Evidence for cryptic northern refugia among high- and temperate-latitude species in Beringia

A response to Stewart and Dalén (2008)

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Abstract Stewart and Dalén (2008) argue that only temperate species were locked in cryptic northern refugia during Pleistocene glacial cycles, while species presently found at high latitudes had much wider distributions during glaciations. We present evidence supporting the existence of cryptic northern refugia that likely harbored both high- and temperate-latitude species in the Bering Sea region. Genetic signals of refugial isolation are found in island populations of rock ptarmigan (*Lagopus muta*), rock sandpiper (*Calidris ptilocnemis*), common raven (*Corvus corax*), and winter wren (*Troglodytes troglodytes*). These species have high-latitude, a mixture of high- and temperate-latitude, and temperate-latitude distributions. In addition, there are no data showing historically larger distributions of the high-latitude rock sandpiper or rock ptarmigan in North America during the Pleistocene. Although exact dating of isolation events is not possible using molecular genetic data, the species we examined have similar genetic signals and thus were isolated at similar times. It is evident that Pleistocene glaciations produced refugial genetic signatures among multiple bird species in the North Pacific Ocean.

Stewart and Dalén (2008) propose that species that are currently distributed at high latitudes such as the rock sandpiper (*Calidris ptilocnemis*) were not isolated in cryptic glacial refugia during the late Pleistocene. They offer instead an interesting semantic argument that counters the idea of high-latitude refugia, where species were isolated in ice-free areas during glacial maxima, with an opposing idea of isolation during warmer periods. They suggest that cold-tolerant species are currently locked in refugia. Because refugia are islands of suitable habitat within a landscape of unsuitable habitat, different fauna and flora will experience variable isolation events as species-specific habitats shift across the

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landscape with climatic change. In this respect, Stewart and Dalén (2008) are correct to draw attention to ways in which high-latitude species might differ from temperate-latitude species in their responses to climatic change. We will show, however, that temperate- and high-latitude landbird species on Bering Sea islands share similar cryptic glacial refugium histories. This suggests that the simple dichotomous treatment of northern versus temperate species that Stewart and Dalén (2008) propose is inaccurate.

Stewart and Dalén's (2008) hypothesis rests on the assumption that high- and temperate-latitude organisms were not isolated in the same areas and by the same factors (glacial ice, changes in sea levels) during glacial cycles. If this were the case, then high- and temperate-latitude species might show two different patterns of isolation in genetic data. We (Pruett and Winker 2005) found that rock sandpipers in the Bering Sea region had genetic signals of refugia (isolation) for several locations, including the Commander Islands, Pribilof Islands/St. Matthew Island, and two locations in the Aleutian Islands (Attu and Adak islands). Here we present genetic evidence using the same molecular marker, the mito-chondrial (mt)DNA cytochrome *b* gene, from other species that are co-distributed with rock sandpipers in the Bering Sea and show genetic patterns of isolation in some of the same locations as rock sandpipers (Fig. 1; see Pruett 2002 and Pruett and Winker 2005 for data collection methods). These species include the high-latitude rock ptarmigan (*Lagopus muta*), the high- and temperate-latitude common raven (*Corvus corax*), and the primarily temperate-latitude winter wren (*Troglodytes troglodytes*). Network diagrams based on cytochrome *b* haplotypes for each species show patterns of isolation (haplotypes only found in that location
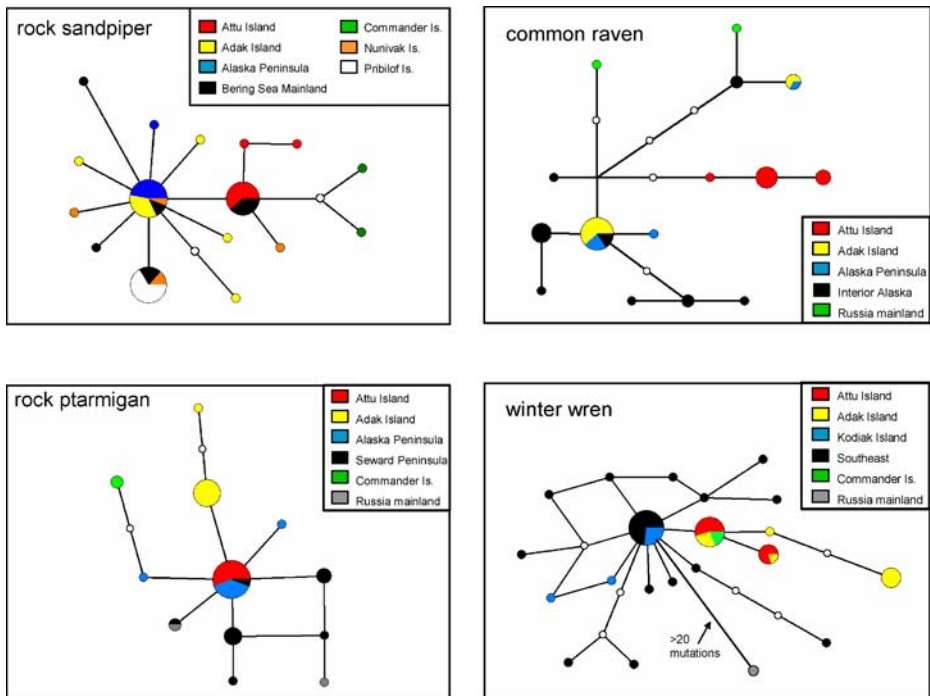

Fig. 1 Haplotype networks based on cytochrome *b* sequence data for four species of birds that are co-distributed in Beringia (see Pruett 2002). Each line represents a single mutation with *small white circles* separating two mutations. *Sizes of colored circles* indicate the number of individuals with that haplotype. Networks were developed using Network 4.1.1.2 (http://www.fluxus-engineering.com/sharenet.htm)

or at very high frequencies in one location) that support a shared Commander Island refugium for rock sandpiper, rock ptarmigan, and possibly winter wren. For example, Commander Island rock sandpipers have two endemic haplotypes, rock ptarmigan have one, and winter wrens have a haplotype that is also found in the Aleutian Islands but not on the Russian mainland nor from other locations in Alaska that were sampled (Fig. 1). Refugia in the Aleutian Islands are also indicated for rock sandpipers, rock ptarmigan, common raven, and winter wren. Divergences across species are similar, with one to four mutations separating possible refugial populations from haplotypes found on the continental mainlands. This supports isolation within a similar time frame for these taxa. Thus, the Aleutian and Commander Islands appear to have harbored populations of these species through past glaciations, and these populations were isolated from Russia and Alaska mainland populations during this time.

Determining historic, ice-age ranges of birds is problematic, with little or no data available. We have used population genetics in lieu of other evidence to determine the impacts that historic factors have had on population attributes such as separation and isolation. Although some high-latitude mammals likely had distributions that extended farther southward during the Pleistocene glacials than at present (FAUNMAP 1996), there is little support for this phenomenon in birds found in Beringia. Stewart and Dalén (2008) propose that because ptarmigan had larger distributions southward in the Palearctic during the Pleistocene, then this was also the case for other high-latitude species of birds like rock sandpipers. They argue that the genetic breaks we found in rock sandpipers correspond to isolation during warm cycles and that during cold cycles rock sandpipers had a much larger distribution. However, currently there are no known fossils of rock sandpipers from the Pleistocene (Gill et al. 2003), and no credible fossils of rock ptarmigan exist from North America during this time interval (Olson 1985; Potapov et al. 2003). The idea that all high-latitude species expanded their distributions southward from Beringia during the glacial cycles is not supported by data. In addition, there are no relictual populations of rock sandpipers farther south than their current distribution (Gill et al. 2003), a phenomenon often associated with Holocene refugial populations of birds. Rock ptarmigan currently have an extremely large Holarctic distribution, and in North America at least it seems difficult to believe that they are currently locked in a refugium (Holder and Montgomerie 1993). In addition, Holder et al. (1999) found support for numerous refugia for rock ptarmigan that coincided with known glacial refugial areas.

Rock sandpipers breed within 30 km of the ocean in upland, treeless habitats and feed along the coast (Gill et al. 2003). Unlike rock ptarmigan, which are found throughout interior Alaska and Russia and have a much larger distribution, rock sandpipers are tied to the coast, and thus their distribution would have fluctuated with available coastline and adjacent treeless habitat. It seems probable that coastal areas in the North Pacific with adjacent treeless habitats provided changing amounts of habitat for rock sandpipers. Also, fluctuations in sea levels probably affected population sizes, through, for example, alternating exposure and inundation of the Bering Land Bridge. Areas farther to the south in North America did not have suitable habitat for rock sandpipers during the Last Glacial Maximum (LGM; Ray and Adams 2001). However, based on current behavior, rock sandpipers do not overwinter in areas that have substantial pack ice. Of the four subspecies of rock sandpiper we studied, only those found in the upper Bering Sea Islands and along the coast, where pack ice extends in the winter, are migratory and spend the winter in ice-free coastal areas farther south (Gill et al. 2003; Pruett and Winker 2005). Large glaciers or areas where pack ice existed year-round, as was found during Pleistocene glacial cycles, would have been inhospitable for rock sandpipers by limiting foraging and breeding habitat.

A word on molecular genetics is also warranted. Within species, we expect the genetic variation in mtDNA sequence data, largely dominated by neutral processes, to be decoupled from differentiation due to selection. Sequence data from mtDNA therefore are not, *a priori*, expected to correlate with named subspecies, which are based on phenotypic differences that are more likely due to selection (see Winker et al. 2007). Thus, Stewart and Dalén's (2008) observation that our mtDNA data did not correspond perfectly with named subspecies is not an important issue. Further, while mtDNA sequence data do provide very useful data to understand historic population attributes, these data do not allow for sufficient temporal resolution to understand events on the scale of interstadials or Heinrich events (Mindell 1997). Stewart and Dalén's (2008) desire for phylogeographic studies to pay more attention to the effects of these shorter-term events within glacial cycles is thus unlikely to occur using existing methods.

In conclusion, we consider the world to be more complex than the scenario Stewart and Dalén (2008) present. Their argument works for some arctic species such as polar bears (*Ursus maritimus*) and glaucous gulls (*Larus hyperboreus*), in which interglacial warming seems to be causing habitat contraction (e.g., Winker et al. 2002:506). But the complexities of Beringian high-latitude communities defy simple categorical treatment. The similarities in genetic patterns of high-latitude and mid-latitude species in the Aleutian and Commander Islands suggests that populations of rock sandpiper, rock ptarmigan, common raven, and winter wren were isolated from their mainland counterparts during the late Pleistocene and quite possibly in the same refugia (Fig. 1). This finding is not surprising, given that these species are currently co-distributed in these areas. Were these refugia isolated by ice, water, or both? Unfortunately we cannot answer this question based on the data at hand, but it is apparent that in Beringia during the late Pleistocene the distribution of species having both temperate- and high-latitude distributions were strongly affected by glacial cycles. These taxa each exhibit the accrual of partitioned genetic diversity at depths associated with past glacial cycles, an expected genetic signature of glacial refugia. It is thus probable that high-latitude islands in Beringia that were at least partially ice free during the LGM served as refugia for both temperate- and high-latitude species currently distributed in these areas.

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