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Auklets on Triangle Island have a relatively constant annual adult survival rate of ~86

To characterize the genetic profile of each sampled population, individuals were genotyped at eight microsatellite loci (Table 1, Hasegawa et al. 2005). All loci were amplified using a 10 μ L single-reaction nested polymerase chain reaction (PCR). Forward primers had a M13 sequence added to the 5' end to allow incorporation of a fluorescently labeled M13(–21) primer (see Schuelke 2000). Reverse primers

may be present in the eastern Pacific with birds on Triangle Is forming a third genetically distinct group (PCA and F_{ST}) and possibly a fourth group on Chowiet Is (PCA). Range-wide patterns are consistent with those found in other marine taxa showing an east–west split in the North Pacific (Cronin et al. 1996; Stanley et al. 1996; Congdon et al. 2000; Holder et al. 2000; Canino et al. 2010; Liu et al. 2011). Most of these species are dependent on land for at least one stage of their life history, while a few rely on shallow waters adjacent to coastlines. The eastern and western lineages of marine taxa are proposed to have originated during the Pleistocene and are maintained to different extents by restricted gene flow. For example, Pacific herring (*Clupea pallasii*) contained two evolutionary lineages that subsequently mixed in the eastern Pacific, yet have remained isolated from a third lineage in the western Pacific (Liu et al. 2011). During the last glacial maximum, the rhinoceros auklets were likely further south or had a reduced range due to the presence of ice throughout much of the North Pacific, with the exception of Beringia, restricting breeding habitat and altering prey distributions. A southwards range shift during the Pleistocene would have isolated the breeding populations into eastern and western Pacific refugia allowing divergence to occur. We cannot rule out the possibility that the east–west split predates the last glacial maximum (LGM) and was maintained during the LGM. To test the hypothesis of an early Pleistocene split, the divergence time needs to be estimated using sequence data.

The observed population genetic structure in rhinoceros auklets likely reflects historical factors and not just contemporary conditions. This scenario is considered likely for species whose current geographic distribution is the result of post-Pleistocene range expansion (Cronin et al. 1996; Stanley et al. 1996; Congdon et al. 2000; Holder et al. 2000; Friesen et al. 2007; Canino et al. 2010; Liu et al. 2011). The current distribution of rhinoceros auklets (BirdLife International 2013) is not continuous. During the nonbreeding season, birds are found along the coastlines of the eastern (California to British Columbia) and western (Japan) Pacific (Fig. 1; BirdLife International 2013), possibly as a result of historical isolation. While the breeding distribution is more fragmented with four clusters of breeding sites (western Sea of Okhotsk, western Aleutian Islands, Gulf of Alaska, and British Columbia/southeast Alaska), population genetic patterns observed here correspond to the auklet's nonbreeding distribution. This is consistent with findings that levels of population genetic structure for seabirds are best explained by their nonbreeding distribution (Burg and Croxall 2001; Friesen et al. 2007).

Contemporary processes and their effects on population differentiation are evident by looking at the time required for newly isolated populations to arrive at

mutation-migration-drift equilibrium and to diverge sufficiently as to lose the genetic imprint of their past association. Indeed, populations of common murre (*Uria aalge*), an alcid whose broad geographic distribution includes the North Pacific, are considered not to be in genetic equilibrium (Morris-Pocock et al. 2008). We found deviations from Hardy–Weinberg proportions in rhinoceros auklets that were not found when the same markers were applied to birds of this species breeding in Japan (Hasegawa et al. 2005) and thus may be modest evidence that these populations are out of mutation-migration-drift equilibrium.

Isolation by distance is an appealing hypothesis for rhinoceros auklets as it is consistent with the stepping-stone model of colonization (Kimura and Weiss 1964), whereby proximate populations are genetically more similar than those located more distantly. It is generally considered the most likely scenario for seabirds and has particular intuitive appeal for coastal species like rhinoceros auklets whose breeding colonies are linearly distributed along the coastline. Range-wide we had weak support for isolation by distance ($R^2 = 0.065$); however, once the western Pacific population was excluded, this pattern disappeared. The small number of sampled populations is likely precluding a valid statistical assessment of isolation by distance in rhinoceros auklets as it offers only a few pairwise population comparisons, and sampling sites were not evenly distributed along the coastline. If the populations are relatively young, genetic

all other populations, including nearby Pine Is (~100 km away). Reductions in gene flow over short geographic distances have been reported for other seabirds (Abbott and Double 2003; Levin and Parker 2012; Welch et al. 2012). Microsatellite analyses of Nazca boobies (*Sula granti*), a seabird restricted to the eastern tropical Pacific, showed that genetic isolation in this species does not correspond to geographic distances (Levin and Parker 2012). Individuals breeding on Espanola show significant allele frequency differences from birds breeding on San Cristobal (~35 km away), but are not significantly different from individuals on Genovesa (~150 km away). Seabirds are generally known for their strong natal philopatry (Friesen et al. 2007), which could promote genetic differentiation among different breeding sites if gene flow were sufficiently limited. For rhinoceros auklets, data from banding hundreds of adult individuals in British Columbia (Hifner unpublished) showed no evidence of dispersal to other sites. However, limited data are available for nestlings and as such dispersal could be occurring prior to recruitment. More information is needed on both post-breeding dispersal and juvenile movement as both would be expected to promote gene flow. As mentioned earlier, at-sea distribution in seabirds is an important factor, and in a number of instances, populations with different nonbreeding distributions are genetically isolated from each other (Burg and Croxall 2001; Friesen et al. 2007; Rayner et al. 2011; Taylor et al. 2011).

different breeding colonies is not known, genotyping samples collected during the winter will help gather this critical information. In addition, as genetic homogeneity of populations at a relatively small spatial scale of this study was rejected, it is reasonable to hypothesize that higher levels of population structure exist across their full geographic range, which spans from California to Japan (Gaston and Dechesne 1996a). More comprehensive sampling in both the eastern and western Pacific is needed to determine whether genetic patterns are the same in the east and west and will better elucidate the extent of population differentiation in rhinoceros auklets at micro-geographic scales. This would be worth investigating to determine whether there are distinct units for conservation purposes on a range-wide scale and, if so, to facilitate the development of genetic tools for determining provenance of fisheries bycatch birds to aid impact assessments and monitoring efforts.

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The conservation implications of the results presented here are somewhat equivocal. Management units as defined by Moritz 1994) are “populations with significant divergence of allele frequencies.” While Pine Is and Lucy Is clearly do not represent management units, Triangle Is is sufficiently divergent from both of them, and the other eastern Pacific breeding sites have to be considered a separate management unit. Furthermore, as PCA shows Chowiet Is in Alaska is separated from the other islands, it may merit separate conservation priority. While structure only detected two clusters, Pritchard et al. (2000) note the program may underestimate the number of clusters when structure is weak. Caution is warranted as the four units represent the minimum number of distinct genetic groups based on our sampling and additional samples from western Alaska in particular, and inclusion of other markers may reveal further population genetic differences in the North Pacific. A more in-depth study with more comprehensive sampling of rhinoceros auklet populations including birds from wintering areas and information on at-sea distributions will aid in the interpretation of our results adding an important temporal component. As the nonbreeding distribution of

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