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The Evolution of Endemic Species in Haida Gwaii

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Highly distinctive and geographically restricted plants and animals characterize the biota of islands. Such endemism results from a complex interplay of geographical, ecological, and evolutionary processes. One of the central tenets of island biogeography is that number of species is reduced compared with equivalent areas on the adjacent mainland, and that the extent of the deficiency is directly proportional to the distance from the mainland and inversely proportional to island size (MacArthur and Wilson 1967). Significant ecological consequences result from this deficiency because species experience reduced competition, which allows for ecological expansion into unoccupied niches. Consequently, island species often exhibit striking morphological and genetic differences from ancestral populations. Galapagos finches and Hawaiian honeycreepers are classic examples of such divergence. Because evolutionary rates can be rapid in such conditions of ecological release (Gingerich 1993), the morphological distinctness may represent geologically recent adaptations to novel habitats rather than long periods of isolation and gradual divergence.

One of the largest and most isolated archipelagos in western North America is Haida Gwaii, and similar to other islands, it exhibits a rich diversity of biologically unique plant and animal taxa. The prevalence of such endemics relative to adjacent continental regions led to an emerging view that areas on or near Haida Gwaii escaped glaciation and allowed survival of these relict forms when other coastal and continental regions were subject to glacial advances during the Pleistocene (Scudder 1989). However reasonable such a view, available geological evidence indicates that Haida Gwaii was subject to major ice cover with few prospects of ice-free areas other than mountaintops, which would not have supported diverse ecological communities (Sutherland-Brown and Nasmith 1962; Clague 1989). If true, this would suggest that the endemism in Haida Gwaii was derived during postglacial times (Holocene) rather than through extended periods of isolation. In this chapter, we consider the conflicting evidence for relictual

versus Holocene origin of endemic animals in Haida Gwaii and summarize recent studies using genetic markers in mitochondrial DNA, which allow times of divergence or antiquity of populations to be estimated.

The endemism of biota in Haida Gwaii is taxonomically and ecologically diverse (Figure 5.1). It occurs in mosses (Schofield 1989), flowering plants (Calder and Taylor 1968), beetles (Kavanaugh 1992), fish (Moodie and Reimchen 1973), birds, and mammals (Foster 1965; Cowan 1989). In virtually all cases, endemics are differentiated from mainland forms to the level of subspecies or, rarely, full species. In this review, we will focus on seven endemic animals: the three-spined stickleback (*Gasterosteus aculeatus*), Dawson caribou (*Rangifer tarandus dawsoni*), black bear (*Ursus americanus carlottae*), marten (*Martes americana nesophila*), Haida short-tailed weasel (*Mustela erminea haidarum*), saw-whet owl (*Aegolius acadicus brooksi*), and ground beetles (*Nebria* spp.). We provide brief descriptions of the life history, distinguishing attributes from mainland source populations, evidence for adaptation, and results for molecular phylogenies for some of the endemics.

Endemic Taxa of Haida Gwaii

Three-spined Stickleback

This small fish is widespread in marine and freshwater habitats of northern latitudes and is extensively studied in ecological, behavioural, and evolutionary disciplines (Bell and Foster 1994). Marine stickleback are anadromous, entering freshwater streams each year for reproduction, and this has led to multiple invasions of freshwater lakes during the recession of ice and establishment of populations restricted to fresh water. Collections of the fish by multiple researchers from throughout Europe, Asia, and North America show evidence for high levels of morphological variability among freshwater populations, much of which is due to genetic differences (see Wootton 1984 for summary). It has become apparent that the sticklebacks from Haida Gwaii exhibit greater morphological variability among lakes than that found throughout the rest of the distribution of the species (Moodie and Reimchen 1973, 1976a; Reimchen 1994a). This extensive variability over such a small geographical area provides a model for evaluating the origin of endemic taxa in Haida Gwaii.

Surveys of 95 percent of all watersheds in Haida Gwaii (Reimchen 1992b, 1994b) have identified stickleback in 110 lakes, most of which occur on northeastern Graham Island, with the remainder in low-elevation lakes on both Graham and Moresby Islands. Collections of stickleback yielded geographically isolated populations with gigantism in body size (Moodie 1972), complete loss of bony armour (Reimchen 1980, 1984), diversity in body pigmentation, and breeding colour ranging from blue iridescence and crim-
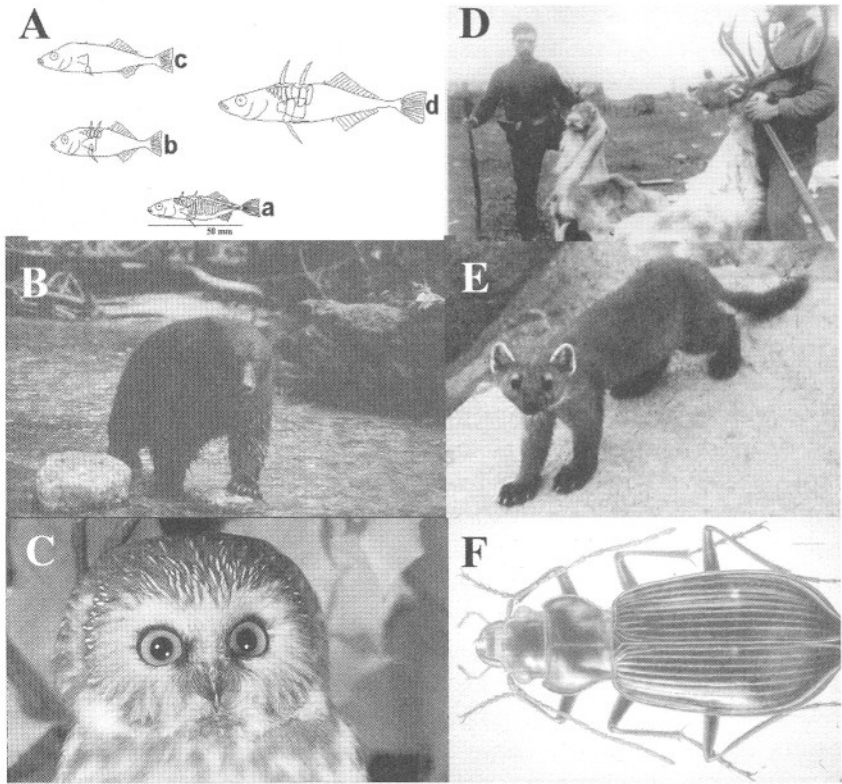
Figure 5.1 Representatives of endemic animals from Haida Gwaii: (A) Three-spined stickleback; (a) ancestral marine form, (b) typical stream and small lake form, (c) unarmoured forms of northeastern Graham Island, (d) giant stickleback from Drizzle Lake, Mayer Lake, Skidegate Lake, and Coates Lake. (B) Coastal black bear. (C) Saw-whet owl (courtesy Bristol Foster). (D) Last Dawson caribou (1908) seen from northern Graham Island (BC Archives F-00235). (E) Marten (courtesy Bristol Foster). (F) *Nebria*.

son displays to black forms (Moodie 1972; Reimchen 1989). Such large differences also occur over short distances within watersheds where genetic interchange among populations is possible (Reimchen et al. 1985).

The majority of highly divergent stickleback are found in the tea-coloured and low-productivity lakes of the Argonaut Plain. This high level of divergent body forms in Haida Gwaii stickleback was consistent with trends found in other endemic species and initially appeared to represent relict populations that diverged during long periods of isolation in ice-free conditions. There is, however, a striking congruence between morphological characteristics of the fish in each lake and ecological attributes of the habitat (Moodie and Reimchen 1976b). These and subsequent studies show strong support for the primary role of natural selection in shaping the characteristics of

the divergent stickleback. Gigantism in body size, independently derived in six different populations, represents a defensive adaptation against gape-limited piscivores such as trout and diving birds (Moodie 1972; Reimchen 1988, 1991). Lateral bony plates on the fish vary extensively in number among populations and are tightly correlated with the presence or absence of predatory trout (Moodie and Reimchen 1976b). Variability in the defensive apparatus ranging from robust development of spines and bony armour to complete loss of spines and armour represents a functional adaptation to the relative proportions of puncturing, compression, and grappling predators in a given lake (Reimchen 1983, 1992a, 1994a). These predator groups correspond to trout, bird, and macroinvertebrate piscivores that forage, capture, and manipulate their prey in a distinctive manner, leading to different defences of the stickleback to each predator. The speed of evolutionary adaptation among these populations may be very high, as there is evidence for yearly and seasonal shifts in morphological traits that respond to yearly and seasonal shifts in predation regime (Reimchen 1995; Reimchen and Nosil 2004). This suggests that the morphological endemism in the Haida Gwaii populations could have developed postglacially without extended periods of isolation.

One of the most distinctive populations of stickleback in Haida Gwaii occurs at Rouge Pond on the Argonaut Plain. These fish are unarmoured and represent the most morphologically derived condition relative to the marine ancestral form (Reimchen 1984). The fish are also unusual in that most have a mucous layer on their body containing thousands of nonpathogenic dinoflagellates of unknown taxonomic affinity (Reimchen and Buckland-Nicks 1990). Recent studies demonstrate that the dinoflagellate has a particularly complex life cycle (Buckland-Nicks and Reimchen 1995) and represents a new species that is apparently restricted globally to a small region of the Argonaut Plain (Buckland-Nicks et al. 1997). The restricted distribution of this atypical dinoflagellate and its association with a highly divergent and unarmoured stickleback is suggestive of extended historical persistence and perhaps a relictual status of this stickleback population.

Molecular studies using mitochondrial DNA have been employed to investigate phylogenetic affinities or relatedness among populations and species (Avise 1994). Ideally, the extent of genetic divergence in the DNA can be used to determine whether endemic species from islands are ancient relictual lineages that survived in ice-free regions or whether they are closely related to mainland forms and therefore of postglacial origin. Two hypotheses for the evolution of Haida Gwaii stickleback are reasonable: (1) that freshwater populations such as the unarmoured stickleback at Rouge Pond and the giant stickleback at Mayer Lake and Drizzle Lake are relictual, from which one would predict major genetic differences among these endemic freshwater populations as well as a major separation between each of these

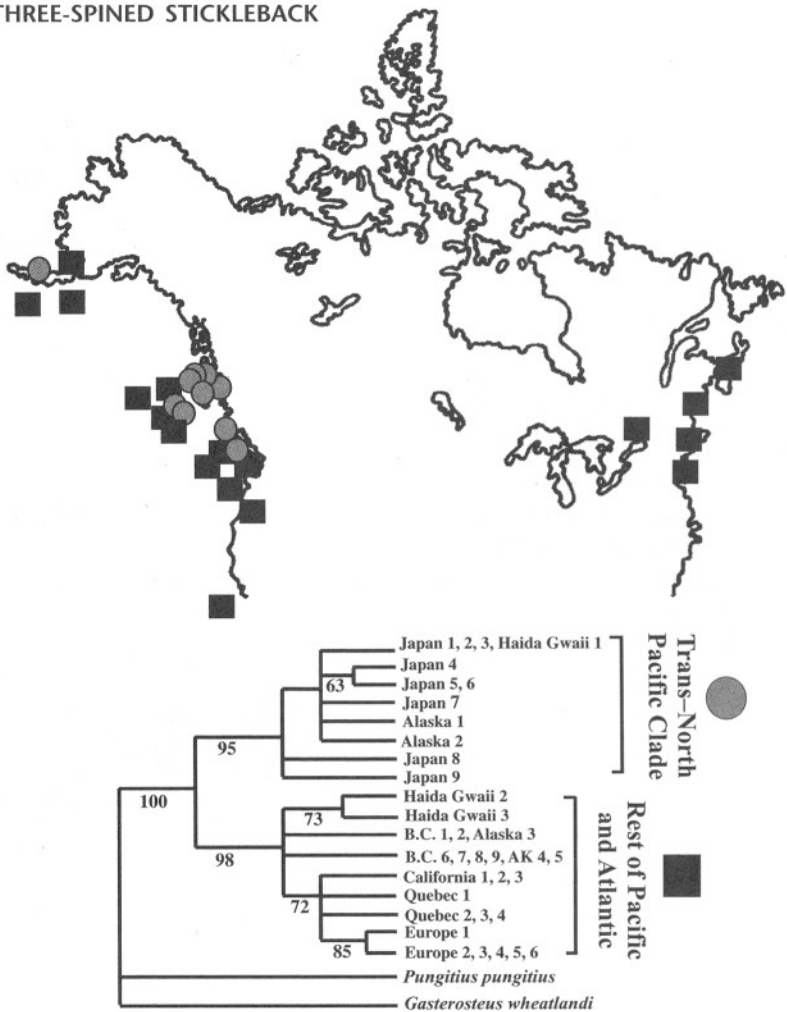**THREE-SPINED STICKLEBACK**

Figure 5.2 Molecular phylogeny of three-spined stickleback and North American geographical distribution of lineages.

populations and the ancestral marine populations; and (2) that freshwater populations are postglacially derived, from which one would predict a single major genetic lineage among all freshwater and marine populations.

Results from genetic studies (Gach and Reimchen 1989; O'Reilly et al. 1993; Orti et al. 1994; Deagle et al. 1996) demonstrate a complex and unanticipated history consistent with both of these hypotheses. Two highly divergent mitochondrial DNA lineages have been identified globally for marine and freshwater stickleback, and these lineages separated from a common ancestor near the beginning of the Pleistocene (Figure 5.2). The Euro–North

American lineage is common and widespread and is found in marine and freshwater habitats around Europe, eastern North America, and western North America, including California, Vancouver Island, Alaska, and most lakes in Haida Gwaii. The latter includes marine ancestral populations as well as highly derived freshwater populations such as the spine-deficient form at Boulton Lake and the giant forms at Mayer Lake and Drizzle Lake. This is consistent with the second hypothesis, that these endemic stickleback in Haida Gwaii are not relics but rather originated from marine ancestors in postglacial (Holocene) periods.

The second mitochondrial lineage identified from the global survey, referred to as the Japanese lineage on the trans–North Pacific clade (Johnson and Taylor 2004), is much more restricted but predominates in Japan and in several localities in Alaska. It is also found in Haida Gwaii lakes, primarily in the northeastern corner of Graham Island and usually in the same lakes as the widely distributed lineage (Figure 5.3). Frequencies of this more restricted lineage are highly variable in Haida Gwaii lakes, with the higher frequencies in localities where stickleback are most dissimilar morphologically to marine ancestral forms. The highest frequency of the Japanese lineage (100 percent) is found in Rouge Pond, where the stickleback are the most divergent from marine ancestors and show the strange association with dinoflagellates. While there is potential for recent transoceanic dispersal of stickleback from Japan (Deagle et al. 1996), the apparent absence of the Japanese lineage in marine waters surrounding Haida Gwaii, combined with the prevalence of this lineage in the most morphologically divergent stickleback populations, suggests that these comprise older and possibly relictual populations, results consistent with the first hypothesis. Recent investigations also show the Japanese lineage on Vancouver Island, but these populations do not exhibit any morphological divergence (Johnson and Taylor 2004).

However, the ponds and lakes containing the most divergent stickleback populations are underlain by glacial outwash gravels (Sutherland-Brown 1968) and are clearly postglacial in origin (Warner 1984). Consequently, the current prevalence of the Japanese lineage in ponds and lakes on the northeastern corner of the Argonaut Plain would suggest early postglacial colonization from adjacent freshwater habitats that persisted during late Pleistocene. These habitats, including large freshwater lakes, occurred on the now submerged continental shelf separating Haida Gwaii from the mainland (Josenhans et al. 1993; Chapter 1) and could have allowed early postglacial colonization by a relictual lineage of the Argonaut Plain.

Dawson Caribou

One of the most interesting endemics known to Haida Gwaii is the now extinct Dawson caribou. The last caribou ever seen on the islands (a herd consisting of two bulls and a cow near Naden Harbour) were shot in 1908
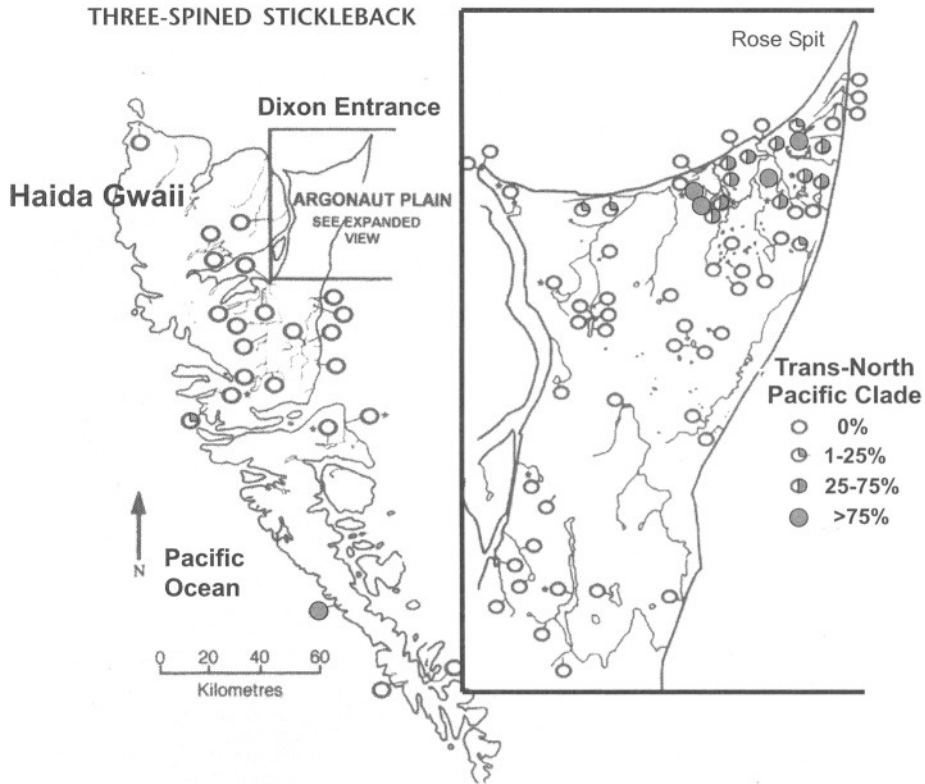
Figure 5.3   Haida Gwaii distribution of two divergent molecular lineages in stickleback.

and the species is believed to have become extinct shortly thereafter (Cowan and Guiget 1978; Banfield 1961). The 1908 specimens of Dawson caribou were small in stature. The antlers on the males were poorly developed and remarkably irregular, while the females lacked antlers altogether, a condition atypical for caribou (Cowan and Guiget 1978). Fossil evidence indicates that Haida Gwaii was inhabited by caribou at least 5500 years BP (Chapters 6 and 13), and there is recent evidence for interglacial presence based on an antler dated at > 40,000 BP (R.W. Mathewes, personal communication). The large diameter and length of these fossil caribou bones indicate close affinity to large-bodied woodland or mountain caribou on the mainland, suggesting that the small stature of the Dawson caribou is of recent origin and not relictual.

Many of the Dawson caribou's divergent characteristics, such as small stature and reduced antlers, are typical of insular ungulates (Foster 1965). This is clearly illustrated by the decrease in body size and reduction in antler size of black-tailed deer introduced to Haida Gwaii in the late 1800s. These morphological changes have been attributed to a variety of factors,

including poor nutrition and lack of predators (Foster 1965) and is possibly an adaptation for improved mobility in dense forest (Lister 1993). Both Foster (1965) and Banfield (1961) considered the Dawson caribou to be a postglacial colonist of Haida Gwaii rather than a glacial relict.

Byun (1998) extracted short mitochondrial DNA (mtDNA) fragments from four museum specimens of Dawson caribou for comparison with mainland caribou. Based on the base sequences from these fragments, Dawson caribou did not have a distinctive mtDNA lineage relative to woodland and mountain caribou on the adjacent mainland. Such results based on short fragment lengths are tentative, but these suggest that the Dawson caribou was a postglacial colonist of Haida Gwaii (Byun et al. 2002).

Black Bear
It has been generally assumed that black bears persisted in refugia south of the Cordilleran Ice Sheet in North America during the Wisconsin glacial advance (Kurtén and Anderson 1980). From these refugia, they recolonized the Pacific Northwest and its offshore islands by 12,000 BP and ultimately differentiated into the various subspecies in this region. Across North America, sixteen subspecies of black bear have been recognized (Hall 1981), seven of which occur in the Pacific Northwest. These subspecies differ principally in skull and tooth morphology. The Haida Gwaii black bear (*U. americanus carlottae*) was originally described as a distinct species by Osgood (1901) based on its robust skull, heavy dentition, and exceptionally large body size. It was later reduced to subspecies status but remains the most morphologically distinct of all coastal bears and the largest black bear in North America.

Cowan and Guiget (1978) and Foster (1965) suggested that the Haida Gwaii bear was a glacial relict, having developed heavy molars and a massive skull in response to foraging on marine resources over long periods of isolation from mainland bears. Given the rapid evolutionary rates observed in many Quaternary mammals (Gingerich 1993), however, the adaptations observed in the Haida Gwaii black bear may have been derived following early postglacial colonization of the islands.

To determine whether Haida Gwaii bears are glacial relicts or recently separated from mainland bears, we undertook an examination of mitochondrial DNA from black bears of western North America. Earlier genetic studies of interior continental black bears (Cronin et al. 1991) suggested that these bears were represented by a single and widespread genetic lineage. If Haida Gwaii black bears are glacial relicts that diverged from other black bears prior to the Fraser Glaciation, then they should be genetically distinct.

Our results are only partially consistent with this hypothesis. Phylogenetic analyses of 719 base pairs of the mtDNA clearly identified two major lineages in black bear, which we distinguish as continental and coastal (Byun

et al. 1997). The continental lineage includes black bears from locations as diverse as Alaska, Alberta, Montana, and Pennsylvania, while the coastal lineage comprises all of the coastal subspecies, including the Haida Gwaii bear, the Kermode bear of the mainland coast, and the Vancouver Island black bear (Figure 5.4). The average sequence divergence within these coastal
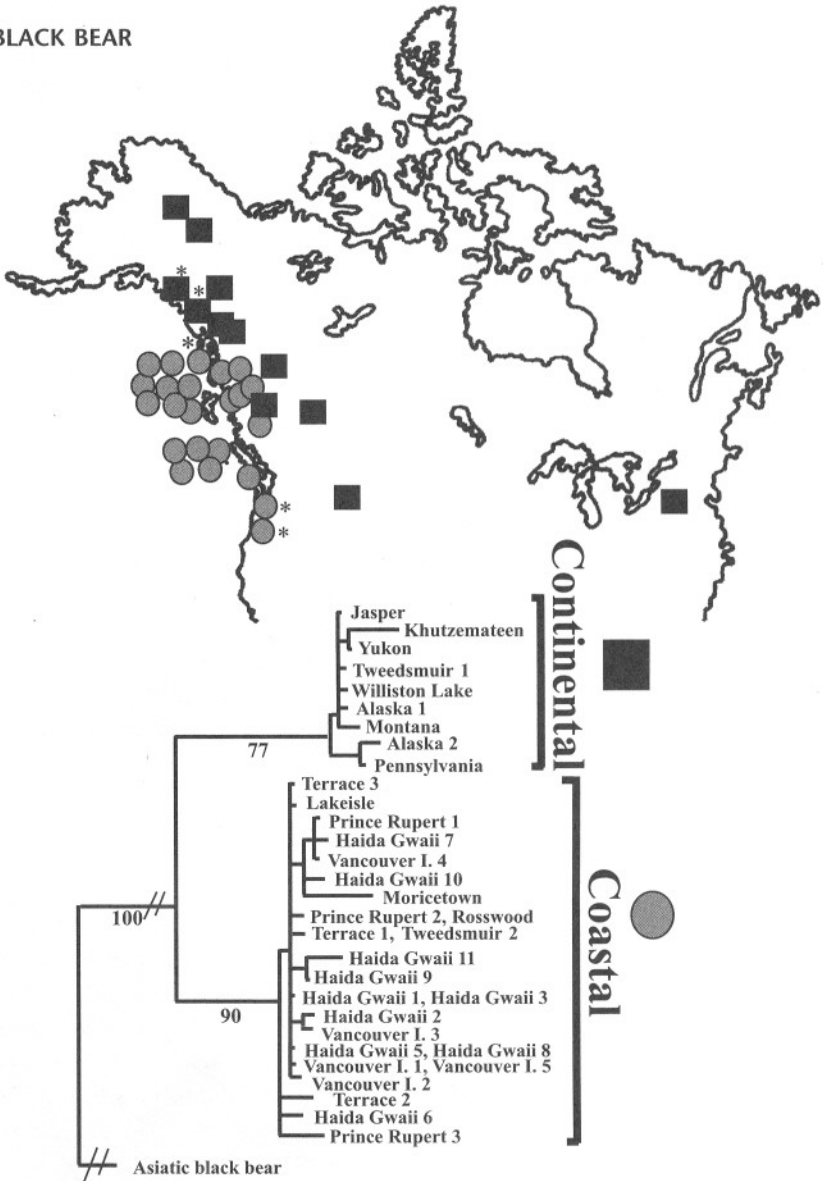
BLACK BEAR

Figure 5.4 Molecular phylogeny of black bear and geographical distribution of lineages.

lineages is low (0.1 percent), suggesting that diversification of the various subspecies in each lineage occurred during the Holocene. In contrast, the average sequence divergence between coastal and continental lineages was high (3.6 percent). Using the standard rate of change for vertebrate mtDNA of 2 percent per million years (Brown 1985), these two lineages apparently diverged 1.8 million years ago. Application of other rate estimates, including those for silent base substitutions and a rate calibrated from *Ursus* subfossils, both yielded divergence times in the range of 360,000 to 1.8 million years ago.

The close genetic affinity of the Haida Gwaii black bear with those from the mainland and Vancouver Island suggests that these bears shared a common ancestor in the early Holocene. Consequently the unique and highly divergent morphology of Haida Gwaii bears relative to the Kermode bear and to the Vancouver Island bear must be postglacially derived and not the product of long-term isolation. Recently discovered skeletal remains from three bears on northwestern Vancouver Island (carbon-dated to 10,000 BP) suggest that early Holocene colonists to Vancouver Island were significantly larger than modern black bears on both Vancouver Island and adjacent continental regions (Nagorsen et al. 1995). If true, then large body size, currently observed in the Haida Gwaii black bear, may be ancestral among the coastal subspecies, perhaps as a foraging adaptation for intertidal resources that currently predominate and would have predominated in the periglacial habitats of the late Pleistocene.

It is generally believed that black bears in the Pacific Northwest are derived from southern Washington (Kurtén and Anderson 1980). Northern dispersal from Washington probably occurred during the late glacial and early Holocene on newly deglaciated landscapes, although somewhat impeded by changing sea levels on the coast and instability of ecosystems at the edge of retreating glaciers. Occurrence of the two highly divergent mtDNA lineages differentiating coastal bears from continental bears contradicts the supposition that black bears in the Pacific Northwest are derived from a single southern refugial population. The divergent lineage restricted to Haida Gwaii, Vancouver Island, and coastal regions of mainland British Columbia suggests that these areas were colonized by the same source population, but one different from the bears that recolonized deglaciated areas on the continent. The current distribution of mtDNA lineages in coastal British Columbia can be most readily interpreted if one assumes that the source population of coastal bears had equal access to Haida Gwaii, the coastal mainland, and Vancouver Island prior to the rise in sea levels.

Two major glacial refugia in the Pacific Northwest are currently recognized, one south of the ice front in Washington and a second in unglaciated parts of Alaska and the Yukon (Pielou 1992). Various lines of evidence

suggest that a third mid-coastal glacial refugium persisted on the now sub-merged continental shelf separating Haida Gwaii from the mainland. Cores taken midway between Haida Gwaii and the mainland indicate that large portions of Hecate Strait were terrestrial and ice-free during the Fraser Glaciation (see Josenhans et al. 1993; Barrie et al. 1993; Josenhans et al. 1995). The coastal plain would have connected Haida Gwaii to the mainland and may have extended far enough south along the mainland to allow access along the coast to Vancouver Island. The distribution of the coastal mtDNA lineage can be explained if the black bear persisted in the Hecate refugium and, during the early stages of deglaciation, recolonized Haida Gwaii, the coastal mainland, and Vancouver Island. Recent molecular studies (Stone and Cook 2000) have also identified the coastal lineage in southeastern Alaska, immediately north of Haida Gwaii, consistent with our suggestions. The coastal lineage is rare further inland, probably since movement into the interior of British Columbia would have been impeded by Cordilleran ice. The rapid rise in sea level in early postglacial times would have further isolated the mainland from Vancouver Island and Haida Gwaii, resulting in the present lineage distribution. The continental lineage, which likely resided south of the Cordilleran Ice Sheet, repopulated the interior regions more effectively due to greater accessibility to the mid-continental corridor, which became more habitable by the Holocene (Pielou 1992). Some black bear populations in interior British Columbia contain both lineages and may represent recent easterly dispersal of the coastal lineage and a westerly or northerly dispersal of the continental lineage (see Stone and Cook 2000).

The early to mid-Pleistocene split between the two black bear mtDNA lineages indicates that they have persisted through multiple glacial and interglacial periods. This is surprising given the numerous population bottlenecks and opportunities for lineage sorting that would occur in a large mammal with low population size (see Avise 1994). These two lineages could have been maintained if they had been reproductively isolated, but there is no evidence to suggest any reproductive barriers. These lineages could also have persisted if they had been geographically isolated for the past 360,000 years. It is not clear how this could have occurred. Given the cyclic pattern of glaciations, the coastal lineage could have been isolated from the continental lineage by surviving in coastal refugia during glacial advances and in Haida Gwaii during interglacials. If true, this would make the Haida Gwaii black bear the ancestral form for the recolonization of the coastal Pacific Northwest (Byun et al. 1997).

Marten

Based on fossil evidence, marten likely crossed to North America from Eurasia via the Bering land bridge during the mid to late Pleistocene (Anderson 1994). These early colonists spread eastward and were subsequently isolated in

eastern North America by the Laurentide Ice Sheet. Following retreat of the glaciers, eastern marten expanded westward but were largely excluded from the Pacific Northwest by a second group of marten, which had independently colonized this region from Eurasia (Anderson 1994; see, however, Stone and Cook 2002). These two colonizing groups are currently recognized as morphotypes *caurina* and *americana*. They are differentiated on the basis of skull characteristics, including shape of the auditory bullae and relative size of the upper molar teeth (Grinnell and Dixon 1926; Hagmeier 1961). *Caurina* occurs in western North America and has greater morphological affinity to a Eurasian ancestor than does the eastern *americana*. Hagmeier (1955) suggested that both morphotypes persisted during the late Pleistocene, with *caurina* isolated from *americana* in west coast refugia.

There are seven subspecies currently recognized within each of the two morphotypes. These subspecies, differentiated by variations in pelage colour, body size, and skull shape, are believed to have originated postglacially (Hagmeier 1955; Foster 1965). Of all the subspecies in North America, the Haida Gwaii marten (*Martes americana nesophila*) is the most distinct. It is the largest marten in North America and is characterized by thick nasal bones, robust molar teeth, orange breast patch, and marked sexual dimorphism (Foster 1965; Giannico and Nagorsen 1989). Both Hagmeier (1955) and Foster (1965) suggest that these characteristics are too distinct to have evolved in postglacial times, suggesting that these morphological features evolved during extended isolation in a refugium in Haida Gwaii.

Phylogenetic analyses of a 311-base-pair fragment of the cytochrome b gene indicate the presence of two distinct marten mtDNA lineages in the Pacific Northwest (Figure 5.5). The coastal lineage was found exclusively in Haida Gwaii and on Vancouver Island while the continental lineage was found on mainland British Columbia and Newfoundland. An average sequence divergence within the coastal lineage of 0.8 percent suggests that the morphological features characterizing both the Haida Gwaii and Vancouver Island marten may have evolved during postglacial times. Similarly, marten of mainland British Columbia exhibit relatively low sequence divergence (0.6 percent) for this molecular marker, again implying that the morphological differences distinguishing each of these continental subspecies evolved within the last 12,000 years.

The average sequence divergence of 1.8 percent between these mtDNA lineages suggests that the continental martens of British Columbia and Newfoundland diverged from marten in Haida Gwaii and on Vancouver Island prior to the Wisconsin glaciation. These results suggest that the biogeographical history of marten in the Pacific Northwest is more complex than previously thought. More recent molecular data on marten from a broader region of the Pacific Northwest (Small et al. 2003) confirm our results of two distinctive lineages. The coastal lineage that we identified in
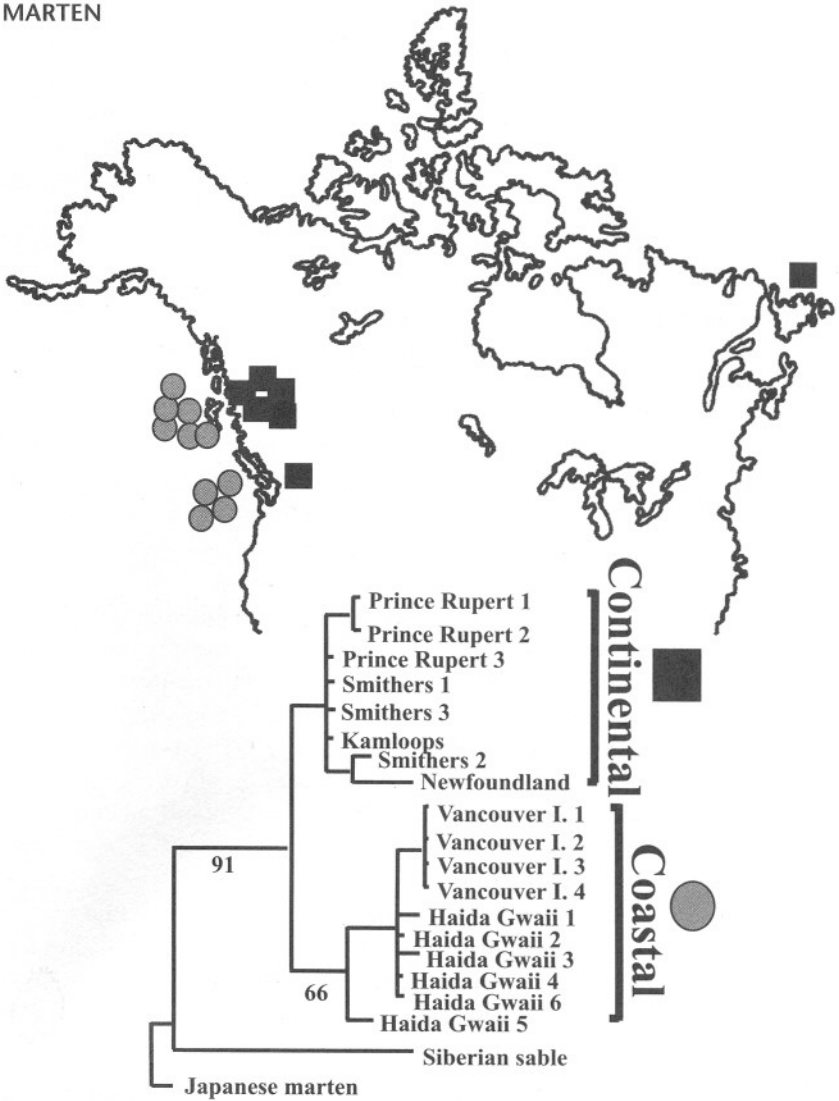
MARTEN

Figure 5.5 Molecular phylogeny of marten and geographical distribution of lineages.

Haida Gwaii and Vancouver Island was also found on Admiralty Island and Kuiu Island in southeastern Alaska. While this lineage was not found on the Alaskan mainland, it was detected in Oregon and southern Montana. Given the broadly similar phylogeographic pattern observed in black bear, the distribution of coastal and continental marten lineages is largely consistent with postglacial recolonization of the Pacific Northwest from both continental and coastal refugia.

Haida Short-tailed Weasel

The short-tailed weasel first appeared in North America from Eurasia during the mid-Pleistocene and spread over Canada and northern United States (Kurtén and Anderson 1980). During the last glacial advance, the short-tailed weasel appears to have persisted both north and south of the Cordilleran Ice Sheet (Kurtén and Anderson 1980). From these refugia, they are believed to have recolonized the Pacific Northwest, undergoing extensive morphological diversification to produce the twenty subspecies identified in North America (Hall 1981). The Haida short-tailed weasel is the most morphologically distinct of all short-tailed weasels, with large body size and proportional difference in the breadth and depth of the rostrum (Cowan and Guiget 1978; Foster 1965; Eger 1990). Like the black bear and marten, the Haida short-tailed weasel is believed to be from a coastal glacial refugium that was distinct from the continental refugia that occurred north and south of the ice sheet (Foster 1965). Alternatively, the Haida short-tailed weasel may not be relictual but part of the Holocene dispersal and differentiation that occurred among many subspecies on the continent.

Mitochondrial DNA was extracted from museum skins of short-tailed weasels collected throughout their North American distribution (Byun 1998). Two predictions are considered. If Haida short-tailed weasels are relictual, then three major lineages would be expected to exist in northwestern North America, representing each of the isolated refugial populations. Alternatively, if Haida short-tailed weasels are recent and derived only from the two major refugia, then only two molecular lineages should occur. Although the data are limited by the short fragment length of DNA and small number of specimens, results from the mtDNA are more consistent with the first hypothesis, as they reveal a Beringian and southern lineage as expected but also a unique lineage for Haida short-tailed weasels, indicating that the attributes of the Haida short-tailed weasel are relictual (Figure 5.6). In fact, phylogenetic reconstructions demonstrate that the Haida weasels may constitute the source populations for postglacial recolonization of British Columbia (Byun 1998), rather than weasels from south of the ice front as previously assumed (Kurtén and Anderson 1980).

Saw-whet Owl

Because of the lack of fossil evidence, little is known about the distribution of various owl species during Wisconsin glaciation (Fedduccia 1996). There is no direct information regarding the postglacial source for the saw-whet owl. Given their high dependence on trees for nesting sites, however, they are considered unlikely to have persisted in the tundra regions north of the Cordilleran Ice Sheet and are most likely to have recolonized northern North America from southern refugia. There are two subspecies of saw-whet owl in North America. One subspecies is found on the continent while the other
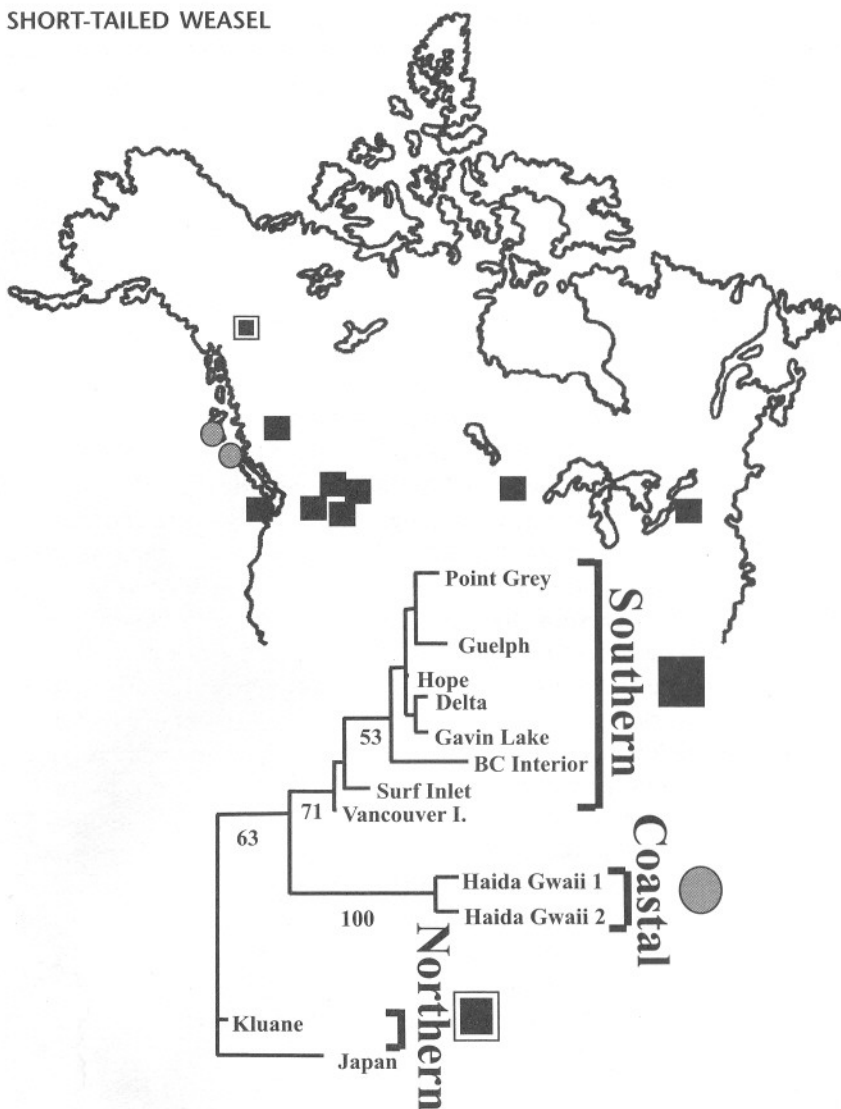
Figure 5.6 Molecular phylogeny of short-tailed weasel and geographical distribution of lineages.

is found in Haida Gwaii. The Haida Gwaii saw-whet owl (*Aegolius acadicus brooksi*) was first described by Fleming in 1916 as a dark, slightly larger race, although Brooks and Swarth (1925) regarded the Haida Gwaii owl to be a distinct insular species. The darker feathers and larger body that characterize the Haida Gwaii owl are typical for insular avifauna (Murphy 1938; Foster 1965) and are considered to have evolved in situ in response to local selective regimes.

Phylogenetic analyses of a 241-base-pair fragment of cytochrome b amplified from DNA isolated from preserved skins indicated little genetic differentiation between the Haida Gwaii saw-whet owl and owls from across Canada.

Ground Beetles

Ground beetles of the *Nebria gregaria* group are distributed in the Pacific Northwest from Haida Gwaii to the Aleutians. Haida Gwaii is inhabited by three species of *Nebria,* one that is restricted to cobble beaches on Graham Island, a second found in similar habitats on Moresby Island, and a third found only in alpine locations on Graham and Moresby Islands and on a mountaintop north of Prince Rupert, BC. These beetles are thought to have survived in ice-free habitats in Haida Gwaii during the Pleistocene, during which their morphological differences developed (Kavanaugh 1992). Their closest relatives occupy beaches on the Alaskan coastline.

There are two lines of evidence that suggest relictual status of these beetles in Haida Gwaii. First, the beetles are flightless and have limited dispersal ability; second, *Nebria* occur across North America and are highly conserved morphologically, suggesting that the differences among Haida Gwaii beetles are unlikely to be of recent origin (Kavanaugh 1992). There are, however, alternate interpretations for the distribution and differentiation of Haida Gwaii *Nebria,* including postglacial colonization and subsequent diversification. The beetles are common on high intertidal and supratidal habitats, including drift logs. Given the abundance of large woody debris in coastal waters and the prevalence of such drift logs in virtually all shorelines in Haida Gwaii (personal observation), it seems plausible that these beetles could have colonized these habitats in this manner. Furthermore, the morphological traits that differentiate the three *Nebria* species in Haida Gwaii are subtle shape differences in the body (Kavanaugh 1992), raising the potential that these represent recent ecological adaptations to the distinctive habitats that the beetles encountered upon colonizing the archipelago.

To differentiate between relictual and recent status, analyses were undertaken (Clarke 1998) of the mtDNA sequence of *Nebria* from Haida Gwaii and from related species on the mainland. One predicts the occurrence of three distinct lineages if the three species are relictual but only a single lineage if the beetles colonized and differentiated postglacially. Results show high genetic similarity among the Haida Gwaii species and suggest that *Nebria* probably colonized the islands and differentiated there during postglacial times (Clarke et al. 2001).

Discussion and Conclusions

Morphological and molecular examination of the major endemic species yields two major results:

1 The morphological features characterizing the endemic forms of highly divergent stickleback, dwarf Dawson caribou, large black bear and marten, dark saw-whet owls, and *Nebria* ground beetles appear to have been derived postglacially. Where more detailed investigations were made on endemics such as the Haida Gwaii stickleback, it is evident that morphological differentiation is not the result of isolation per se but rather due to natural selection and adaptation to the distinct ecological habitats found in the archipelago.

2 Genetic data of a mid-Pleistocene split of vertebrate taxa and geographic distribution of the mitochondrial lineages of stickleback, black bear, marten, and short-tailed weasel cumulatively suggest that a refugium existed on the continental shelf off the central coast of British Columbia. Genetic data are consistent with geological and stratigraphic data demonstrating that the continental shelf separating Haida Gwaii from the mainland contained a large ice-free area during the glacial maximum (Josenhans et al. 1993, 1995; Chapter 1). The assemblage of taxa that might have persisted here during the last glaciation, including top-level carnivores such as bear and marten, suggests that this refugium was ecologically productive and likely an important source area for the postglacial recolonization of northwestern North America. Recent cave discoveries in southern Haida Gwaii show both black bear and brown bear fossil material, with preliminary dates as old as 11,500 BP and 14,000 BP, respectively (Chapter 6). This unambiguous evidence of two bear species in Haida Gwaii during the early Holocene is concordant with our interpretation based on molecular data.

If the coastal refugium was a major source area that influenced the phylogeographic distributions of these endemics, then other species in the Pacific Northwest should have been affected similarly. There are additional data to suggest that this is the case. Molecular studies of brown bear (*Ursus arctos*) show two divergent lineages, one found throughout Europe, Asia, and North America and a second lineage largely restricted to Admiralty, Baranof, and Chicagof Islands in Alaska immediately north of Haida Gwaii (Talbot and Shields 1996). Protein analyses of sockeye salmon have also suggested that three genetic lineages exist in northwestern North America that may correspond to northern, southern, and coastal refugia (Wood et al. 1994).

In addition to these molecular studies, data from other disciplines point to similar conclusions. There are currently eighteen disjunct liverworts, twelve disjunct mosses, and nine vascular plants found only in the Pacific Northwest. In addition, seven disjunct bryophytes in North America are found only in Haida Gwaii. The strong affinity of many of these disjunct bryophytes with bryophytes found in western Europe or southeastern Asia

suggests that they are relics of formerly more widespread species, possibly dating back to the Tertiary Period (over 2.5 million years old). The persistence of these suspected relics and disjuncts in Haida Gwaii is considered evidence for continuity during multiple Pleistocene glacial advances (Calder and Taylor 1968; Ogilvie and Roemer 1984; Schofield 1989). Perhaps even more compelling is evidence of early deglaciation on the east coast of Graham Island near 16,000 BP, followed by rapid recolonization of a plant community. Because of the absence of any known source areas in the region at this time of glacial maximum, it was suggested by Warner et al. (1982) that these plants dispersed from well-established plant communities in a nearby coastal refugium.

There are alternate interpretations of our molecular data. It is possible that the rare mitochondrial lineage detected in the unarmoured stickleback is not relictual but rather a second postglacial colonizing event. This is possible because the rare lineage was detected in samples of stickleback from the mid-Pacific, raising the possibility of recent colonization (Deagle et al. 1996). However, the combination of this lineage in headwater lakes on the northeastern corner of the Argonaut Plain and the highly derived morphology of the fish is suggestive of extended isolation. The presence of divergent mtDNA lineages in Haida Gwaii in black bear, marten, and short-tailed weasel might be solely due to northward dispersal from southern populations (Demboski et al. 1999). If this had occurred, the dispersal would have to have occurred during the early stages of deglaciation, prior to sea level rises. Massive glacial lakes (Lake Missoula and Lake Columbia) (Pielou 1992), high sea levels, and large rivers would have severely impeded northward movement, particularly for small-bodied and uncommon apex predators such as marten and weasel. On the coast, eustatic and isostatic changes resulted in flooding of the Puget Lowland about 11,500 to 13,500 BP (Easterbrook 1992). From about 13,000 BP to 9000 BP, sea levels rose along the eastern shores of Haida Gwaii, isolating Haida Gwaii from the mainland (Josenhans et al. 1995; Chapter 2). These changes were exacerbated by tilting of tectonic plates that effectively increased sea levels along the coastal mainland while decreasing sea levels further west (Chapter 1). Furthermore, the divergent lineages of black bear, marten, and short-tailed weasel in Haida Gwaii suggest that these lineages dispersed from nearby source populations and not from southern refugia over 600 kilometres away (see Byun et al. 1999 for a review of arguments).

The current most plausible interpretation for the high similarity of molecular lineages in Haida Gwaii, Vancouver Island, and coastal British Columbia and major differences from interior continental lineages is persistence of a complex ecosystem on the continental shelf that provided the source populations for the postglacial recolonization of the Pacific

Northwest during the Holocene. Subsequent morphological differentiation among colonists to Haida Gwaii, the coastal mainland, and Vancouver Island probably comprises ecological adaptation to the distinctive selective regimes of each region in the Pacific Northwest.