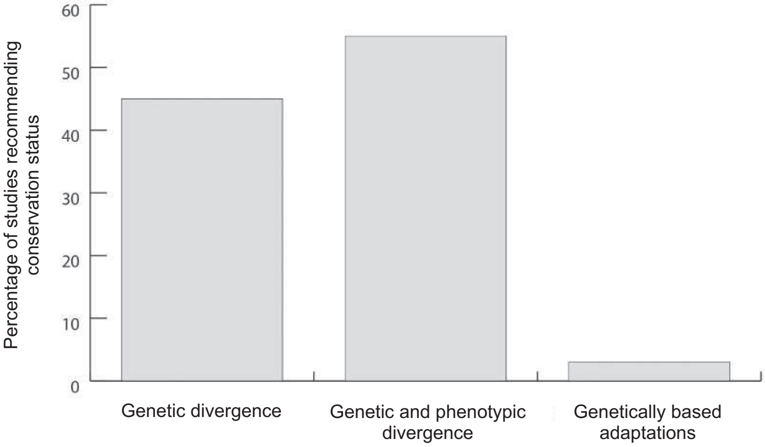

Fig. 1. Most studies of island taxa use genetic data alone for ESU designation. While some studies include data on morphological differences, there remains a paucity of studies that test whether these phenotypic differences are genetically based and adaptive prior to making conservation recommendations.

mainland population or other surrounding island populations. Of the 39 studies, 45% used genetic distance as the sole criterion for delineating a conservation unit, and 55% based their designation on evidence of genetic and phenotypic differentiation (Fig. 1). Bottin et al. (2007) was the only study to demonstrate that the phenotypic traits unique to an insular population represented genetically based, adaptive differentiation, as opposed to phenotypically plastic differences caused by environmental effects. In the 39 studies, an ESU definition focusing on neutral genetic divergence was applied much more frequently for insular populations than was ESU frameworks that integrate data on neutral genetic and adaptive phenotypic differentiation. Moreover, most studies documenting genetic divergence at neutral loci showed genetic differentiation as significant differences in allele or haplotype frequencies, rather than demonstrating reciprocal monophyly (but see Kanthaswamy et al. 2006, Hoglund et al. 2011; Appendix).

We suggest that management strategies on islands should transition to putting a greater emphasis on adaptive differentiation. We are particularly concerned with cases where populations are distributed on multiple adjacent islands or where populations are found on islands and nearby mainland locations. In such cases, insular populations are likely to exhibit neutral genetic divergence relatively quickly, even in the presence of some gene flow, because of initial founder effects and subsequent genetic drift.

We propose a modified version of the framework described by Crandall et al. (2000) for delineating ESUs on continental islands and on island archipelagos. Our framework is aligned with Crandall et al. (2000) in that populations must be genetically differentiated (rejecting genetic exchangeability). However, we put greater emphasis on the need to demonstrate that observed phenotypic differences are both genetically based and adaptive (i.e., increase fitness). We deemphasize the requirement that a population must have a unique ecological role that is nonexchangeable with sister populations on adjacent islands or the mainland. We also argue that even if island populations do not qualify as ESUs using our framework, they may still warrant some level of conservation prioritization, depending on the degree of neutral, phenotypic, and adaptive divergence from mainland or other island populations (see “Summary and Recommendations” and Table 1). The 3 components of this modified framework are (1) neutral genetic divergence, (2) phenotypic divergence, and (3) genetically based local adaptation; and we present the data required to test these criteria.

Neutral Genetic Divergence

Despite our *a priori* expectation that most insular populations should show some degree of

TABLE 1. Criteria for delineating evolutionarily significant units (ESUs) and conservation priority for insular populations based on neutral genetic, phenotypic, and adaptive divergence. Supporting evidence for divergence or designation as an ESU (yes), failure to find evidence for divergence or ESU (no), missing data (no data), and unresolved (?).

Lines of evidence			Conclusion	
Neutral genetic divergence	Phenotypic divergence	Genetically based adaptive divergence	Evolutionarily significant unit	Conservation priority
yes	yes	yes	yes	highest
yes	yes	no data	?	higher
yes	no data	no data	?	high
no	yes	yes	no	high
yes	yes	no	no	mid
yes	no	no	no	low
no	yes	no data	no	low
no	yes	no	no	low
no	no	no	no	lowest

genetic differentiation, we recognize the importance of neutral genetic data to confirm isolation of island populations. Therefore, as a first step in identifying insular endemic populations, we recommend comparing genetic divergence at neutral loci across island and mainland populations or between island populations. We also agree with the recommendation of Crandall et al. (2000) for measuring genetic differentiation on both historical and recent time scales. The magnitude of recent genetic differentiation is expected to vary among taxa due to differences in life history and dispersal abilities and thus should be considered with reference to the level of genetic differentiation between species, subspecies, and populations in other parts of the taxon's range (Oliva-Tejera et al. 2006).

Traditionally, phylogeographic studies use mitochondrial, chloroplast, or nuclear DNA sequence data to infer deeper historical relationships among populations, whereas landscape genetic studies use microsatellite loci to quantify genetic structure on more recent time scales. Both approaches have been applied to delineate island ESUs (Appendix). Gene flow can also be estimated from measurements of genomic variation across populations based on single-nucleotide polymorphisms (SNPs), thereby allowing characterization of adaptive differentiation (Luikart et al. 2003, Hohenlohe et al. 2010, De Wit et al. 2012).

Phenotypic Divergence

The second component of our framework addresses variation in morphological, behavioral, or demographic traits among islands and between continental island and mainland populations. The first step in documenting adoptive differentiation is quantifying divergence in phenotypic traits that are easily measured, and this practice has been applied to several island studies to date (Appendix). Insular populations often exhibit the insular syndrome: a suite of morphological, life history, or behavioral traits that appear to be adaptive for island environments (e.g., Postma and van Noordwijk 2005). Divergence in traits used for courtship and mating might also reveal island populations that are in the early stages of speciation (West-Eberhard 1983, Coyne and Orr 2004). However, the mere detection of unique phenotypic traits is not sufficient for establishing whether adaptive differentiation has occurred. We recommend that these data be used to frame hypotheses and develop appropriate tests for local adaptation.

Local Adaptation

The third component of our framework requires testing whether island populations are adaptively differentiated from mainland or other island populations. Many studies include phenotypic divergence as supporting evidence for subspecific or ESU designation of island populations (Fig. 1). However, few test whether these differences are the products of adaptive evolution (Appendix), which testing requires that traits have a genetic basis and confer a fitness benefit in the local environment (Funk and Fa 2006). Experimental, genomic, and field studies can elucidate patterns of local adaptation. Below we describe several different approaches that can be applied to determine whether observed phenotypic differences of island populations are genetically based local adaptations with fitness consequences.

Identifying Adaptive Differentiation

EXPERIMENTAL STUDIES.—Reciprocal transplant (RT) and common garden (CG) experiments are the most common approaches for investigating local adaptation (reviewed by Kawecki and Ebert 2004, Rader et al. 2005). These experimental designs are well suited for sessile or small organisms (e.g., plants, some insects, and small vertebrates; Losos et al. 2000) and are powerful for distinguishing evolved responses from environmentally mediated ones. A review of RT and CG experiments detected high levels of adaptive variation in marine taxa, but few of those studies were evaluated in an ESU framework (Conover et al. 2006), emphasizing the disconnect between studies of adaptive variation and conservation. RT and CG experiments can be challenging to conduct on vertebrates, especially species of conservation concern (Mittelbach et al. 1999, Ballentine and Greenberg 2010, Herczeg and Valimaki 2011, Svanback and Eklov 2011). In light of this limitation, we propose that in situations where RT and CG experiments are not feasible, population genomic and field studies be used to determine the genetic basis of phenotypic differences observed between island and mainland populations.

POPULATION GENOMIC STUDIES.—Population genomics is a powerful approach for characterizing adaptive differentiation among island populations (Hudson 2008, Morozova and Marra 2008, Stapley et al. 2010). Sequencing SNPs can be used to identify adaptively divergent populations and to study reproductive isolation and incipient speciation processes (Nosil and Feder 2012), and this method has been validated for known divergent ecotypes (Lumley and Cusson 2013). One approach is to compare genetic distances across thousands of loci to identify outlier loci, presumably under divergent selection, to characterize adaptive differentiation among populations (Luikart et al. 2003, Funk et al. 2012). Ideally, many loci of adaptive significance should be examined to quantify overall adaptive differentiation in response to the multiple dimensions of environmental variation. We advise against using few genes of known function because this does not characterize overall adaptive differentiation (Funk et al. 2012). Genomic data are rapidly becoming more affordable and easier to obtain, which will increase the importance of population genomics in conservation (Allendorf et al. 2010, Lumley and Cusson 2013). For example, one can conduct a population genomic study using RAD tag technology for $50 to $100 per individual (Allendorf et al. 2010), a cost that is less than many long-term monitoring programs.

FIELD STUDIES.—Studies that measure selection or test whether divergent traits are adaptive in the field can help distinguish between local adaptation and phenotypic plasticity, especially in cases where funding is limited and RT and CG experiments are not feasible. Field research, particularly behavioral studies, need not be invasive or time consuming, contrary to assertions by some evolutionary biologists (e.g., Zink 2007). For example, Peluc et al. (2008) used a simple experimental design to demonstrate in one field season that the unique nest-site selection behavior exhibited by Orange-crowned Warblers (*Oreothlypis celata*) on Santa Catalina Island reflected the birds' ability to respond plastically to variation in the nest-predator community, rather than a genetically based phenotypic differentiation. Quantifying patterns of morphological and life history variation among populations typically requires more intensive, long-term study (e.g., Radar et al. 2005). For example, selection gradient analysis of marked individuals can help identify whether divergent traits are under selection (Lande and Arnold 1983). Closely related species could act as proxies for an insular population that is not amenable to experimental studies. (Friesen et al. 2006, Bottin et al. 2007).

Applying the Framework

Combining data on genetic and phenotypic divergence with considerations of local adaptation will make it possible to set appropriate priorities for conservation management on islands. Such an approach may require more effort in determining ESUs but could improve efficiency in delineating ESUs, particularly as population genomics become more feasible and cost effective. We will also gain a deeper understanding of the processes that drive adaptive genetic differentiation by explicitly considering and quantifying the continuum of genetic divergence that is expected for island populations connected by varying levels of gene flow and exposed to varying levels of divergent selection.

We make specific recommendations in Table 1 for ranking populations based on the degree of neutral, phenotypic, and adaptive differentiation compared to other island and mainland populations. We define an ESU as a population that shows both genetic divergence at neutral loci and adaptive, genetically based phenotypic differences. Assuming that the demographic characteristics among populations are equal, we place the highest conservation priority on populations where evidence exists for adaptive genetic differentiation, even when tests for the genetic basis of phenotypic divergence are pending. Mid-priority is assigned to populations that are genetically isolated and that exhibit phenotypically plastic differentiation from neighboring populations. Populations that are divergent at neutral loci but have no phenotypic or adaptive differences are lower priority. Populations that show no detectable differentiation at neutral genetic loci (even with sufficiently variable loci) but exhibit phenotypic differences (e.g., Ballentine and Greenberg 2010) should have some conservation value. Populations that are indistinguishable both genetically and phenotypically are not considered a distinct ESU and are the lowest conservation priority. We suggest that this ranking system be used to identify island populations that are most deserving of limited economic resources for biodiversity conservation efforts. Nonetheless, other factors must also be considered when making decisions about conservation prioritization, including population status, our ability to influence population viability through management actions, management objectives of different land owners, and socioeconomic factors.

Beyond prioritization, data on neutral versus adaptive genetic differentiation can also inform the management of populations that have been identified as a conservation priority. For instance, insular populations are particularly susceptible to the demographic and genetic consequences of small population sizes, especially when anthropogenic stressors reduce numbers below historic levels. Translocation of individuals from neighboring populations is one management strategy to consider in those situations. This strategy has the potential to ameliorate demographic stochasticity or inbreeding depression but could also lead to outbreeding depression if the translocated individuals originate from an adaptively divergent population. Outbreeding depression is most likely when populations are adaptively divergent and least likely when they only differ at neutral loci (Frankham et al. 2011). The benefit of demographic or genetic rescue may outweigh the potential cost of outbreeding depression for a population undergoing severe declines, but information on the degree of adaptive population divergence could still be valuable for management.

We recognize that identifying conservation units at the intraspecific level can be challenging with real-world data and pressing management concerns. The degree of population-level divergence can fall along a spectrum that ranges from slight divergence at neutral loci, to adaptive phenotypic divergence, to incipient speciation. These gradations in divergence should be translated into priority management categories. However, insular populations require a particularly strong emphasis on identifying and understanding patterns of adaptive divergence, not just neutral genetic divergence.

CASE STUDIES ON THE CALIFORNIA CHANNEL ISLANDS

The California Channel Islands have been the focus of intensive conservation management over recent decades. Here, we highlight 2 case studies of species of conservation concern to demonstrate how our framework for delineating ESUs could be applied toward their management.

Loggerhead Shrike

San Clemente Island is home to an endemic population of Loggerhead Shrike (*Lanius ludovicianus mearnsi*) that was driven nearly extinct by habitat destruction due to livestock grazing and other anthropogenic land-use disturbances. This population was listed under the U.S. Endangered Species Act (ESA) in 1977 (USFWS 1977), and the population size dropped to an estimated low of 14 individuals in 1998 (USFWS 2009). Since then, an intensive and costly management program ($25 million from 1993 to 2008; DOD 2010) has involved invasive species removal, management of shrike breeding habitat, captive breeding, and the removal or eradication of 5 species of native shrike predators (Elliot and Popper 1999). The population increased to nearly 200 individuals by 2009 (including juveniles and nonbreeding adults) but remains listed under the ESA due to small population size and other ongoing threats (USFWS 2009).

The management actions used to conserve shrikes on San Clemente Island have been controversial, in part because of their cost and their impact on other native vertebrate species, including the endemic island fox (*Urocyon littoralis,* Roemer and Wayne 2003), and the debate over the population's genetic distinctiveness. *Lanius l. mearnsi* was described by Ridgeway (1903) and later Miller (1931) based on plumage and morphological characters. Subsequent genetic studies concluded that the San Clemente shrikes are genetically distinct from populations on the mainland and on the northern Channel Islands (Mundy et al. 1997, Eggert et al. 2004, Caballero and Ashley 2011). However, genetic analyses of museum specimens collected in the late 1800s and early 1900s have detected a decline in genetic diversity over time, and those specimens have a different genetic composition than the postmanagement birds sampled after 1990. Moreover, the postmanagement population of *L. l. mearnsi* is more genetically distinct from the mainland and other islands than was the historical population. Thus, the apparent genetic distinctiveness of *L. l. mearnsi* may reflect, to a certain extent, the effects of genetic drift during the extreme population bottleneck of the past century, as well as the effects of population management since 1990—a situation that may warrant very different management strategies than would be the case for a population with strong historical isolation.

Two questions arise regarding future conservation of shrikes on San Clemente Island: (1) whether continued investment in intensive management is still justified and (2) whether the management strategy for *L. l. mearnsi* should involve genetic rescue via shrikes from other populations. These 2 questions invoke both the logistical and philosophical complications surrounding conservation management. Our framework provides an objective template to help with these decisions. San Clemente Island shrikes would be recognized as "higher" conservation priority (one level below "highest"; Table 1) but not designated as an ESU (Table 1) based on currently available data (evidence of both genetic and phenotypic divergence). For this population to be designated formally as an ESU, further studies of adaptive differentiation would be needed to show that shrikes on San Clemente Island have evolved genetically based local adaptations and have diverged from the mainland population and other islands in the archipelago. The decision about whether to pursue genetic rescue also relies on understanding whether or not the source and receiving populations share genetically based adaptive variation. The introduction of alleles from another island via captive breeding or translocation could result in maladapted offspring if the source population was locally adapted to divergent environmental conditions. Studies of adaptive variation in Channel Island shrikes would provide these answers.

Island Fox

Consistent with the insular syndrome (Lomolino 2005), the island fox has evolved a much smaller body size compared to its mainland ancestor, the gray fox (*Urocyon cinereoargenteus*; Collins 1993). Island foxes are found on 6 of the 8 Channel Islands. Subspecies status was granted to foxes on each of those islands based on interisland differences in morphology and neutral genetic structure (Gilbert et al. 1990, Wayne et al. 1991, Collins 1993). However, we do not know whether the morphological differences observed between islands (Collins 1993) are a product of local adaptation (e.g., to different climate regimes or different community composition), genetic drift in small founder populations, or phenotypic plasticity.

In the early 2000s, these subspecific designations were central to management decisions after catastrophic population declines of foxes on 4 of the Channel Islands. Captive breeding programs were established for each of the affected subspecies on their respective islands, and each was listed as endangered under the ESA in 2004 (USFWS 2004). Additional intensive management actions included a vaccination program for canine distemper, the removal of Golden Eagles (*Aquila chrysaetos*) from the northern Channel Islands, and the reintroduction of Bald Eagles (*Haliaeetus leucocephalus*), which through agonistic interactions may deter *A. chrysaetos* (Morrison 2008). These management programs ultimately proved successful. Fox populations have rebounded on all 4 of the affected islands, although population monitoring and vaccination efforts continue (Coonan et al. 2010).

The island fox example provides the opportunity to evaluate whether, given the same data, the previous designations of island populations (based on Gilbert et al. 1990) and our framework reach the same conclusions regarding the conservation priority of island foxes. As with the San Clemente Island shrikes, our framework would not have identified each island fox population as an ESU due to lack of evidence of adaptive differentiation but would have classified the islands as "higher" priority, owing to evidence of genetic and phenotypic divergence. Resource managers followed the precautionary principle, given the limited data on local adaptation in the island fox populations. Going forward, however, limited resources for conservation management and new knowledge may call for a different approach.

The island fox is likely a "conservation-reliant" species (Scott et al. 2005) that will require continued monitoring and active management for long-term persistence (Coonan et al. 2010). All 6 *U. littoralis* populations have low levels of genetic variation (Wayne et al. 1991) and thus may lack the adaptive variation to survive future environmental changes (Allendorf and Luikart 2007). Although we currently have no evidence of inbreeding depression on any of the islands, managers have recognized that a future conservation option may include translocations between islands, with the goal of genetically rescuing fox populations (Coonan et al. 2010). If this is deemed a potentially necessary strategy, then knowledge of the degree of adaptive population divergence between islands will be critical for developing an effective translocation strategy and for understanding the potential risks of outbreeding depression.

CONCLUSIONS

The shrike and fox examples both involved intensive, costly management programs that were aimed at saving island-endemic populations. The population crashes were relatively sudden, particularly in the case of the island fox, and strategies were developed based on existing subspecies delineations and data on conservation threats. Our goal here is not to question the management actions of the past but to suggest that future management of these species might be enhanced by knowledge of the degree of adaptive population divergence between island populations. The recent anthropogenically driven population crashes have led to a decline in already low genetic diversity in both the shrike and fox (e.g., Frankham 1997). If future conservation management requires translocation in order to maintain population viability, managers would benefit from knowledge of the degree of local adaptation to the conditions on each island. Further, research on adaptive divergence could be important for prioritizing limited conservation funds. For instance, it may or may not be worth spending millions of dollars to save the genetic diversity contained within a remnant population of 20 individuals if those individuals are not genetically distinct and locally adapted compared to populations on neighboring islands. Questions like this are difficult to answer and ultimately require a consideration of factors ranging from relative priority of *neutral* genetic diversity versus *adaptive* genetic diversity to societal values.

Island populations and species are particularly vulnerable to local extirpation due to isolation, small population sizes, climate change, and the introduction of nonnative species. The framework we have presented here could aid in the identification and conservation of vulnerable insular taxa. Our framework may also be useful for delineating intraspecific conservation units for mainland taxa that inhabit "habitat islands" that are susceptible to the same genetic and demographic threats as true islands (Knowles 2001, Holycross and Douglas 2007, Bech et al. 2009). Ultimately, we believe that given limited conservation funding, knowledge of adaptive differentiation is essential for developing sound conservation strategies, particularly for geographically isolated populations.

ACKNOWLEDGMENTS

We thank E. Fisher, K. Hoke, and S. Fitzpatrick for insightful comments on previous versions of this manuscript. JMR and KML were supported by funding from The Nature Conservancy and the Smithsonian Institution during the writing of this manuscript.

LITERATURE CITED

AGUDO, R., C. RICO, F. HIRALDO, AND J.A. DONAZAR. 2011. Evidence of connectivity between continental and differentiated insular populations in a highly mobile species. Diversity and Distributions 17:1–12.

ALLENDORF, F.W., P.A. HOHENLOHE, AND G. LUIKART. 2010. Genomics and the future of conservation genetics. Nature Reviews Genetics 11:697–709.

ALLENDORF, F.W., AND G. LUIKART. 2007. Conservation and the genetics of populations. Blackwell Publishing, Oxford, United Kingdom.

ANDO, H., S. KANEKO, H. SUZUKI, K. HORIKOSHI, H. TAKANO, H. OGAWA, AND Y. ISAGI. 2011. Genetic diversity of the Japanese Wood Pigeon, *Columba janthina,* endemic to islands of East Asia, estimated by newly developed microsatellite markers. Zoological Science (Tokyo) 28:891–896.

BALAKRISHNAN, C.N., S.L. MONFORT, A. GAUR, L. SINGH, AND M.D. SORENSON. 2003. Phylogeography and conservation genetics of Eld's deer (*Cervus eldi*). Molecular Ecology 12:1–10.

BALLENTINE, B., AND R. GREENBERG. 2010. Common garden experiment reveals genetic control of phenotypic divergence between swamp sparrow subspecies that lack divergence in neutral genotypes. PLOS ONE 5(4): e10229.

BARTON, N.H. 1996. Natural selection and random genetic drift as causes of evolution on islands. Philosophical Transactions of the Royal Society of London Series B–Biological Sciences 351:785–794.

BECH, N., J. BOISSIER, S. DROVETSKI, AND C. NOVOA. 2009. Population genetic structure of Rock Ptarmigan in the 'sky islands' of French Pyrenees: implications for conservation. Animal Conservation 12: 138–146.

BIOLLAZ, F., N. BRUYNDONCKX, G. BEUNEUX, M. MUCEDDA, J. GOUDET, AND P. CHRISTE. 2010. Genetic isolation of insular populations of the Maghrebian bat, *Myotis punicus,* in the Mediterranean Basin. Journal of Biogeography 37:1557–1569.

BLONDEL, J. 2000. Evolution and ecology of birds on islands: trends and prospects. Vie Et Milieu–Life and Environment 50:205–220.

BOTTIN, L., J. TASSIN, R. NASI, AND J.-M. BOUVET. 2007. Molecular, quantitative and abiotic variables for the delineation of evolutionary significant units: case of sandalwood (*Santalum austrocaledonicum* Vieillard) in New Caledonia. Conservation Genetics 8:99–109.

BOWEN, L., AND D. VANVUREN. 1997. Insular endemic plants lack defenses against herbivores. Conservation Biology 11:1249–1254.

BUTAUD, J.-F., F. RIVES, D. VERHAEGEN, AND J.-M. BOUVET. 2005. Phylogeography of eastern Polynesian sandalwood (*Santalum insulare*), an endangered tree species from the Pacific: a study based on chloroplast microsatellites. Journal of Biogeography 32:1763–1774.

CABALLERO, I.C., AND M.V. ASHLEY. 2011. Genetic analysis of the endemic Island Loggerhead Shrike, *Lanius ludovicianus anthonyi.* Conservation Genetics:1485–1493.

[CDFG] CALIFORNIA DEPARTMENT OF FISH AND GAME. 2002. Status review of California coho salmon north of San Francisco: report to the California Fish and Game Commission. Candidate Species Status Review Report 2002-3. 231 pp.

CAUJAPE-CASTELLS, J., A. MARRERO-RODRIGUEZ, M. BACCARANI-ROSAS, N. CABRERA-GARCIA, AND B. VILCHES-NAVARRETE. 2008. Population genetics of the endangered Canarian endemic *Atractylis arbuscula* (Asteraceae): implications for taxonomy and conservation. Plant Systematics and Evolution 274:99–109.

CHAN, C.H., K.N. BALLANTYNE, H. AIKMAN, D. FASTIER, C.H. DAUGHERTY, AND G.K. CHAMBERS. 2006. Genetic analysis of interspecific hybridisation in the world's only Forbes' Parakeet (*Cyanoramphus forbesi*) natural population. Conservation Genetics 7:493–506.

CIOFI, C., M.A. BEAUMONT, I.R. SWINGLAND, AND M.W. BRUFORD. 1999. Genetic divergence and units for conservation in the Komodo dragon *Varanus komodoensis.* Proceedings of the Royal Society of London Series B–Biological Sciences 266:2269–2274.

COLLINS, P.W. 1993. Taxonomic and biogeographic relationships of the island fox (*Urocyon littoralis*) and gray fox (*U. cinereoargenteus*) from western North America. Pages 351–390 *in* F.G. Hochberg, editor, Third California Islands Symposium: recent advances in research on the California Islands. ISBN-13: 978-0936494050.

CONOVER, D.O., L.M. CLARKE, S.B. MUNCH, AND G.N. WAGNER. 2006. Spatial and temporal scales of adaptive divergence in marine fishes and the implications for conservation. Journal of Fish Biology 69:21–47.

COONAN, T.J., C.A. SCHWENN, AND D.K. GARCELON. 2010. Decline and recovery of the island fox: a case study for population recovery. Cambridge University Press, Cambridge, United Kingdom.

COYNE, J.A., AND H.A. ORR. 2004. Speciation. Sinauer Associates, Sunderland, MA.

CRANDALL, K.A., O.R.P. BININDA-EMONDS, G.M. MACE, AND R.K. WAYNE. 2000. Considering evolutionary processes in conservation biology. Trends in Ecology and Evolution 15:290–295.

CRUZ, F., V. CARRION, K.J. CAMPBELL, C. LAVOIE, AND C.J. DONLAN. 2009. Bio-economics of large-scale eradication of feral goats from Santiago Island, Galapagos. Journal of Wildlife Management 73:191–200.

[DOD] UNITED STATES DEPARTMENT OF DEFENSE. 2010. Threatened and endangered species on DoD lands. U.S. Department of Defense, Natural Resources Conservation Program, Washington, DC.

DE WIT, P., M.H. PESPENI, J.T. LADNER, D.J. BARSHIS, F. SENECA, H. JARIS, N.O. THERKILDSEN, M. MORIKAWA, AND S.R. PALUMBI. 2012. The simple fool's guide to population genomics via RNA-Seq: an introduction to high-throughput sequencing data analysis. Molecular Ecology Resources 12:1058–1067.

DUDANIEC, R.Y., B.E. SCHLOTFELDT, T. BERTOZZI, S.C. DONNELLAN, AND S. KLEINDORFER. 2011. Genetic and morphological divergence in island and mainland birds: informing conservation priorities. Biological Conservation 144:2902–2912.

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.

ELLIOT, T., AND B. POPPER. 1999. Predator management report for the protection of the San Clemente Loggerhead Shrike. Natural Resources Management Branch, United States Navy, Southwest Division Naval Facilities Engineering Command, editor. San Diego, CA.

FAY, J.J., AND M. NAMMACK. 1996. Policy regarding the recognition of distinct vertebrate population segments under the Endangered Species Act. Federal Register 61:4722–4725.

FLOYD, C.H., D.H. VAN VUREN, K.R. CROOKS, K.L. JONES, D.K. GARCELON, N.M. BELFIORE, J.W. DRAGOO, AND B. MAY. 2011. Genetic differentiation of island spotted skunks, *Spilogale gracilis amphiala.* Journal of Mammalogy 92:148–158.

FOUQUET, A., D.M. GREEN, B. WALDMAN, J.H. BOWSHER, K.P. MCBRIDE, AND N.J. GEMMELL. 2010. Phylogeography of *Leiopelma hochstetteri* reveals strong genetic structure and suggests new conservation priorities. Conservation Genetics 11:907–919.

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

FRANKHAM, R., J.D. BALLOU, M.D.B. ELDRIDGE, R.C. LACY, K. RALLS, M.R. DUDASH, AND C.B. FENSTER. 2011. Predicting the probability of outbreeding depression. Conservation Biology 25:465–475.

FRASER, D.J., AND L. BERNATCHEZ. 2001. Adaptive evolutionary conservation: towards a unified concept for defining conservation units. Molecular Ecology 10: 2741–2752.

FRIESEN, V.L., J.A. GONZALEZ, AND F. CRUZ-DELGADO. 2006. Population genetic structure and conservation of the Galapagos Petrel (*Pterodroma phaeopygia*). Conservation Genetics 7:105–115.

FUNK, S.M., AND J.E. FA. 2006. Phylogeography of the endemic St. Lucia whiptail lizard *Cnemidophorus vanzoi:* conservation genetics at the species boundary. Conservation Genetics 7:651–663.

FUNK, W.C., J.K. MCKAY, P.A. HOHENLOHE, AND F.W. ALLENDORF. 2012. Harnessing genomics for delineating conservation units. Trends in Ecology and Evolution 27:489–496.

GILBERT, D.A., N. LEHMAN, S.J. O'BRIEN, AND R.K. WAYNE. 1990. Genetic fingerprinting reflects population differentiation in the California Channel Island fox. Nature 344:764–767.

GOLDMAN, R.L., L.P. GOLDSTEIN, AND G.C. DAILY. 2008. Assessing the conservation value of a human-dominated island landscape: plant diversity in Hawaii. Biodiversity and Conservation 17:1765–1781.

GONZALEZ, J.A., C. MONTES, J. RODRIGUEZ, AND W. TAPIA. 2008. Rethinking the Galapagos Islands as a complex social-ecological system: implications for conservation and management. Ecology and Society 13. http://hdl.handle.net/10535/2456

GROOM, M.J., G.K. MEFFE, AND C.R. CARROLL, EDITORS. 2005. Principles of conservation biology. 3rd edition. Sinauer Associates, Sunderland, MA.

HERCZEG, G., AND K. VALIMAKI. 2011. Intraspecific variation in behaviour: effects of evolutionary history, ontogenetic experience and sex. Journal of Evolutionary Biology 24:2434–2444.

HILL, A., C. GREEN, AND E. PALACIOS. 2012. Genetic diversity and population structure of North America's rarest heron, the Reddish Egret (*Egretta rufescens*). Conservation Genetics 13:535–543.

HOGLUND, J., J.K. LARSSON, C. CORRALES, G. SANTAFE, D. BAINES, AND G. SEGELBACHER. 2011. Genetic structure among Black Grouse in Britain: implications for designing conservation units. Animal Conservation 14:400–408.

HOHENLOHE, P.A., P.C. PHILLIPS, AND W.A. CRESKO. 2010. Using population genomics to detect selection in natural populations: key concepts and methodological considerations. International Journal of Plant Sciences 171:1059–1071.

HOLYCROSS, A.T., AND M.E. DOUGLAS. 2007. Geographic isolation, genetic divergence, and ecological nonexchangeability define ESUs in a threatened sky-island rattlesnake. Biological Conservation 134: 142–154.

HUDSON, M.E. 2008. Sequencing breakthroughs for genomic ecology and evolutionary biology. Molecular Ecology Resources 8:3–17.

JOHNSON, J.A., R.T. WATSON, AND D.P. MINDE. 2005. Prioritizing species conservation: does the Cape Verde Kite exist? Proceedings of the Royal Society B–Biological Sciences 272:1365–1371.

JOHNSON, T.H., AND A.J. STATTERFSFIELD. 1990. A global review of island endemic birds. Ibis 132:167–180.

KANTHASWAMY, S., J.D. KURUSHIMA, AND D.G. SMITH. 2006. Inferring *Pongo* conservation units: a perspective based on microsatellite and mitochondrial DNA analyses. Primates 47:310–321.

KAWAKAMI, K., S. HARADA, T. SUZUKI, AND H. HIGUCHI. 2008. Genetic and morphological differences among populations of the Bonin Islands White-eye in Japan. Zoological Science (Tokyo) 25:882–887.

KAWECKI, T.J., AND D. EBERT. 2004. Conceptual issues in local adaptation. Ecology Letters 7:1225–1241.

KIER, G., H. KREFT, T.M. LEE, W. JETZ, P.L. IBISCH, C. NOWICKI, J. MUTKE, AND W. BARTHLOTT. 2009. A global assessment of endemism and species richness across island and mainland regions. Proceedings of the National Academy of Sciences of the United States of America 106:9322–9327.

KNOWLES, L.L. 2001. Did the Pleistocene glaciations promote divergence? Tests of explicit refugial models in montane grasshoppers. Molecular Ecology 10: 691–701.

KRETZMANN, M.B., N. CAPOTE, B. GAUTSCHI, J.A. GODOY, J.A. DONAZAR, AND J.J. NEGRO. 2003. Genetically distinct island populations of the Egyptian vulture (*Neophron percnopterus*). Conservation Genetics 4:697–706.

LANDE, R., AND S.J. ARNOLD. 1983. The measurement of selection on correlated characters. Evolution 37: 1210–1226.

LHUILLIER, E., J.-F. BUTAUD, AND J.-M. BOUVET. 2006. Extensive clonality and strong differentiation in the insular Pacific tree *Santalum insulare*: implications for its conservation. Annals of Botany (London) 98: 1061–1072.

LLOYD, B.D. 2003. Intraspecific phylogeny of the New Zealand short-tailed bat *Mystacina tuberculata* inferred from multiple mitochondrial gene sequences. Systematic Biology 52:460–476.

LOMOLINO, M.V. 2005. Body size evolution in insular vertebrates: generality of the island rule. Journal of Biogeography 32:1683–1699.

LOSOS, J.B., D.A. CREER, D. GLOSSIP, R. GOELLNER, A. HAMPTON, G. ROBERTS, N. HASKELL, P. TAYLOR, AND J. ETTLING. 2000. Evolutionary implications of phenotypic plasticity in the hindlimb of the lizard *Anolis sagrei.* Evolution 54:301–305.

LOVETTE, I.J., E. BERMINGHAM, AND R.E. RICKLEFS. 1999. Mitochondrial DNA phylogeography and the conservation of endangered Lesser Antillean *Icterus orioles.* Conservation Biology 13:1088–1096.

LUIKART, G., P.R. ENGLAND, D. TALLMON, S. JORDAN, AND P. TABERLET. 2003. The power and promise of population genomics: from genotyping to genome typing. Genetics 4:981–994.

LUMLEY, L.M., AND M. CUSSON. 2013. Linking adaptation, delimitation of evolutionarily significant units (ESUs), and gene function: a case study using hemlock looper ecotypes. Systematic Entomology 38:428–439.

MARTIN, J.-L. 1992. Niche expansion in an insular bird community: an autecological perspective. Journal of Biogeography 19:375–381.

MCFADDEN, K.W., M.E. GOMPPER, D.G. VALENZUELA, AND J.C. MORALES. 2008. Evolutionary history of the critically endangered Cozumel dwarf carnivores inferred from mitochondrial DNA analyses. Journal of Zoology 276:176–186.

MILLER, A.H. 1931. Systematic revision and natural history of the American shrikes (*Lanius*). University of California Publications in Zoology 38:11–242.

MITTELBACH, G.C., C.W. OSENBERG, AND P.C. WAINWRIGHT. 1999. Variation in feeding morphology between pumpkinseed populations: phenotypic plasticity or evolution? Evolutionary Ecology Research 1:111–128.

MORITZ, C. 1994. Defining evolutionarily significant units for conservation trends. Ecology and Evolution 9: 373–375.

______. 2002. Strategies to protect biological diversity and the evolutionary processes that sustain it. Systematic Biology 51:238–254.

MOROZOVA, O., AND M.A. MARRA. 2008. Applications of next-generation sequencing technologies in functional genomics. Genomics 92:255–264.

MORRISON, S.A. 2008. Reducing risk and enhancing efficiency in non-native vertebrate removal efforts on islands: a 25 year multi-taxa retrospective from Santa Cruz Island, California. *In:* USDA National Wildlife Research Center Symposia: managing vertebrate invasive species. University of Nebraska, Lincoln, NE.

MORRISON, S.A., T.S. SILLETT, C.K. GHALAMBOR, J.W. FITZPATRICK, D.M. GRABER, V.J. BAKKER, R. BOWMAN, C.T. COLLINS, P.W. COLLINS, K.S. DELANEY, ET AL. 2011. Proactive conservation management of an island-endemic bird species in the face of global change. BioScience 61:1013–1021.

MUNDY, N.I., C.S. WINCHELL, AND D.S. WOODRUFF. 1997. Genetic differences between the endangered San Clemente Island Loggerhead Shrike *Lanius ludovicianus mearnsi* and two neighbouring subspecies demonstrated by mtDNA control region and cytochrome *b* sequence variation. Molecular Ecology 6:29–37.

NEIGEL, J., AND J.C. AVISE. 1986. Phylogenetic relationships of mitochondrial DNA under various demographic models of speciation. *In:* E. Nevo and S. Karlin, editors, Evolutionary processes and theory. Academic Press, New York, NY.

NOSIL, P., AND J.L. FEDER. 2012. Genomic divergence during speciation: causes and consequences. Introduction. Philosophical Transactions of the Royal Society B–Biological Sciences 367:332–342.

O'CORRY-CROWE, G., B.L. TAYLOR, T. GELATT, T.R. LOUGHLIN, J. BICKHAM, M. BASTERRETCHE, K.W. PITCHER, AND D.P. DEMASTER. 2006. Demographic independence along ecosystem boundaries in Steller sea lions revealed by mtDNA analysis: implications for management of an endangered species. Canadian Journal of Zoology–Revue Canadienne De Zoologie 84:1796–1809.

OHARA, K., M. TAKAGI, M. HASHIMOTO, K. MIYAZAKI, AND K. HIRASHIMA. 2008. DNA markers indicate low genetic diversity and high genetic divergence in the landlocked freshwater goby, *Rhinogobius* sp YB, in the Ryukyu Archipelago, Japan. Zoological Science (Tokyo) 25:391–400.

OLIVA-TEJERA, F., J. CAUJAPE-CASTELLS, J. NAVARRO-DENIZ, A. REYES-BETANCORT, S. SCHOLZ, M. BACCARANI-ROSAS, AND N. CABRERA-GARCIA. 2006. Patterns of genetic divergence of three Canarian endemic *Lotus* (Fabaceae): implications for the conservation of the endangered *L. kunkelii.* American Journal of Botany 93:1116–1124.

PAGE, T.J., J.C. MARSHALL, AND J.M. HUGHES. 2012. The world in a grain of sand: evolutionarily relevant, small-scale freshwater bioregions on subtropical dune islands. Freshwater Biology 57:612–627.

PATIRANA, A., S.A. HATCH, AND V.L. FRIESEN. 2002. Population differentiation in the Red-legged Kittiwake (*Rissa brevirostris*) as revealed by mitochondrial DNA. Conservation Genetics 3:335–340.

POSTMA, E., AND A.J. VAN NOORDWIJK. 2005. Gene flow maintains a large genetic difference in clutch size at a small spatial scale. Nature 433:65–68.

PELUC, S.I., T.S. SILLETT, J.T. ROTENBERRY, AND C.K. GHALAMBOR. 2008. Adaptive phenotypic plasticity in an island songbird exposed to a novel predation risk. Behavioral Ecology 19:830–835.

PULLIN, A.S., AND G.B. STEWART. 2006. Guidelines for systematic review in conservation and environmental management. Conservation Biology 20:1647–1656.

RADER, R.B., M.C. BELK, D.K. SHIOZAWA, AND K.A. CRANDALL. 2005. Empirical tests for ecological exchangeability. Animal Conservation 8:239–247.

REYNOLDS, R.G., G.P. GERBER, AND B.M. FITZPATRICK. 2011. Unexpected shallow genetic divergence in turks island boas (*Epicrates c. chrysogaster*) reveals single evolutionarily significant unit for conservation. Herpetologica 67:477–486.

RIDGEWAY, R. 1903. Descriptions of new genera, species and subspecies of American birds. Proceedings of the Biological Society of Washington 16:105–111.

ROBINSON-WOLRATH, S.I., AND I.P.F. OWENS. 2003. Large size in an island-dwelling bird: intraspecific competition and the dominance hypothesis. Journal of Evolutionary Biology 16:1106–1114.

ROEMER, G.W., AND R.K. WAYNE. 2003. Conservation in conflict: the tale of two endangered species. Conservation Biology 17:1251–1260.

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

SATO, J.J., S.P. YASUDA, AND T. HOSODA. 2009. Genetic diversity of the Japanese marten (*Martes melampus*) and its implications for the conservation unit. Zoological Science 26:457–466.

SCOTT, J.M., D.D. GOBLE, J.A. WIENS, D.S. WILCOVE, M. BEAN, AND T. MALE. 2005. Recovery of imperiled species under the Endangered Species Act: the need for a new approach. Frontiers in Ecology and the Environment 3:383–389.

SHAFER, A.B.A., K.S. WHITE, S.D. COTE, AND D.W. COLTMAN. 2011. Deciphering translocations from relicts in Baranof Island mountain goats: is an endemic genetic lineage at risk? Conservation Genetics 12: 1261–1268.

SHAFFER, M.L. 1981. Minimum population sizes for species conservation. BioScience 31:131–134.

SHIMIZU, T. 2008. Geographic differentiation of *Cobitis shikokuensis* inferred from mtDNA RFLP analysis. Ichthyological Research 55:101–111.

SLIKAS, B., S.L. OLSON, AND R.C. FLEISCHER. 2002. Rapid, independent evolution of flightlessness in four species of Pacific Island rails (Rallidae): an analysis based on mitochondrial sequence data. Journal of Avian Biology 33:5–14.

SMITH, W., I.A.W. SCOTT, AND J.S. KEOGH. 2007. Molecular phylogeography of Rosenberg's goanna (Reptilia:

Varanidae: *Varanus rosenbergi*) and its conservation status in New South Wales. Systematics and Biodiversity 5:361–369.

STAPLEY, J., J. REGER, P.G.D. FEULNER, C. SMADJA, J. GALINDO, R. EKBLOM, C. BENNISON, A.D. BALL, A.P. BECKERMAN, AND J. SLATE. 2010. Adaptation genomics: the next generation. Trends in Ecology and Evolution 25:705–712.

SVANBACK, R., AND P. EKLOV. 2011. Catch me if you can: predation affects divergence in a polyphenic species. Evolution 65:3515–3526.

TAKADA, M., AND K. TACHIHARA. 2009. Comparisons of age, growth, and maturity between male and female, and diploid and triploid individuals in *Carassius auratus* from Okinawa-jima Island, Japan. Aquatic Conservation: Marine and Freshwater Ecosystems 19:806–814.

TARR, C.L., AND R.C. FLEISCHER. 1999. Population boundaries and genetic diversity in the endangered Mariana crow (*Corvus kubaryi*). Molecular Ecology 8:941–949.

TAYLOR, M.L., N. BUNBURY, L. CHONG-SENG, N. DOAK, S. KUNDU, R.A. GRIFFITHS, AND J.J. GROOMBRIDGE. 2012. Evidence for evolutionary distinctiveness of a newly discovered population of sooglossid frogs on Praslin Island, Seychelles. Conservation Genetics 13:557–566.

TOPP, C.M., AND K. WINKER. 2008. Genetic patterns of differentiation among five landbird species from the Queen Charlotte Islands, British Columbia. Auk 125:461–472.

[USFWS] UNITED STATES FISH AND WILDLIFE SERVICE. 1977. Determination that seven California Channel Island animals and plants are either endangered species or threatened.

______. 2004. Endangered and Threatened wildlife and plants; listing the San Miguel Island fox, Santa Rosa Island fox, Santa Cruz Island fox, and Santa Catalina Island fox as Endangered.

______. 2009. San Clemente Loggerhead Shrike *Lanius ludovicianus mearnsi.* 5-Year review: summary and evaluation. Carlsbad Fish and Wildlife Office, Carlsbad, CA.

WALKER, M.L., S.E. CHIRHART, A.F. MOORE, R.L. HONEYCUTT, AND I.F. GREENBAUM. 2006. Genealogical concordance and the specific status of *Peromyscus sejugis.* Journal of Heredity 97:340–345.

WAPLES, R.S. 1991. Pacific salmon, *Oncorhynchus* spp., and the definition of "Species" under the Endangered Species Act. Marine Fisheries Review 53.

______. 1995. Evolutionarily significant units and the conservation of biological diversity under the Endangered Species Act. Pages 8–27 *in* J.L. Nielson, editor, Evolution and the aquatic ecosystem: defining units in population conservation. American Fisheries Society.

______. 1998. Evolutionarily significant units, distinct population segments and the Endangered Species Act: reply to Pennock and Dimmick. Conservation Biology 12:718–721.

WAYNE, R.K., S.B. GEORGE, D. GILBERT, P.W. COLLINS, S.D. KOVACH, D. GIRMAN, AND N. LEHMAN. 1991. A morphological and genetic-study of the island fox, *Urocyon littoralis.* Evolution 45:1849–1868.

WEST-EBERHARD, M.J. 1983. Sexual selection, social competition, and speciation. Quarterly Review of Biology 58:155–183.

WHITTAKER, R.J., AND FERNANDEZ-PALACIOS. 2008. Island biogeography: ecology, evolution, and conservation. 2nd edition. Oxford University Press, Oxford, United Kingdom.

WOOD, B. 2000. Room for nature? Conservation management of the Isle of Rum, UK and prospects for large protected areas in Europe. Biological Conservation 94:93–105.

WOOLFIT, M., AND L. BROMHAM. 2005. Population size and molecular evolution on islands. Proceedings of the Royal Society B–Biological Sciences 272: 2277–2282.

WU, Y.C., H. LI, F.S. ZOU, AND Y.C. HSU. 2011. Lineages differentiation and population structure of the Light-vented Bulbul *Pycnonotus sinensis* in China based on mitochondrial DNA and microsatellite analysis. Integrative Zoology 6:387–398.

ZINK, R.M. 2004. The role of subspecies in obscuring avian biological diversity and misleading conservation policy. Proceedings of the Royal Society of London Series B–Biological Sciences 271:561–564.

______. 2007. Ecological exchangeability versus neutral molecular markers: the case of the Great Tit. Animal Conservation 10:369–373.

Received 26 April 2013
Accepted 28 February 2014

Appendix on page 410.

APPENDIX. A Web of Knowledge literature search shows that empirical studies of island populations use variable criteria to designate a population as an evolutionarily significant unit. For each study, we include (1) the conservation unit (UNIT) recommended by the authors for the island, with respect to mainland or nearby island: evolutionary significant unit (ESU), management unit (MU), distinct population segment (DPS), conservation unit (CU), or no conservation status (NONE); (2) evidence of genetic divergence at mtDNA/chloroplast DNA (mtDNA) provided as reciprocal monophyly (MONO), haplotypic differentiation (HAPL) and/or microsatellite divergence (MSAT); (3) phenotypic divergence (phenotype) and/or measures of phenotypic divergence that included social signals or other traits related to fitness (Fitness); and (4) whether the studies included a test for adaptive variation (Adapt) among islands, or between island and mainland populations. See literature cited for full citation. Additional codes: Yes (Y), No (N), shallow (S), not done (ND), or ND but inferred (NDi).

Island/island archipelago	Taxon	UNIT	mtDNA	MSAT	Phenotype	Fitness	Adapt	Reference
Turk and Caicos Islands	Turks Island boa (*Epicrates c. chrysogaster*)	ESU	S	S	ND	ND	ND	Reynolds et al. 2011
Polynesia	Sandalwood (*Santalum insulare*)	ESU	ND	Y	ND	ND	ND	Butaud et al. 2005
Komodo Island	Komodo dragon (*Varanus komodoensis*)	MU/ESU	ND	Y	ND	ND	ND	Ciofi et al. 1999
California Channel Islands	Spotted skunk (*Spilogale gracilis amphiala*)	ESU	ND	Y	N	ND	ND	Floyd et al. 2011
Lesser Antilles	Lesser Antillean Oriole (*Icterus* spp.)	ESU	MONO	ND	Y	Y	ND	Lovette et al. 1999
Cozumel	Pygmy raccoon (*Procyon pygmaeus*), dwarf coati (*Nasua nelsoni*)	MU	S	ND	Y	ND	ND	McFadden et al. 2008
Hainan Island	Eld's deer subspecies (*Cervis eldi*)	ESU	Y	ND	Y	ND	ND	Balakrishnan et al. 2003
New Caledonia	Sandalwood (*Santalum austrocaledonicum*)	CU	Y	Y	Y	Y	Y	Bottin et al. 2007
Kangaroo Island and Australia	Superb Fairywren subspecies (*Malurus cyaneus*)	ESU	ND	Y	Y	Y	ND	Dudaniec et al. 2011
Australia	Multiple freshwater fish and crustacean species[a]	MU	N	ND	ND	ND	ND	Page et al. 2012
Corsica and Sardinia	Maghrebian bat (*Myotis punicus*)	ESU	Y	Y	ND	ND	ND	Biollaz et al. 2010
Islands of East Asia	Japanese Wood Pigeon (*Columba janthina*)	CU	ND	Y	ND	ND	ND	Ando et al. 2011
Gran Canaria	Canarian Asteraceae shrub (*Atractylis arbuscula*)	ESU	HAPL	ND	Y	Y	ND	Caujape-Castells et al. 2008
Chatham Island and Mangere Island	Forbes' Parakeet (*Cyanoramphus forbesi*)	ESU	HAPL	Y	Y	Y	ND	Chan et al. 2006
Islands of New Zealand	*Leiopelma* frogs	ESU	MONO	Y	ND	ND	ND	Fouquet et al. 2010
Galápagos Islands	Galápagos Petrel (*Pterodroma phaeopygia*)	ESU	HAPL	Y	Y	Y	NDi	Friesen et al. 2006
San Lucia island	San Lucia whiptail lizard (*Cnemidophorus vanzoi*)	ESU	HAPL	Y	Y	N	ND	Funk and Fa 2006
Great Inagua	Reddish Egret (*Egretta rufescens*)	ESU	ND	Y	Y	Y	ND	Hill et al. 2012
Cape Verde Islands	Cape Verde Kite (*Milvus milvus fasciicauda*)	NONE	N	ND	Y	ND	ND	Johnson et al. 2005
Bonin Islands	Bonin White-eye (*Apalopteron familiare*)	ESU	HAPL	ND	Y	ND	ND	Kawakami et al. 2008

APPENDIX. Continued.

Island/island archipelago	Taxon	UNIT	mtDNA	MSAT	Phenotype	Fitness	Adapt	Reference
Borneo and Sumatra	Orangutan (*Pongo pygmaeus* ssp.)	MU	HAPL	Y	Y	ND	ND	Kanthaswamy et al. 2006
Eastern Polynesia	Sandalwood (*Santalum insulare*)	MU	HAPL	Y	ND	ND	ND	Lhuillier et al. 2006
New Zealand	Short-tailed bat (*Mystacina tuberculata*)	Y	HAPL	ND	N	N	ND	Lloyd 2003
Alaska and Aleutian Islands	Steller sea lion (*Eumetopias jubatus*)	DPS	HAPL	ND	ND	ND	ND	O'Corry-Crowe et al. 2006
Ryukyu Archipelago	Goby (*Rhinogobius* sp.)	ESU	HAPL	Y	ND	ND	ND	Ohara et al. 2008
Bering Sea Islands	Red-legged Kittiwake (*Rissa brevirostris*)	ESU	HAPL	ND	ND	ND	ND	Patirana et al. 2002
Mediterranean Sea	Egyptian Vulture (*Neophron percnopterus*)	NO	MONO	Y	Y	ND	ND	Agudo et al. 2011
Mediterranean Sea	Egyptian Vulture (*Neophron percnopterus*)	MU	MONO	Y	Y	ND	ND	Kretzmann et al. 2003
Baranof Island	Mountain goat (*Oreamnos americanus*)	ESU	S	Y	ND	ND	ND	Shafer et al. 2011
Shikoku Island	Japanese spinous loach (*Cobitis shikokuensis*)	ESU	HAPL	ND	Y	Y	ND	Shimizu 2008
Kangaroo Island	Rosenbergs goanna (*Varanus rosenbergi*)	ESU	MONO	ND	Y	ND	ND	Smith et al. 2007
Ryukyu Archipelago	Carassius goldfish (*Carassius auratus*)	ESU	MONO	ND	Y	Y	ND	Takada and Tachihara 2009
Guam and Rota	Mariana Crow (*Corvus kubaryi*)	ESU	MONO	Y	ND	ND	ND	Tarr and Fleischer 1999
Seychelles	Sooglassid frog (*Sooglossus* sp.)	ESU	MONO	ND	Y	ND	ND	Taylor et al. 2012
Queen Charlotte Islands	5 avian endemics[a]	ESU	MONO	ND	Y	Y	ND	Topp and Winker 2008
Sea of Cortés	Endemic mouse (*Peromyscus* spp.)	ESU	MONO	Y	Y	Y	ND	Walker et al. 2006
Hainan, Taiwan, and Ryukyu islands	Light-vented Bulbul (*Pycnonotus sinensis*)	ESU	HAPL	Y	Y	Y	ND	Wu et al. 2011
Japan	Japanese marten (*Martes melampus*)	ESU	HAPL	ND	ND	ND	ND	Sato et al. 2009

[a] See reference for publications that include more than 2 taxa.