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COASTAL REFUGIA AND POSTGLACIAL RECOLONIZATION ROUTES: A REPLY TO DEMBOSKI, STONE, AND COOK

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For the past fifty years, there has been considerable speculation that a coastal refugium existed in the Pacific Northwest during the last glaciation (Wisconsin glaciation). Initially these speculations, which were based on surveys of both faunal (McCabe and Cowan 1945; Foster 1965) and floral (Calder and Taylor 1968; Ogilvie and Roemer 1984; Ogilvie 1989; Schofield 1989) endemism and disjunct plant distributions (Schofield 1965, 1984; Calder and Taylor 1968; Ogilvie and Roemer 1984; Ogilvie 1989, 1997), pointed to Haida Gwaii (previously known as the Queen Charlotte Islands) as the site of this refugium. However, geological data directly contradicted such speculations because abundant erratics, cirques, and striations on Haida Gwaii indicate that this archipelago experienced substantial ice cover during the late Wisconsin (Sutherland Brown and Nasmith 1962). Investigations of the endemic populations of stickleback (*Gasterosteus*) on the islands strongly indicate local adaptation to site-specific habitats (Reimchen 1994) as well as strong suggestion for the postglacial origin of the divergent populations (Moodie and Reimchen 1976). In response to this controversy, we initiated a broad molecular survey of some of Haida Gwaii's putative glacial relicts to determine whether mtDNA phylogeography could shed some light on this long-standing problem. In 1997, we reported the existence of two black bear (*Ursus americanus*) lineages, which we designated as coastal and continental. The coastal lineage was largely restricted to the coast (Haida Gwaii, Vancouver Island, coastal mainland of British Columbia, and the Olympic Peninsula), whereas the continental lineage was widely distributed throughout North America. From this phylogeographic pattern we suggested that (1) this pattern in western North America was the result of postglacial recolonization from two source areas: a refugium south of the ice front and coastal refugia on the continental shelf possibly adjacent to Haida Gwaii, which is consistent with previous predictions; and (2) the morphological attributes that differentiate black bear subspecies from coastal British Columbia (*carlotta*, *kermodei*, *altifrontalis*, and *vancouveri*) arose from a common ancestor sometime after the Wisconsin glaciation.

Demboski et al. have argued that the phylogeographic pattern that we uncovered in the North American black bear is an artifact of incomplete sampling. As such, they argue that our suggestion that this pattern may have been influenced by dispersal from a coastal refugium is premature. Their argu-

ment is based on their finding that the coastal haplotypes of marten (*Martes americana*) and vagrant shrew (*Sorex vagrans*) also occur in continental regions. They also cite similar findings within the brown bear (*U. arctos*), where a divergent haplotype originally identified on the Admiralty, Baranof, and Chicagof Islands in Alaska (Talbot and Shields 1996) has been found on the mainland. We also noted (Byun et al. 1997; Byun 1999) that the coastal black bear haplotype may also be present in California (Wooding and Ward 1997) and Montana (Cronin et al. 1991; Paetkau and Strobeck 1996).

It is possible that the mtDNA phylogeographic pattern identified in black bears that comprises a coastal and a continental lineage has nothing to do with coastal refugia. Limited sampling is a typical problem in phylogeographic studies and increasing sampling area always provides a more detailed picture of distribution. However, our suggestion of a coastal refugium was based both on molecular evidence as well as information outside of the field of molecular phylogeography. We will briefly outline this evidence.

Point 1.—There are currently 18 disjunct hepatics and 12 disjunct mosses found in the Western Hemisphere only on Haida Gwaii, the Pacific Coast of British Columbia, and adjacent Alaska. In addition to this, seven disjunct bryophytes are found only in North America on Haida Gwaii. Strong affinity of many of these disjunct bryophytes with bryophytes found in western Europe or southeastern Asia is suggestive that they may be relicts of ancient flora, possibly dating back to the Tertiary. Persistence of these suspected relicts on Haida Gwaii was suggested by Schofield (1984) to be evidence that suitable habitat continued to exist during multiple Pleistocene glacial advances. Although the current distribution of these bryophytes might be the result of postglacial dispersal from mainland refugia, it was considered unlikely because of the lack of readily dispersible diaspores and absence of significant asexual reproduction, which limits these species to local populations. In addition to bryophytes, at least nine vascular plants are known to be disjunctly distributed. Ogilvie and Roemer (1984) and Calder and Taylor (1968) proposed that Haida Gwaii was likely to have been a late Wisconsin refugium for these plant species.

Point 2.—While local ice sheets on Haida Gwaii began to recede about 16,000 years ago, surrounding areas were experiencing a glacial maximum. Pollen profiles taken from the

northeastern coast of Haida Gwaii (Cape Ball) demonstrates a diverse and rapid colonization of this area when it became deglaciated. The rate of colonization and the diversity of plants (sedges, Asteraceae, Ericales, Caryophyllaceae, rushes, and pondweeds) that were established at Cape Ball when adjacent areas were supposedly inundated by ice strongly suggests the existence of a nearby and not yet identified coastal source area (Warner et al. 1982).

Point 3.—Recent sonar data and sedimentary cores provides physical proof that the continental shelf, currently submerged beneath Hecate Strait, was terrestrial, free of ice, and also possessed freshwater lakes during the last glacial maximum 15,000 years ago (Barrie et al. 1993; Josenhans et al. 1993, 1995).

Point 4.—The black bear mtDNA phylogeographic pattern is largely congruent with other phylogeographic patterns obtained for independent species such as sockeye salmon (*Oncorhynchus nerka*; Wood et al. 1994), brown bear (*U. arctos*; Talbot and Shields 1996), and short-tailed weasel (*Mustela erminea*; S. A. Byun, B. F. Koop, and T. E. Reimchen, unpubl. ms.). Furthermore there has been indications from *Tellinia grandiflora* (chloroplast DNA) suggesting that its phylogeographic pattern might have been influenced by postglacial dispersal from coastal refugia (Soltis et al. 1991, 1997). A divergent mtDNA lineage of sticklebacks (*Gasterosteus aculeatus*) was discovered on Haida Gwaii (Gach and Reimchen 1987) and subsequent work determined that this lineage was disjunctly distributed in a few locales in Alaska and Japan (O'Reilly et al. 1993; Orti et al. 1994). Although it is possible that the presence of this lineage is the result of ongoing gene flow via oceanic populations (Deagle et al. 1996), its apparent restriction to particular locales in the Pacific Northwest and original divergence during the early Pleistocene despite the great potential for intermixing is suggestive of coastal refugia. Such congruency of phylogeographic patterns implies a common biogeographical history (Avice 1994) and argues against spurious events like lineage sorting or founder events.

Point 5.—Northward dispersal from southern refugia was a significant problem at the time of glacial retreat. Such dispersal probably began during the early stages of deglaciation but massive recessional lakes (Lake Missoula and Lake Columbia; Pielou 1992), floods, and marine transgression severely impeded northward movement. On the coast, eustatic and isostatic changes resulted in massive flooding of the Puget Lowland about 11,500 to 13,500 years ago (Easterbrook 1992). From about 13,000 BP to 9000 BP, sea levels rose along the Coast Mountains and eastern shores of Haida Gwaii, respectively. These changes were exacerbated by tilting of tectonic plates which effectively increased sea levels along the coastal mainland while decreasing sea levels further west. Furthermore, as a higher trophic level species, the black bear would have experienced significant ecological inertia as colonization would have required at least the establishment of primary producers.

Although it is possible that the presence of divergent mtDNA haplotypes on Haida Gwaii in black bear, marten, and short-tailed weasel is solely due to northward dispersal from southern source populations, it is unusual that all of these carnivores, organisms that are extremely poor island colonizers (Carlquist 1974), could have successfully colo-

nized the most isolated archipelago of the Pacific Northwest during postglacial periods. Furthermore, if Haida Gwaii was postglacially recolonized from mainland source populations, then its biota can only be about 12,000 years old. This is at odds with its high disproportion of carnivores, a feature characteristic of old and long-established island communities (Carlquist 1974). We think that this feature might be attributed to the derivation of some populations on Haida Gwaii from the adjacent coast, which have maintained continuity for at least the duration of the Wisconsin glaciation.

It is important to note that each piece of evidence, including our black bear data, does not provide proof that a biologically significant refugium did exist on the coast. However, collectively they present a powerful case that late Wisconsin glacial history of northwestern North America needs to be seriously reexamined. The only evidence that would prove the continuity of coastal habitats during the last glacial advance would be a continuous Wisconsin sequence of either microfossils or pollen. However, the lack of such a sequence is not surprising if this refugium was located on the continental shelf and is now underwater.

We believe that the occurrence of coastal haplotypes in continental regions does not allow for comment on the issue of coastal refugia. Such occurrences are not necessarily surprising given the thousands of years in which these species have had to disperse. This is especially true in species with large home ranges, like the black bear and marten. As we have suggested before (Byun et al. 1997; Byun 1999), it is the frequency of occurrence that is important. We examined 11 black bear individuals from Haida Gwaii and five individuals from Vancouver Island. All 16 individuals had the coastal haplotype. We also sequenced portions of the cytochrome *b* gene (307 bp) from 12 marten (S. A. Byun, B. F. Koop, and T. E. Reimchen, unpubl. data) and identified coastal and continental lineages. However, we examined six individuals from Haida Gwaii and four from Vancouver Island. All 10 individuals possessed the coastal haplotype. Examination of 30 short-tailed weasels (143–673 bp), encompassing eight subspecies (S. A. Byun, B. F. Koop, and T. E. Reimchen, unpubl. ms.) produced a similar result. Three lineages corresponding roughly to coastal, southern, and northern refugia were identified. All six weasels from Haida Gwaii possessed a haplotype divergent by about 2.5% from haplotypes that characterized both northern and continental weasels. Assuming that the frequency of a particular haplotype will be concentrated near its source area, then these haplotypes probably dispersed from somewhere along the northwestern coast in close vicinity to Haida Gwaii. This coastal refugium that we suspect existed on the continental shelf during the late Wisconsin was probably part of a series of coastal refugia that were likely to have been intermittently connected through fluctuations in ice margins and sea levels. This coastal corridor probably allowed some degree of gene flow among coastal populations, thus accounting for the high frequency of coastal haplotypes in areas adjacent to Haida Gwaii.

Our 1997 paper tried to make two points: (1) local adaptation to different ecological conditions has been of greater importance to the formation of black bear subspecies than vicariance events that occurred during the Pleistocene glacial

advances; and (2) that the distribution of black bear coastal and continental haplotypes, even with outliers in Montana and California, is consistent with the hypothesis that black bear recolonized the Pacific Northwest from at least two refugia: a southern refugium and a refugium on the continental shelf now beneath Hecate Strait. Demboski et al. (1999) offer no evidence to contradict these suppositions.

There is no dispute about the phylogeographic break that exists in the Pacific Northwest across a multitude of taxa (for review, see Soltis et al. 1997, Byun 1999). We have offered a testable hypothesis to account for these congruent molecular patterns based on our understanding of past and current research in paleobotany, plant and animal surveys, sonar profile data, and molecular phylogeography.

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