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NEWS AND COMMENTARY

Restricted dispersal of seabirds at small geographic scales

No island hopping for Hawaiian petrels

TM Burg and AB Martin

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Understanding the mechanisms of population differentiation is critical to studying evolutionary ecology, speciation and population connectivity. Gene flow via dispersal ultimately determines the levels and patterns of population differentiation for any species. Seabirds present an enigma with respect to dispersal potential and realized gene flow. They are capable of traveling tens of thousands of kilometers either on single foraging trips or during the non-breeding season, yet they are highly philopatric often returning not only to their natal island, but to their natal colony to breed. Their longevity (some live >50 years) and delayed sexual reproduction make using traditional mark-recapture methods to study dispersal more challenging. Molecular markers allow researchers to study multigenerational movements by measuring gene flow. Most of the population genetic studies on seabirds have found evidence of gene flow among breeding sites at small geographic scales (Friesen *et al.*, 2007a). In order for populations to become, and remain, genetically homogenous, only a few individuals per generation need to be exchanged between breeding sites. Some seabirds do show evidence of restricted gene flow, however, these are often geographically clustered (for example, New Zealand seabirds), species with restricted dispersal (for example, flightless cormorant) or species with temporally segregated breeding (for example, band-rumped storm petrel) (Friesen *et al.*, 2007a and references therein; Duffie *et al.*, 2009; Friesen *et al.*, 2007b).

A recent study by Welch *et al.* (2012) provides valuable insights into patterns of gene flow in the endangered Hawaiian petrel (*Pterodroma sandwichensis*), an endemic species found in one of the world's biodiversity hotspots. The authors investigated population genetic structure using samples from one extirpated and four extant colonies on separate islands. Two of the three molecular markers contained significant genetic differences among all four of the modern breeding sites in the Hawaiian archipelago. Interestingly, the extirpated population on Molokai was not genetically different from the contemporary population on the adjacent island of Lanai. In contrast to other studies examining population structure in highly mobile seabirds, these authors have found evidence for restricted gene flow (0.01–8 migrants per generation) among the four extant Hawaiian petrel breeding sites, some separated by <100 km.

Island archipelagos, particularly Hawaii and the Galapagos, are well known for their high levels of endemism and isolated populations; however, most studies on those islands focus on organisms with restricted dispersal potential (for example, happy-face spiders, Gillespie and Oxford, 1998). So what is restricting gene flow in a species like the Hawaiian petrel capable of traveling 10 000 km from moving to a breeding site 75–500 km away? Barriers to gene flow in seabirds include land masses, even as small as the Isthmus of Panama, and colony-specific foraging areas. No obvious physical barriers for seabirds exist between any of the Hawaiian Islands raising the possibility of behavioural (for example, foraging distribution at-sea) or other non-physical dispersal barriers. Alternatively, the patterns of genetic differentiation may be the result of genetic drift caused by population bottlenecks or founder effects. Population estimates for Hawaiian petrels are difficult to obtain because of their nocturnal behavior, remote nesting burrows and difficult terrain. Many of the nesting areas remain undiscovered and although current population estimates are in the 'many thousands' (Carlile *et al.*, 2003), this does not rule out historical bottlenecks. Little is known about historical population size, as the first breeding sites were not reported until 1953.

Hawaiian petrels forage over a large area from the Aleutian Islands off Alaska to the equatorial Pacific. It appears that birds from two of the colonies studied by Welch *et al.* (2012) forage in different areas and the authors discuss this in their paper. Differences in nitrogen signatures suggest the Hawaii birds forage further south during their molt than the Kauai birds, and both forage in different areas during chick-rearing (Wiley *et al.*, 2012). Many seabirds have a well-developed sense of smell, which aids in foraging, navigation and homing. Nevitt (2008) proposed seabird chicks are able to learn odors from food brought back to them by their parents and use this information later in life for homing, mate choice and foraging, thereby potentially enforcing differences that may exist among colonies due to foraging behaviour.

In addition to possible differences in foraging behavior, variation in morphology, vocalizations and breeding phenology exist among each of the four contemporary breeding sites (Judge, 2011); all of these are potential reproductive isolation mechanisms. It is possible that these differences arose as the result of local adaptation and now act as isolating mechanisms creating the genetic patterns seen by Welch *et al.* (2012), or genetic drift created the observed morphological and behavioral differences and they are maintained by reduced gene flow. Vocal and morphological cues are important during courtship and mating in some seabirds. Each of the extant Hawaiian petrel colonies has a unique vocal repertoire, and this may act to discourage mixing. In addition, birds from Maui are larger and breed 26–30 days

Dr TM Burg and AB Martin are at the Department of Biology, University of Lethbridge, 4401 University Drive, Lethbridge, Alberta, Canada T1K 3M4.
E-mail: theresa.burg@uleth.ca

earlier. The size differences may be attributed to differential food allocation during chick rearing or access to food as adults. The behavioral and morphological differences, combined with an earlier breeding time at one of the colonies (as seen in other species, Friesen *et al*., 2007b), may help to explain some of the reductions in gene flow detected by Welch *et al*. (2012), but further studies are required to test these hypotheses.

Another interesting finding by Welch *et al*. (2012) concerns the extirpated colony on Molokai. Despite the genetic and phenotypic differences in extant populations, the extirpated Molokai population was not genetically distinct from the extant population on the adjacent island of Lanai ~15 km away. Welch *et al*. (2012) raise the possibility of historical movement by survivors from Molokai to Lanai. Populations on both of these islands were declining because of the introduced animals and habitat degradation. Following the removal of introduced goats and habitat restoration on Lanai, a large colony of Hawaiian petrels was discovered. Although the absence of genetic differences between these two colonies does not mean they exchanged genes, it does raise the possibility of historical connections.

The movement of individuals to a new or existing population is not unprecedented in seabirds. The black-browed albatross (*Thalassarche melanophris*) recently colonized Campbell Island where the closely related, endemic Campbell albatross (*T. impavida*) is found (Moore *et al*., 1997). These two species now interbreed off the coast of New Zealand despite a number of morphological differences. Another example of dispersal and divergence is the shy albatross, which is thought to have arisen through a dispersal of white-capped albatross ancestor to Tasmania (Abbott and Double, 2003). What is needed in the case of the Hawaiian petrel to conclusively determine whether birds from Molokai moved to Lanai or merged with a remnant population are historical samples from Lanai. By comparing the two sets of historical samples with the extant Lanai birds, one would be able to determine whether the modern Lanai birds are transplants from Molokai or a historical merger. If it was a merger of two genetically distinct populations, it raises a series of questions including: what is keeping extant Hawaiian petrel colonies genetically isolated, what caused the merger: was it a change in ocean conditions and why did the two colonies merge?

Welch *et al*.'s (2012) study opens the door to future studies on seabirds examining at-sea distribution, formation of new colonies, foraging behavior and the role of vocalization in speciation. What prezygotic isolating mechanisms (for example, spatial segregation or temporal differences in breeding phenology) are restricting dispersal and ultimately gene flow?

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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