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A phylogeographic perspective on endemism in the Alexander Archipelago of southeast Alaska

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Abstract

Conservation plans for the North Pacific Coast are beginning to acknowledge that the old-growth forests remaining on the extensive archipelagos of the region may require a new management paradigm. Extensive timber harvesting activities on these islands may impact wildlife populations and be particularly detrimental to the large number of endemics. Because insular biotas have suffered a disproportionate number of documented extinctions worldwide, the documentation of taxonomic validity and spatial distribution of endemics should be a priority for management efforts. To date, few North Pacific coastal endemics have been reevaluated since their original descriptions. This study provides an independent view of endemism in the Alexander Archipelago of southeast Alaska through a phylogeographic assessment of eight species of mammals (*Sorex monticolus*, *Glaucomys sabrinus*, *Microtus longicaudus*, *Clethrionomys rutilus*, *Clethrionomys gapperi*, *Martes americana*, *Mustela erminea*, *Ursus americanus*). The molecular data (mitochondrial sequence variation of the cytochrome b gene) suggest a dynamic history of faunal interchange in the region. While some purported endemics show minimal levels of genetic divergence from other conspecific populations, other taxa appear to be more divergent than recognized by current taxonomy. Some species in the region are comprised of multiple clades or evolutionarily significant units. These reciprocally monophyletic lineages may be the result of multiple Holocene invasions (neoendemics) or they may have persisted in refugia (paleoendemics) in the region during Pleistocene glacial advances. This emerging historical perspective should have direct implications for the management of these endemic taxa.

Keywords: Alexander Archipelago; Endemism; Mammals; Phylogeography; Southeast Alaska

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1. Introduction

The impact of timber harvests in old-growth forests along the North Pacific Coast has been fervently debated, focusing largely on the fate of a few old-growth associated species (e.g. Forsman et al., 1996). Missing from this debate has been recognition that a substantial portion of the temperate old-growth biome occurs across large oceanic archipelagos that support numerous endemics (Heusser, 1989; MacDonald and Cook, 1996; Cook and MacDonald, 2001). An assessment of the taxonomic validity and distribution of these endemics, many thought to be restricted to a few islands, would provide a foundation for understanding the magnitude of human impacts on extinction-prone biotas of these islands. We are using molecular genetic methods to focus on the issue of endemism in one of the larger sets of islands, the Alexander Archipelago of southeast Alaska (Fig. 1).

Southeast Alaska is near the northern extreme of the extensive Pacific Northwest temperate rain forest belt. It includes approximately 16,000 km of coastline and >2000 named islands, including seven of the 10 largest in the United States. During the Pleistocene southeast Alaska was repeatedly covered by glaciers (Mann and Hamilton, 1995), which played an important role in shaping species assemblages and biogeography of the region (Klein, 1965; Heaton et al., 1996; Conroy et al., 1999). This coastal region may have been a crossroads for mammals originating in refugia in Beringia and the mid-latitudes of North America (MacDonald and Cook, 1996). A number of species reach the northern or

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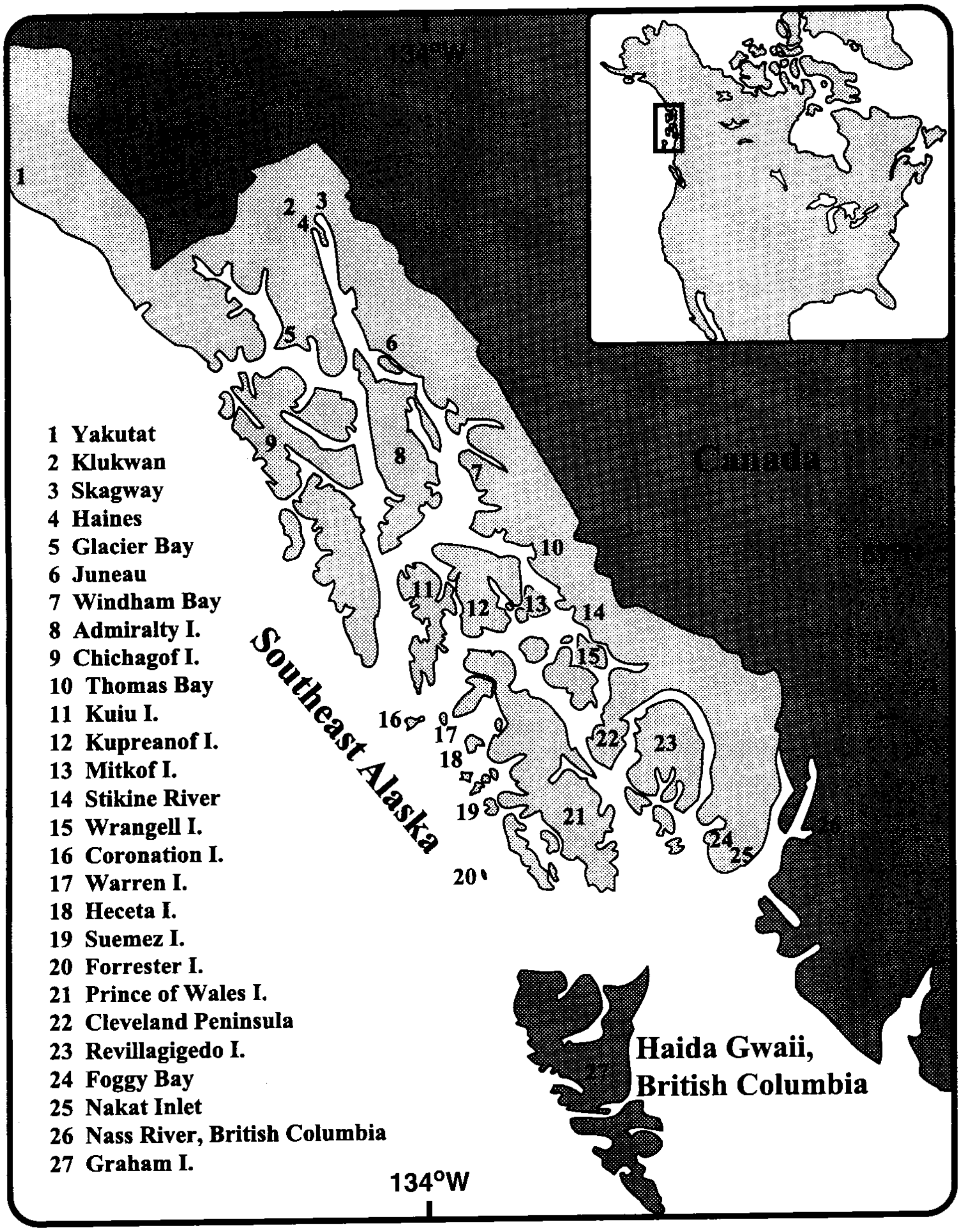


Fig. 1. Map of Southeast Alaska and northern coastal British Columbia showing major islands of the Alexander Archipelago and Haida Gwaii (Queen Charlotte) Islands. Islands and primary localities are noted for specimens examined.

southern limits of their North American distributions in southeast Alaska (MacDonald and Cook, 1996; Parker et al., 1997). Whether or not the region was historically important in the intercontinental movement of northern mammals (including humans) or in the persistence of relict populations during Pleistocene glacial advances remains controversial (Rogers et al., 1991; Heaton et al., 1996; Demboski et al., 1999). These issues, however, do have direct implications for the identification and management of a potentially endemic biota.

Combined with the forests of coastal British Columbia, southeast Alaska includes approximately one-quarter of the world's remaining temperate rainforest (Alaback, 1988, 1991). Extensive timber harvests on private lands and long-term timber contracts on public lands were the subject of public debate that eventually led to management reforms (Tongass Timber Reform Act, 1990). Subsequent controversy over timber practices and their impact on wildlife populations contributed to the long delay of a new 10-year Forest Plan (Durbin, 1999). Previous timber-management policy in southeast Alaska failed to address the relationship between resource extraction and potential impact on unique taxa. Of the 107 mammalian species or subspecies known from the region, 24 are currently considered endemic to southeast Alaska; 12 other taxa are largely confined to the region (MacDonald and Cook, 1996). Federal policy (Tongass Land Management Plan, 1997) now recognizes the insular nature of the biota of the Tongass National Forest, but the question of how to define and manage endemics remains unresolved.

Assessment of genetic relationships provides a basis for testing taxonomic validity and defining geographic distribution of suspected endemic taxa. Many of the original taxonomic descriptions for endemic mammals in this region were the result of morphologic analyses based on relatively small sample sizes (Table 1). For example, the description of *Mustela erminea seclusa*, an endemic subspecies known only from Suemez Island, was based on one specimen (Hall, 1944). With few exceptions (e.g. Allard and Greenbaum, 1988; Hogan et al., 1993; Demboski et al., 1998), the status of these endemics has not been reevaluated. In this paper, we explore aspects of endemism in the Alexander Archipelago and adjacent mainland of southeast Alaska from historical or evolutionary perspectives. We use mitochondrial DNA (mtDNA) sequences from eight species (and 34 subspecies) of mammals to provide a preliminary overview of levels of endemism and historical issues related to the conservation of mammals in southeast Alaska. An appreciation for the biogeographic history of a region can complement existing conservation paradigms and assist in the design of comprehensive management plans (Avise, 1994).

2. Materials and methods

2.1. Specimens examined

Samples (Appendix) resulting from field inventories conducted between 1991 and 1999 are archived in the Alaska Frozen Tissue Collection of the University of Alaska Museum. Additional samples are from the Museum of Southwestern Biology and New Mexico Museum of Natural History. In each case, we chose a subsample that represented the major lineages (previously identified from larger sampling efforts) from southeast Alaska for the phylogeographic analyses. Expanded studies that provide additional sampling details for each taxon are identified in the individual accounts.

1. *Sorex monticolus* — nine *S. monticolus* representing six subspecies (*alascensis, elassodon, longicauda, malitosus, obscurus, setosus*) from nine localities (three island, six mainland) were examined with *Sorex vagrans* (as an outgroup). Representatives were drawn from a larger study ($n = 70$) based on more extensive geographic sampling of the species including specimens from throughout the range of the species in western North America (Demboski and Cook, 2000).

Table 1
List of the mammals endemic to southeast Alaska (Hall, 1981; updated by Nagorsen, 1990, Wilson and Reeder, 1993) including their documented distribution (MacDonald and Cook, 1996), number of specimens of original description (n), and current conservation status based on listing by the International Union for the Conservation of Nature and Natural Resources[a]

Taxon	Distribution	n	Status
Sorex monticolus malitiosus	Warren I., Coronation I.	21	
Sorex alaskanus	Glacier Bay	2	
Marmota caligata vigilis	Glacier Bay	8	DD
Tamiasciurus hudsonicus picatus	Southeast Alaska	36	
Glaucomys sabrinus griseifrons	Prince of Wales I.	2	EN
Castor canadensis phaeus	Admiralty I.	6	DD
Peromyscus keeni hylaeus	Alexander Archipelago, Coastal Mainland	163	
Peromyscus keeni oceanicus	Forrester I.	2	
Peromyscus keeni sitkensis	Baranof I., Chichagof I., Coronation I., Warren I., Duke I.	54	
Clethrionomys rutilus glacialis	Glacier Bay	18	
Clethrionomys gapperi stikinensis	Stikine River Delta, Cleveland Peninsula	29	
Clethrionomys gapperi wrangeli	Wrangell I., Sergief I, Stikine River Delta	31	
Clethrionomys gapperi solus	Revillagigedo I.	13	DD
Microtus pennsylvanicus admiraltiae	Admiralty I.	53	
Microtus oeconomus sitkensis	Baranof I., Chichagof I.	10	DD
Microtus longicaudus coronarius	Coronation I., Warren I., Forrester I.	22	DD
Canis lupus ligoni	Southeast Alaska	27	
Ursus americanus pugnax	Southeast Alaska	9	
Mustela erminea alascensis	Coastal Mainland	24	DD
Mustela erminea initis	Baranof I., Chichagof I.	6	DD
Mustela erminea celenda	Prince of Wales I., Long I., Dall I.	25	DD
Mustela erminea salva	Admiralty I.	26	DD
Mustela erminea seclusa	Suemez I.	1	DD
Mustela vison nesolestes	Alexander Archipelago	3	

[a] None is currently included in the United States Fish and Wildlife Service list of Threatened and Endangered Species; however, several are recognized by IUCN Specialist Groups as needing additional review. Categories of threat are defined by IUCN (1994) and include DD (data deficient) and EN (endangered)

2. *Glaucomys sabrinus* — a total of eight *G. sabrinus* representing three subspecies (*griseifrons, zaphaeus, yukonensis*) was examined from eight localities (five islands and three mainland). *Glaucomys sabrinus fuliginosus* (Washington) was included as an outgroup. These samples were drawn from Demboski et al. (1998) and from analyses of additional sampling ($n=30$) from 22 localities (13 island, nine mainland) in western North America (Bidlack, unpublished).
3. *Microtus longicaudus* — a total of nine *Microtus longicaudus* representing four subspecies (*coronarius, littoralis, macrurus, vellerosus*) was included (three island, six mainland); *Microtus montanus* was included as an outgroup. These representatives were drawn from a study of geographic variation of *Microtus longicaudus* ($n=111$) from the conterminous United States, British Columbia, Yukon Territory, and Alaska including 63 localities (24 island, 39 mainland; Conroy and Cook, 2000).
4. *Clethrionomys rutilus* and *Clethrionomys gapperi* — a sample of *C. rutilus* from Finland and three samples representing two North American subspecies (*dawsoni, glacialis*) from three mainland localities was examined. These were drawn from a larger study of 78 individuals from 11 localities (one island, 10 mainland; Cook et al., ms; Runck, unpublished). A total of six *C. gapperi* representing five subspecies (*cascadensis, phaeus, solus, stikinensis, wrangeli*) and six localities (two island, four mainland) were examined. These representatives were chosen from a sample of 454 individuals from 48 localities (12 island, 26 mainland; Cook, unpublished; Runck, unpublished) extending from North Carolina to the West Coast. *Clethrionomys rufocanus* was included as an outgroup.
5. *Martes americana* — a total of eight samples representing four subspecies (*actuosa, caurina, kenaiensis, nesophila*) and six localities (three island, three mainland) was examined. *Martes martes* was included as an outgroup. These were drawn from a larger study ($n=680$) of geographic variation in marten representing 28 localities (14 island, 14 mainland) across the species range in North America (Stone, 2000).
6. *Mustela erminea* — a total of nine *Mustela erminea* representing seven subspecies (*alascensis, arctica, celenda, initis, richardsonii, salva, seclusa*) from four islands and five mainland sites was examined; *Mustela putorius* was included as an outgroup. These samples were taken from a study of 210 individuals representing 45 localities (13 island, 32 mainland) across the species range in western and central North America (Fleming and Cook, 2000).
7. *Ursus americanus* — a total of eight *U. americanus* representing three subspecies (*altifrontalis, americanus, pugnax*) and seven localities (three island, four mainland) was examined; *Ursus thibetanus* was included as an outgroup. These samples were drawn from a study of geographic variation in black bears ($n=74$) that represented 18 localities (five island, 13 mainland) across the species range in western North America (Stone and Cook, 2000).

2.2. DNA extraction, amplification, and sequencing

Genomic DNA was extracted from frozen tissue using a sodium chloride extraction protocol modified from Miller et al. (1988). Double-stranded polymerase chain reaction (PCR) usually entailed 35 cycles [94°C (10 s), annealing at 45–50°C (15 s), extension at 72°C (45 s)]. Amplification of cytochrome b, cycle sequencing, and automated sequencing analyses followed standard protocols (Lessa and Cook, 1998). All PCR experiments included negative controls. Complete or partial sequences of cytochrome b were obtained from 15 taxa endemic to southeast Alaska and another 19 subspecies not endemic to the region.

2.3. Sequence and phylogenetic analysis

Sequences were examined, assembled based on overlapping regions, and aligned using Sequence Navigator (Applied Biosystems, Inc., version 1.01). Nucleotide composition, numbers of variable sites, and divergence estimates (uncorrected *P*) between lineages were obtained using PAUP* (Swofford, 1999). Equal-weighted parsimony trees (not shown) and neighbor-joining trees using Kimura (1980) two-parameter distances were constructed using PAUP*. Bootstrap replicates (500) assessed the strength of suggested relationships.

3. Results

All sequences exhibited patterns of nucleotide compositional bias common to mammalian cytochrome b sequences (e.g. Irwin et al., 1991; Ma et al., 1993). Observed substitutions were not evenly distributed across sites, but were most abundant in third positions and least numerous in second positions of codons. These biases are expected for PCR amplifications of genuine, functional sequences of the mtDNA cytochrome b gene. For each species, genetic divergence among lineages (reciprocally monophyletic clades) was characterized as either shallow ($<0.5\%$ uncorrected $P\times100$) or deep ($>2\%$). Distinct clades were identified as coastal, continental, or Beringian. Coastal clades had distributions restricted to Pacific coastal islands, adjacent coasts, or western North America. Clades with broad inland distributions spanning the majority of a species range across North America, were termed continental, although the entire continental range has not been sampled in all cases. Beringian clades were those restricted largely to extreme northwestern North America and into Far East Russia.

1. *S. monticolus* — dusky shrews in southeast Alaska were represented by two deeply divergent clades (coastal and continental) within southeast Alaska (Fig. 2A) that differed by approximately 4.6–5.3%. The coastal lineage was represented by southeast Alaska island and mainland populations and also included an individual from the Cascade Range in Washington. The continental clade included two northern southeast Alaska mainland populations (Haines and Yakutat) and an interior Alaska (Fairbanks) individual. These patterns of divergence are not reflected in currently recognized subspecific taxonomy for southeast Alaska (Alexander, 1996). Contact between these clades may occur in the Lynn Canal region.
2. *G. sabrinus* — two shallow lineages were identified within southeast Alaska (Fig. 2B). All individuals sampled on Prince of Wales, Barrier, Kosciusko, Dall, Suemez, Heceta, Orr, Tuxekan and El Capitan islands (POW complex) shared two basepairs that are distinctive from other flying squirrels examined in southeast and interior Alaska (Demboski et al., 1998). These diagnostic mutations, although minor, were consistent with the designation of the subspecies *Glaucomys sabrinus griseifrons* (Howell, 1934).
3. *Microtus longicaudus* — two deep lineages occurred within southeast Alaska. One (coastal) was found primarily on the Alexander Archipelago, extreme northern mainland of the region and extended into the southern corner of interior Alaska. The continental lineage was restricted in southeast Alaska to the mainland south of Haines (Fig. 2C) and extended into the central region of interior Alaska. These ranges do not correspond to the original subspecies descriptions for the region *(Microtus longicaudus coronarius* and *Microtus longicaudus littoralis*). Samples from the type localities for both of these subspecies (Coronation Island and Prince of Wales Island) were within the coastal clade. The coastal lineage was found beyond the three islands originally described for *Microtus longicaudus coronarius* (Hall, 1981; Conroy, 1998; Conroy and Cook, 2000).

   These clades represent a significant amount of intraspecific divergence for this species (2.1–2.4%). These lineages have been found in sympatry near Haines.
4. *C. rutilus* and *C. gapperi* — *C. rutilus* from southeast Alaska exhibited minimal levels of intraspecific genetic divergence relative to conspecific populations adjacent to southeast Alaska (Fig. 2D). Conversely, populations of *C. gapperi* exhibited higher levels of intraspecific divergence in southeast Alaska and this may be indicative of an earlier colonization of the region. Patterns of divergence were consistent with subspecific designations for *C. gapperi;* however, levels of divergence were low. Some specimens identified morphologically as *C. gapperi* in the zone of contact had cytochrome b haplotypes characteristic of *C. rutilus*, a situation

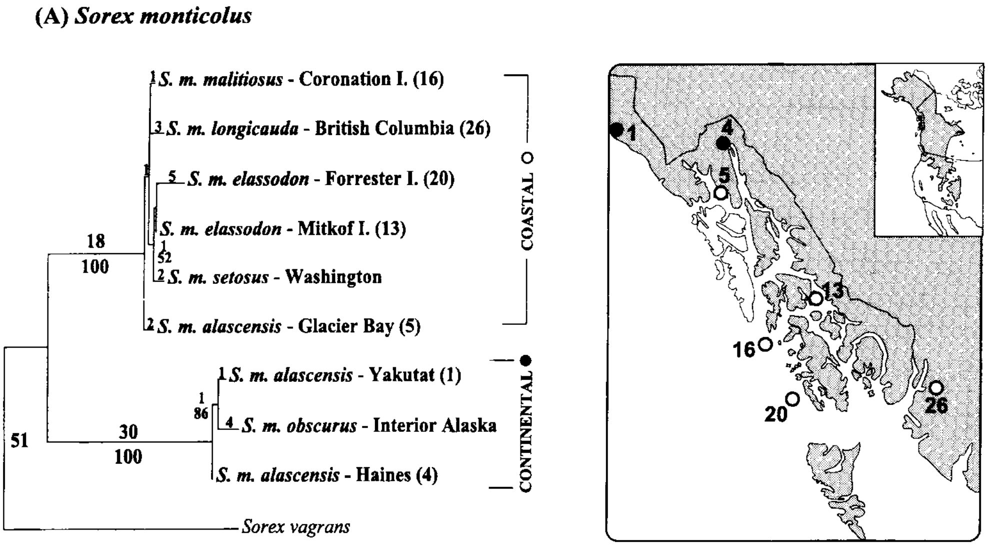
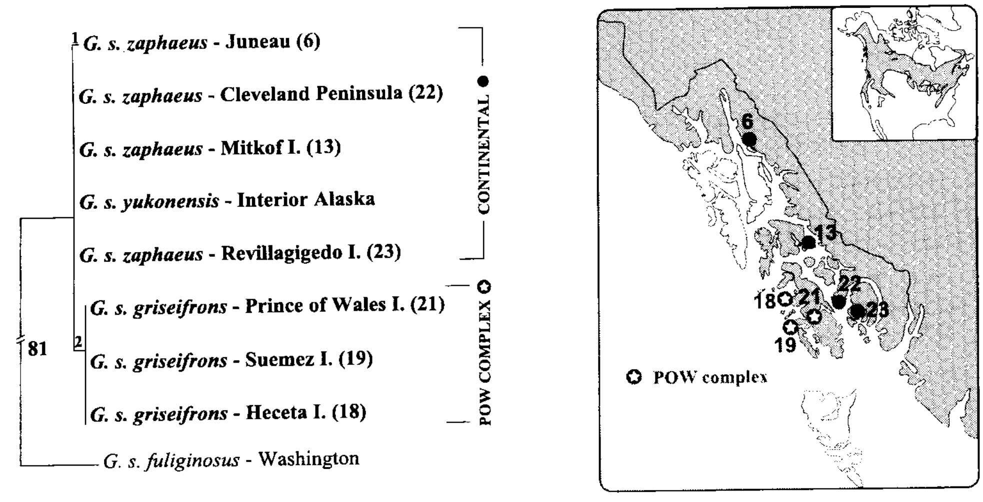
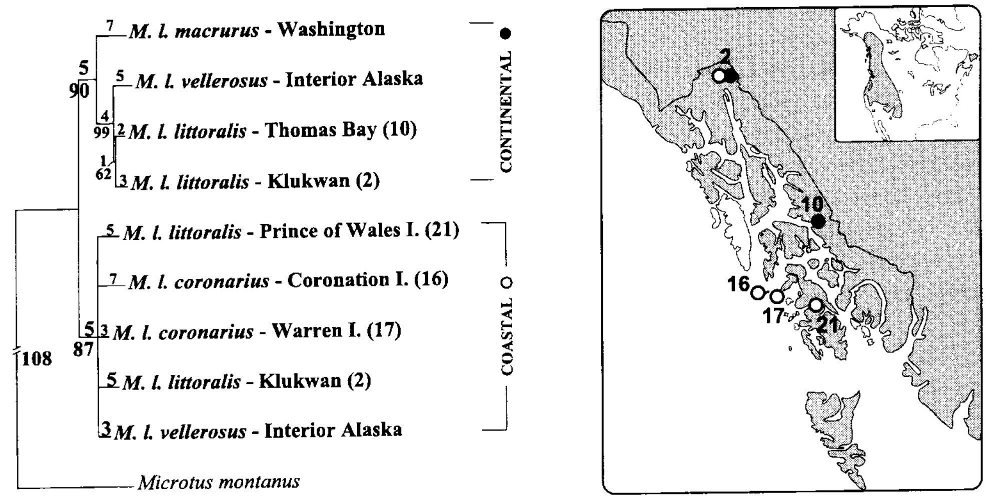

(A) *Sorex monticolus*

Fig. 2. Shaded map of southeast Alaska showing distribution of continental (solid circles) and coastal (white circles) lineages next to neighbor-joining trees for; (A) *Sorex monticolus*; (B) *Glaucomys sabrinus*; (C) *Microtus longicaudus*; (D) *Clethrionomys gapperi* and *C. rutilus*; (E) *Martes americana*; (F) *Mustela erminea*, and (G) *Ursus americanus*. For *Mustela erminea*, a third lineage (Beringian) exists in southeast Alaska. Numbers on the maps (and in parentheses on the trees) refer to the numbered localities in Fig. 1.

(B) *Glaucomys sabrinus*



(C) *Microtus longicaudus*



(D) *Clethrionomys*

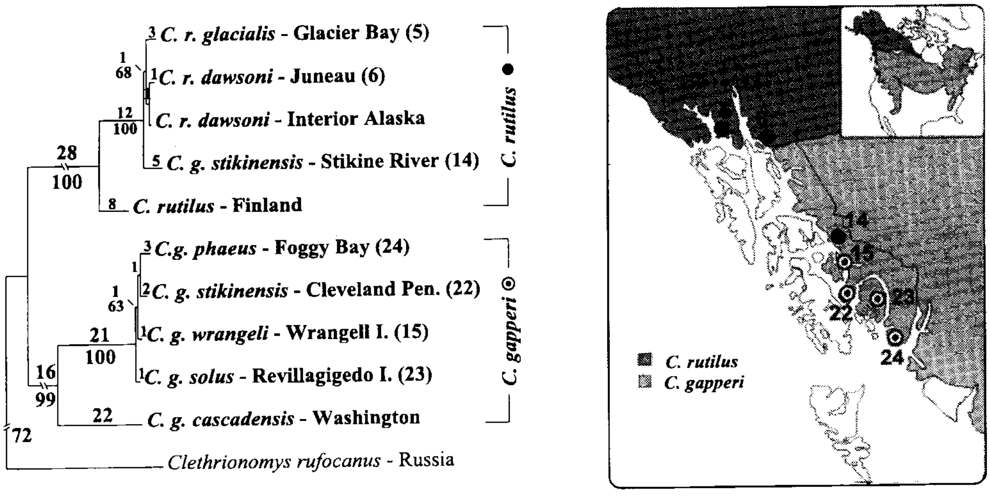
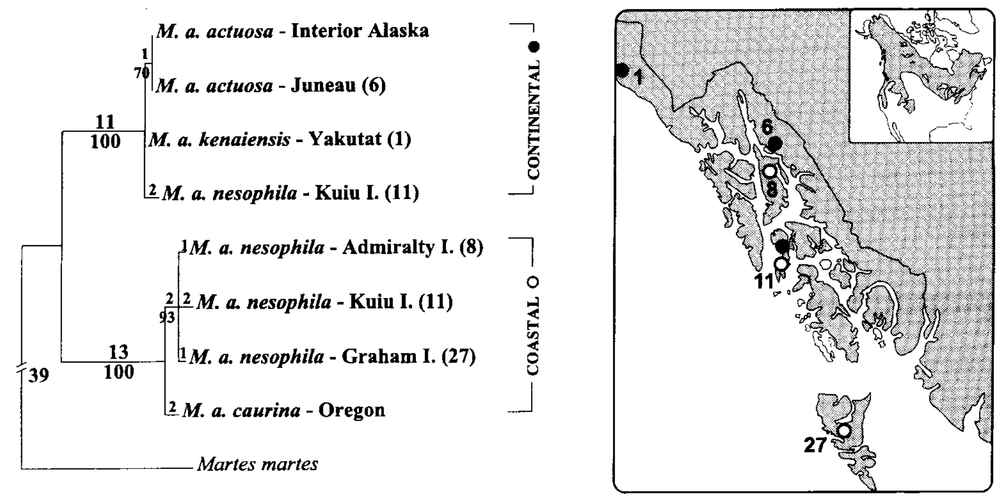
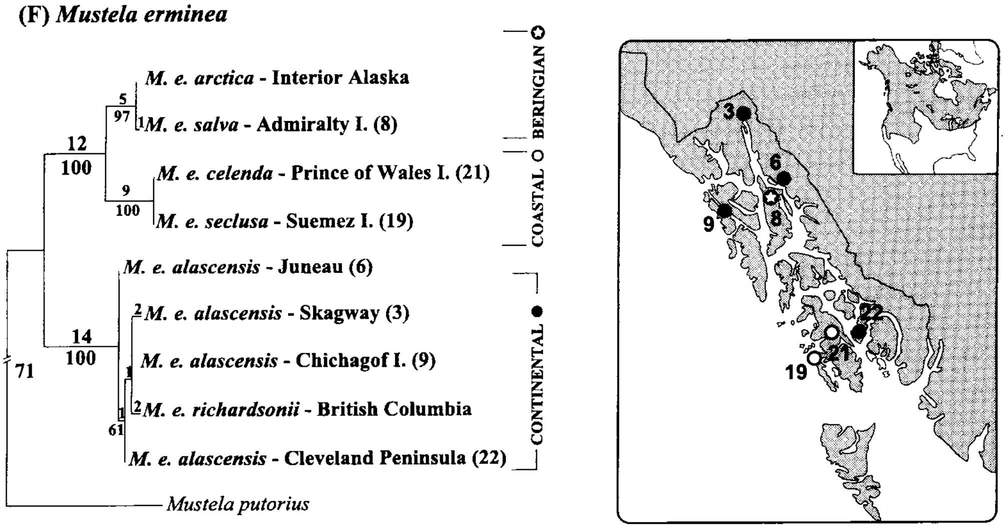


Fig. 2. *(continued)*

(E) ***Martes americana***



(F) ***Mustela erminea***



(G) ***Ursus americanus***

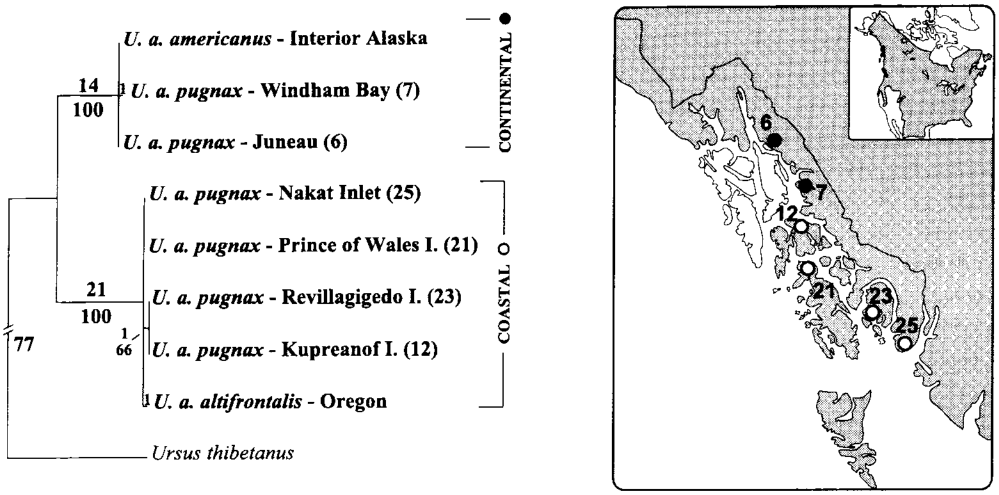


Fig. 2. (*continued*)

previously identified in contact zones between other species of *Clethrionomys* (e.g. Tegelström, 1987).

5. *Martes americana* — two deep lineages, corresponding to the 'caurina' (coastal) and 'americana' (continental) subspecies groups of North America, have been identified in southeast Alaska (Fig. 2E). One subspecies *(Martes americana nesophila;* 'caurina' subspecies group) has been described for most of the area, while *Martes americana kenaiensis* ('americana' subspecies group) was thought to be limited to the northwestern region of southeast Alaska. Contrary to the current taxonomic framework (Hall, 1981), our molecular data indicates that the 'caurina' (coastal) lineage occurs on only two islands in southeast Alaska, whereas the 'americana' (continental) lineage is more widespread. The coastal lineage is found further south on Haida Gwaii (Queen Charlotte Islands) and Vancouver islands of British Columbia and along the Pacific Coast to northern California. The continental lineage is distributed throughout the mainland and islands of southeast Alaska (with the exception of Admiralty Island), northward to central Alaska and eastward to the Atlantic Coast (Stone, 2000). Inter-lineage divergence was approximately 2.7–2.8%.
6. *Mustela erminea* — four island and one mainland subspecies have been described for southeast Alaska (Hall, 1944). The molecular data identified three deep lineages in the region (Fig. 2F). A continental lineage was found on Chichagof and Baranof Islands (subspecies *Mustela erminea initis)*, several nearshore islands (i.e. Mitkof, Wrangell, Etolin, and Revillagigedo islands), the southeast Alaska mainland from Skagway to Hyder (subspecies *Mustela erminea alascensis)*, and south and east into British Columbia, Alberta, and the contiguous United States to at least Wisconsin and New Mexico. The Beringian lineage occurred on Admiralty Island (subspecies *Mustela erminea salva)* in southeast Alaska and further north in interior Alaska (e.g. Fairbanks), southcentral (e.g. Anchorage) Alaska, and Far East Russia (Fleming and Cook, 2001). A coastal lineage was found on Prince of Wales Island (subspecies *Mustela erminea celenda)* and Suemez Island (subspecies *Mustela erminea seclusa)*. The continental clade was approximately 3.0–3.8% divergent from the other two, while the Beringian and coastal lineages were about 1.5% divergent from one another.
7. *U. americanus* — a single subspecies was thought to exist in southeast Alaska (*Ursus americanus pugnax*; Hall, 1981); however, two deep lineages (coastal and continental) were found (Fig. 2G). The coastal lineage was distributed throughout the southern half of southeast Alaska (including southern islands such as Kupreanof, Prince of Wales and Revillagigedo) southward along the Pacific Coast. The continental lineage extended through the northern half of the southeast Alaska mainland into interior Alaska, southward to Oregon and eastward to the Atlantic Coast (Wooding and Ward, 1997; Stone and Cook, 2000). Inter-lineage variation ranged between 3.4 and 3.5% suggesting a deep divergence within black bear.

Five of eight species have deep divergences with four *(S. monticolus, Microtus longicaudus, Martes americana, Ursus americanus)* comprised of two clades, coastal and continental, and one *(Mustela erminea)* showing a third, Beringian, clade. The other three species *(C. rutilus, C. gapperi, G. sabrinus)* show no or only minimal levels of divergence. A plot of divergence values between lineages within each species (Fig. 3) indicates very low levels of differentiation between the southeast Alaska lineages of *G. sabrinus* relative to levels of divergence found within the other taxa with multiple lineages in the region.

Does the existing taxonomic framework, which identifies several endemic organisms, provide an adequate foundation for conservation efforts in the region? Our intention is not to provide a detailed review of the taxonomy of particular species, but rather to provide a preliminary view of phylogeographic variation for several co-occurring mammals that have been reported as endemic to southeast Alaska. By comparing the individual patterns for several species, we can begin to examine general processes that may be responsible for shaping and maintaining diversity (e.g., Moritz and Bermingham, 1998). This presents an opportunity to identify distinctive conservation management units within complex landscapes (Avise, 1996). We begin by examining the generality of phylogeographic patterns.

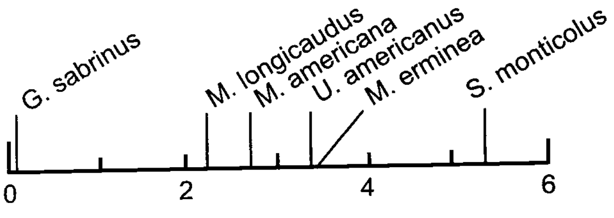


Fig. 3. Uncorrected *P* distance values (average *P* × 100) for major phylogeographic split between coastal and continental lineages based on sequence variation in the mitochondrial cytochrome b gene. The divergence between the *Glaucomys sabrinus griseifrons* populations on the Prince of Wales Island complex and all other southeast Alaska populations was included to show the low level of divergence that characterizes neoendemics in the region. Similarly, low divergence values were found (but not shown) for insular populations of *Clethrionomys gapperi* when compared to mainland populations.

3.1. Phylogeographic patterns

Genetic relationships within these eight taxa suggest two common themes for the post-Pleistocene colonization history of southeast Alaska: single lineages (or evolutionarily significant units; Moritz, 1994), or multiple lineages with distinct origins. The geographic source for these distinctive lineages (i.e. the location of refugial populations during full glacial advances) may have been Beringia (northern), North Pacific Coastal (relictual), or at least two distinct southern refugia at mid-latitudes (west coastal or eastern). Based on the fossil record from the late-Pleistocene, we suspect that some of these colonizers originated from Beringia (e.g. *C. rutilus),* while others may have colonized from the distinctive southern refugia (e.g. two lineages of *U. americanus).*

4. Discussion

4.1. Single lineages

C. rutilus exhibits minimal levels of genetic divergence when compared to conspecific populations outside of southeast Alaska, perhaps reflecting recent colonization (late Holocene) of southeast Alaska. Similarly, Demboski (1999) found minor divergence across southeast Alaskan populations of *Sorex cinereus* in his assessment of mitochondrial DNA variation. We hypothesize that these species entered the region through colonization routes that opened following the retreat of glacial barriers in trans-mountain corridors (e.g. Taku River). These would be the most recent colonizers of the region and none would be identified as endemic. Similarly, most of the 'continental lineages' identified by mitochondrial sequences also show close affinities to populations east of the Coast Range, suggesting they are recent arrivals.

Other Holocene colonizers may have arrived earlier from the south along a coastal route and these have begun to differentiate since their arrival (neoendemics). Low, but consistent, levels of genetic divergence indicates that this in situ divergence is post-glacial. Thus, nominal endemic subspecies may accurately reflect these minimal levels of differentiation (e.g. *G. s. griseifrons;* Demboski et al., 1998). Forest-dependent species, in particular, probably did not colonize the region until coastal coniferous forests were established between about 7500 and 12,000 years before present (BP; Ager, 1983; Heusser, 1985; Fedje and Josenhans, 2000). Subspecific differentiation in *C. gapperi* may be included in this suite of neoendemics based on the low, but diagnostic, levels of genetic differentiation that characterize the four subspecies in southeast Alaska. In contrast, other described endemic subspecies (e.g. *U. a. pugnax)* appear suspect based on mtDNA, suggesting the need for a closer look at the original distinguishing characters, the development of additional markers, and wider sampling throughout the region.

4.2. Multiple lineages

S. monticolus, Microtus longicaudus, Martes americana, Mustela erminea, and *U. americanus* are represented by more than one reciprocally monophyletic lineage in southeast Alaska. A similar finding was reported for *Ursus arctos* (Talbot and Shields, 1996). Strikingly, the intraspecific comparisons of lineages within *S. monticolus* reveal levels of divergence higher than those documented for interspecific comparisons among congeners (Demboski, 1999). In this case, the existing taxonomic framework may severely underestimate diversity (i.e. some nominal species actually may comprise multiple species) and management efforts based on this shaky foundation may lead to loss of diversity (Daugherty et al., 1990). Within such species, the independent lineages apparently originated or were maintained in separate ice-free refugia during full-glacial maxima. Elevated levels of intraspecific differentiation for several lineages (Fig. 3) suggest the possibility that the origin of these predates the Pleistocene, as suspected for some passerine birds (Klicka and Zink, 1997). It would be premature, however, to use a molecular clock approach across these taxa given our limited knowledge of issues such as fluctuations in effective population size, ancestral polymorphism, and other species-specific characteristics (Ayala, 1999). Furthermore, most of these taxa lack a fossil record sufficient to calibrate divergence estimates.

Do some of these divergent lineages represent paleoendemics (i.e. did they persist as relictuals in the region during full glacial advances)? *S. monticolus, Microtus longicaudus, U. arctos, U americanus,* and *Martes americana* show levels of differentiation that may be greater than recognized by the existing taxonomy. Three distinctive lineages of *Mustela erminea* occur in the region including one endemic, but our sampling of this organism is limited along much of the North Pacific Coast. Divergent lineages within these species may indicate the possibility of persistent refugia along the Pacific Northwest coast (Heusser, 1989; Rogers et al., 1991; O'Reilly et al., 1993; Heaton et al., 1996; Byun et al., 1997); however, the location of potential refugia remains speculative. Extensive geographic sampling and use of independent genetic markers are needed to clarify this issue (Demboski et al., 1999).

High faunal turnover indicated by the fossil record (e.g. Heaton and Grady, 1991, 1993; Heaton et al., 1996), combined with the emerging history of Late Quaternary glaciation (e.g. Mann and Hamilton, 1995; Barrie and Conway, 1999) and high levels of intraspecific genetic differentiation, point to a dynamic zoogeographic history for the region. This history is consistent with the hypothesis that most extant coastal and continental lineages are post-Pleistocene colonizers of the region. Several mammals present prior to the last glacial maximum (ca. 18,000 BP) no longer occur in southeast Alaska, including *Lemmus trimucronatus, Rangifer tarandus,* and *Alopex lagopus.* Other species (e.g. *Marmota caligata, U. arctos,* and *U. americanus)* were present before and after this time, but have not been documented during its maximal advance (13,000–20,000 BP; Heaton et al., 1996). Assessments of nested structure of extant species on the Alexander Archipelago also were consistent with this dynamic history (Conroy et al., 1999) because colonization ability, rather than extinction, apparently has shaped patterns of species richness in the region for mammals.

4.3. *Taxonomy versus phylogeography*

In several cases (e.g. *G. s. griseifrons*; Demboski et al., 1998), the original subspecies descriptions (based on morphological characters) were corroborated and the geographic range better defined by the genetic perspective. The relationship between taxonomy and genetic divergence for other endemic subspecies or species is less clear (Fig. 2). For example, two subspecies of *Microtus longicaudus* (*coronanius* and *littoralis*) were described from the Alexander Archipelago, yet only a single distinctive mitochondrial lineage (island clade) was found there. For *Mustela erminea,* five subspecies were described as endemic to the region, yet three lineages were identified and only one of these was endemic to Southeast Alaska. In contrast, several subspecies of other species (e.g. *U. a. pugnax*) were found to include multiple lineages. These results suggest the need for careful revisions. Morphological and molecular studies still rely on relatively small sample sizes, particularly considering the complex landscape. The high divergence estimates for some lineages (Fig. 3) probably predate the last glacial advance (and perhaps most of the Pleistocene), indicating that the mitochondrial signal has been preserved through the repeated retraction, advance, and probable contact of these lineages. This pattern of deep divergence extends across several species and appears to be the result of common historical processes. Within a few species (e.g. *Microtus longicaudus*), the distinctive lineages overlap minimally and the dynamics of these limited contact zones should be investigated with independent markers.

4.4. *Implications for conservation and management*

Island faunas have elevated rates of extinction that are often linked to habitat conversion or the introduction of exotics (Diamond, 1989). The highest concentration of North Pacific Coastal endemics is found along the coasts of British Columbia and southeast Alaska (Cook and MacDonald, 2001). Our results indicate that some of these taxa may be valid and spatially restricted to a few islands (endemic), while the validity of other taxa is questionable. Continued assessment of the geographic extent of these endemic lineages is needed, in combination with taxonomic revisions based on concordance across a suite of characters (Grady and Quattro, 1999).

These emerging historical perspectives have direct implications for the management of endemics. When the mapped lineages for each species are compared, we find that some species share geographic discontinuities in southeast Alaska among lineages (*S. monticolus, Microtus longicaudus, Martes americana, U. americanus*). Coincident phylogeographic breaks suggest a common history of colonization of the North Pacific Coast and these areas should be a significant consideration for management and conservation (Avise, 1994; Moritz and Faith, 1998). At a minimum, distinctive regions should be managed independently given that they support reciprocally monophyletic lineages and thus, distinctive regional biotas.

5. Summary and future prospects

These mitochondrial data, in combination with the late Pleistocene fossil record and history of glaciation, suggest a dynamic history of faunal interchange along the North Pacific Coast. While some purported endemics show minimal levels of genetic divergence, other morphologically cryptic populations are more divergent than recognized by current taxonomy. In the region, species may be represented by multiple lineages due to Holocene invasions or persistence in coastal refugia (relictuals) during glacial advances (Demboski et al., 1999). In addition, we find a repeated pattern of coastal and continental clades in co-distributed taxa.

This preliminary view of genetic variation in selected mammals should be expanded in several critical ways. First, divergence estimates are based on a single mitochondrial marker and need to be further evaluated with larger sample sizes and tested with independent markers such as those rapidly being developed for the nuclear genome. Various problems have been identified in past attempts to use a single molecular marker to characterize the biogeographic history of organisms. In particular, the use of only maternally inherited mtDNA has been criticized (e.g. Paetkau et al., 1998). Additional work should aim to test these results by developing perspectives based on nuclear loci for each of these taxa.

Second, the generality of coincident patterns should be thoroughly explored in other co-distributed taxa. For example, Soltis et al. (1997) found significant phylogeographic breaks in plants of the Pacific Northwest although their sampling did not coincide with ours.

Third, the relationship between the divergence of molecular markers and the divergence of populations (our key interest here) is unclear. Ancestral polymorphism and fluctuating effective populations, among other factors, may impact estimates of temporal divergence. Similarly, comparisons of divergence values among species and estimates of confidence intervals may be affected by these parameters or others (e.g. differing mutation rates).

Conservation strategies should be based on a solid evolutionary foundation such as that provided by phylogeography. Although federal laws mandate the conservation of diversity, the existing taxonomic framework for this complex archipelago may not adequately describe the evolutionarily significant units within the region. Surprisingly high levels of genetic divergence within several Pacific Northwest species and the repeated coastal/continental pattern of differentiation indicate the need for a new paradigm for management, particularly given the large-scale habitat modification that the region has experienced. Further testing of the generality of these phylogeographic patterns provides an opportunity to build this framework.

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Appendix

Voucher specimens are deposited in the Alaska Frozen Tissue Collection, University of Alaska Museum (AFTC or UAM) or Museum of Southwestern Biology Frozen Biological Materials Collection (NK). All DNA sequences have been deposited in GenBank (AF or U accession number). *Sorex monticolus* (n = 9): Alaska: interior — AFTC5929 (AF154539); Yakutat — AFTC6396 (AF23 8008); Haines — AFTC4588 (AF23 8009); Glacier Bay — AFTC5217 (AF23 7997); Mitkof I. — AFTC2498 (AF154541); Coronation I. — AFTC5205 (AF237996); Forrester I. — AFTC16733 (AF238000); British Columbia: AFTC12687 (AF238005); Washington: AFTC14460 (AF154545); *Sorex vagrans:* AFTC2463 (AF154551); *Glaucomys sabrinus* (n=9): Alaska: interior — AFTC14089 (AF030394); Juneau — AFTC27332 (AF271668); Mitkof I. — AFTC14100 (AF030394); Heceta I. — AFTC16874 (AF271672); Suemez I. — AFTC26426 (AF271671); Prince of Wales I. — AFTC26326 (AF271670); Cleveland Peninsula — AFTC25176 (AF271669); Revillagigedo I. — AFTC27093 (AF271673); Washington: AFTC5451 (AF030389); *Microtus longicaudus* (n = 9): Alaska: interior — AFTC 15867 (AF187189), UAM3553 (AF187216); Klukwan — AFTC8034 (AF187202), AFTC8038 (AF187217); Thomas Bay — AFTC5270 (AF187201); Coronation I. — AFTC4485 (AF187213); Warren I. — AFTC8347 (AF187214); Prince of Wales I. — AFTC4503 (AF187207); Washington: NK3135 (AF187180); *Microtus montanus:* NK55041 (AF119280); *Clethrionomys rutilus* (n = 4): Alaska: interior — AFTC4853 (AF119274); Glacier Bay — AFTC6486 (AF272631); Juneau — AFTC7052 (AF272632); Finland: AFTC3 130 (AF272638); *Clethrionomys gapperi* (n=6): Alaska: Stikine River — AFTC2644 (AF272637); Wrangell I. — AFTC2780 (AF272636); Cleveland Peninsula — AFTC26033 (AF272634); Revillagigedo I. — AFTC4995 (AF272635); Foggy Bay — AFTC4267 (AF272633); Washington: NK3221 (AF272639); *Clethrionomys rufocanus:* Russia: AFTC 15469 (AF272640); *Martes americana* (n=8): Alaska: interior — AFTC53 (AF154964); Yakutat — AFTC10769 (AF268272); Juneau — AFTC14952 (AF154965); Admiralty I. — AFTC14470 (AF154968); Kuiu I. — AFTC17541 (AF268273), AFTC17533 (AF268274); British Columbia: Graham I. — AFTC20601 (AF154969); Oregon: AFTC15936 (AF154972); *Martes martes*: AFTC17559 (AF154975); *Mustela erminea* (n=9): Alaska: interior — AFTC17863 (AF271060); Skagway — AFTC8750 (AF271067); Juneau — AFTC14967 (AF271063); Admiralty I. — AFTC24060 (AF271061); Chichagof I. — AFTC24063 (AF271064); Suemez I. — AFTC26441 (AF271068); Prince of Wales I. — AFTC17789 (AF271062); Cleveland Peninsula — AFTC25049 (AF271066); British Columbia: AFTC 16024 (AF271065); *Mustela putorius:* (AF057128); *Ursus americanus* (n=8): Alaska: interior — AFTC895 (AF268258); Juneau — AFTC1458I (AF268262); Windham Bay — AFTC14582 (AF268261); Kupreanof I. — AFTC1 8535 (AF268267); Prince of Wales I. — AFTC14078 (AF268264); Revillagigedo I — AFTC20101 (AF268266); Nakat Inlet — AFTC24096 (AF268263); Oregon: AFTC21 119 (AF268270); *Ursus thibetanus:* (U23558).

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