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Review

Conservation of highly fragmented systems: The north temperate Alexander Archipelago

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ABSTRACT

The Alexander Archipelago of Southeast Alaska encompasses over 2000 named islands that extend along 600 km of the North Pacific Coast. This review summarizes recent research on mammals of this largely unexplored region. Field inventories followed by preliminary molecular genetic analyses of selected mammals demonstrate substantial spatial structure consistent with both the dynamic geologic history of this boreal region and the highly insular landscape. New views of taxonomic diversity, biogeographic history, and contemporary population connectivity lay a framework for managing and conserving this complex biome. First, repeated Pleistocene glacial advances along the coast fragmented species, leaving clear genetic signatures and a strongly diversified fauna. Organisms recolonized the coast following deglaciation from multiple northern (Beringia), southern (West Coast and Continental) or North Pacific Coastal refugia. Several species are composed of multiple, genetically distinctive lineages (in some cases, incipient or new species) due to independent colonization histories from distinct, divergent source populations. Second, the insular landscape of the Alexander Archipelago has produced highly endemic populations. These centers of endemism should be thoughtfully managed as hotspots of lineage diversity. Until a better understanding of connectivity among these divergent populations is developed, each island should be considered an independent biological unit. Finally, industrial logging, mining, human encroachment, tourism, wildlife consumption, and invasive species should be stringently monitored and regulated with respect to impact on island endemics and ecosystems. A new conservation paradigm for the Tongass National Forest should be developed that is built around the recognition of the complexity of this incomparable island archipelago of the North Pacific. In particular, recognition of high diversity and endemism should be central to management plans.

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“No excursion that I know of may be made into any other American wilderness where so marvelous an abundance of noble, newborn scenery is so charmingly brought to view as on the trip through the Alexander Archipelago... so numerous are the islands that they seem to be sown broadcast.” John Muir, 1915

1. Introduction

Investigations of island systems around the world, such as the Galapagos, have provided key insights to fundamental questions in evolution, ecology and conservation. Of the 50 top “hotspots for biodiversity” defined by Conservation International, 70% are on islands. Islands are experiencing some of the highest rates of change in the world, but many island systems do not have proper management strategies, and have fallen victim to problems related to anthropogenic disturbance. Those impacts have led to massive loss of organisms, species extinctions, and disruption of ecosystems (Vitousek et al., 1995; Quammen, 1996). Unfortunately, our baseline understanding of what, where, and why with regard to biotic diversity in many archipelagos remains rudimentary, crippling our ability to assess and respond to perturbations. Knowledge of the relatively few island systems that have been thoroughly investigated has provided key insights in evolution and ecology, including fine-tuning our ability to predict the consequences of perturbations elsewhere.

Intensive studies of island systems also demonstrate that insular faunas are typically distinctive (endemic) and that

Table 1 – Lineage diversity (reciprocally monophyletic clades) has been assessed for 15 Southeast Alaska mammals based on mtDNA and nucDNA variation

Species	mtDNA *n*	# mtDNA lineages SE Alaska	nucDNA *n*	# nucDNA Lineages SE Alaska	References
Black bear	74	2	289	2	Byun et al. (1997), Stone and Cook (2000), Peacock (2004)
Brown bear	317	2	261	1	Talbot and Shields (1996), Paetkau et al. (1998), Barnes et al. (2002)
Wolf	325	1 (E[a])	221	1	Weckworth et al. (2005); unpublished manuscript
Wolverine	159	1 (E)	–	–	Tomasik and Cook (2005)
American marten	462	1	301	1	Small et al. (2003), Stone and Cook (2002), Stone et al. (2002)
Coastal marten	218	2 (2E)	112	2 (2E)	Small et al. (2003), Stone and Cook (2000), Stone et al. (2002)
Ermine	210	3 (1E)	–	–	Fleming and Cook (2002)
Northern flying squirrel	118	2 (1E)	233	2	Demboski et al. (1998), Bidlack and Cook (2001), Bidlack and Cook (2002)
Keen’s mouse	257	2	–	–	Lucid and Cook (2004)
Tundra vole	214	1	63	1	Galbreath and Cook (2004)
Long-tailed vole	111	2	–	–	Conroy and Cook (2000)
Southern red-backed vole	449	1	15	1	Runck (2001), Runck and Cook (2005)
Northern red-backed vole	38	1	8	1	Runck (2001), Cook et al. (2004)
Montane shrew	70	2	–	–	Demboski and Cook (2001)
Cinereus shrew	46	1	–	–	Demboski and Cook (2003)

Sample sizes are reported for each species for the two classes (mitochondrial and nuclear) of molecular studies. E represents a reciprocally monophyletic lineage.

endemics are highly susceptible to extirpation and eventually extinction. Insular endemics are prone to extinction (Reid and Miller, 1989; Burkey, 1995) because they are vulnerable to habitat loss and fragmentation, introduction of exotics, and over exploitation (harvesting). Worldwide, more than 60% of documented vertebrate extinctions have occurred on islands (Diamond, 1989; Olson, 1989; Case et al., 1992; Steadman, 1995).

Fragmentation characterizes the expansive archipelagos of the North Pacific coastal landscape of North America. These systems pose significant challenges for natural resource management because of their complexity, but the challenges have scarcely been articulated, and rarely incorporated into management plans. Recent investigations point to a complex set of factors that drive species richness (Conroy et al., 1999), distribution (MacDonald and Cook, 1996),

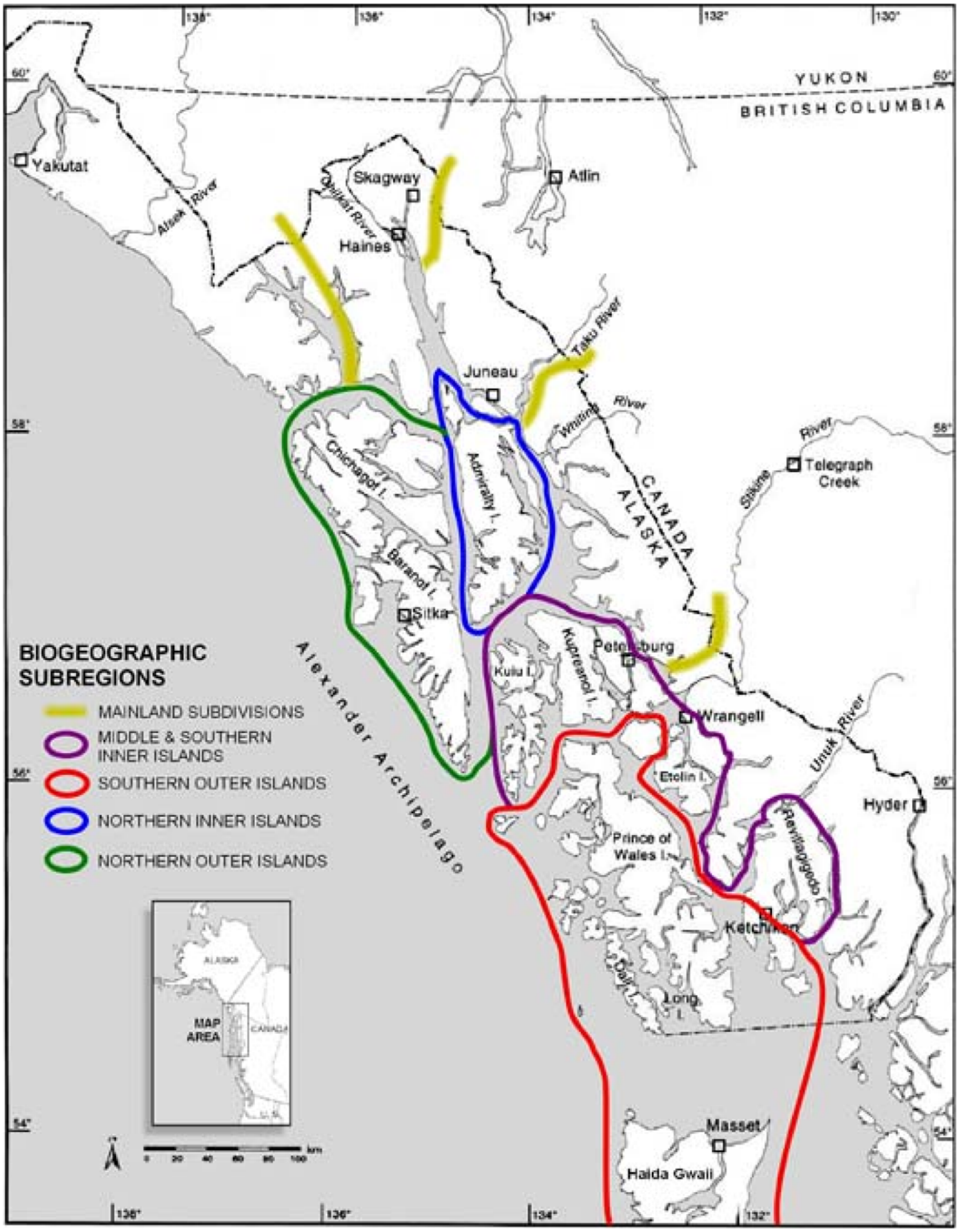

Fig. 1 – Southeast Alaska encompasses distinctive and isolated mammalian subregions along the North Pacific Coast of North America. Proposed biogeographic subregions are modified slightly from MacDonald and Cook (1996) on the basis of recent molecular phylogeographic studies that show close genetic relationships between some mammals on the Prince of Wales Island complex and the Queen Charlotte Islands (Bidlack and Cook, 2001; Fleming and Cook, 2002).

endemism (Cook and MacDonald, 2001; Cook et al., 2001), historical biogeography (Weckworth et al., 2005) and contemporary connectivity (Small et al., 2003) on these North Pacific islands. These factors will need to be addressed if these ecosystems, and associated high primary productivity and biomass (Alaback, 1995), are to remain intact and healthy.

Basic research efforts focused on mammals over the past 15 years have resulted in a series of publications (Table 1) that provide a preliminary view of diversity along the North Pacific Coast. We primarily restrict our focus to the coastal region along the panhandle of Alaska, a region that encompasses the Alexander Archipelago (Fig. 1); however, there are a number of parallels that can be drawn with other North Pacific archipelagos, especially the nearby Haida Gwaii islands of British Columbia. The Alexander Archipelago is one of the largest temperate archipelagos worldwide with more than 2000 named islands (including 4 of the 10 largest islands in the US). We call attention to unique challenges associated with managing biotic diversity on the archipelago and highlight the urgency of incorporating an "island" perspective into resource plans for the region.

Little attention has been paid to impending threats to the endemic fauna of archipelagos of the North Pacific Coast (Nagorsen, 2004), primarily because limited documentation has been available on the status of insular species (Cook and MacDonald, 2001). The few studies published on island organisms along the coast of nearby British Columbia (Nagorsen, 1994; Shank, 1999) have documented extinctions (*Rangifer tarandus dawsoni* last seen on Haida Gwaii in 1908) or endangerment (Vancouver Island marmot, *Marmota vancouverensis*, 20 adult individuals in 2000) of insular populations and species (COSEWIC, 2005). In general, however, management plans for public lands in British Columbia (Paquet et al., 2004) and Southeast Alaska (e.g., Tongass Land Management Plan, 1997) still have not sufficiently addressed the "island" issue.

In this review, we summarize the major points emerging from field inventories and molecular (phylogeographic) studies of a variety of mammals across the Alexander Archipelago. We then raise issues related to effective management of this north temperate island system in an effort to stimulate discussion (and action) related to current and future disturbances.

2. Mammalian research

2.1. Field inventories

Small mammals were sampled on over 100 islands and at numerous sites along the mainland of Southeast Alaska using standardized inventory methods (MacDonald and Cook, 1996, unpublished manuscript; Cook et al., 2005) each July and August between 1991 and 1999. These materials represent geographically extensive and site intensive collections. Each mammal was assigned a GPS locality, unique field identifier, and all tissues, parasites, and other subsamples were linked to the original voucher specimen (skeletal preparations, as whole bodied spirit-preserved or as dried study skins). Inventory crews preserved tissues (heart, liver, kidney, spleen, and lung), and embryos in liquid nitrogen. State and federal agency personnel and private individuals provided large series of specimens, especially material from larger game or furbearer species. Three species, the fisher (*Martes pennanti*), cougar (*Puma concolor*), and heather vole (*Phenacomys intermedius*), were documented as new to Alaska during that time (MacDonald and Cook, 1996; MacDonald et al., 2004). All materials were archived at the University of Alaska Museum of the North in Fairbanks and are available for further analyses (http://arctos.database.museum).

2.2. Phylogeographic analyses

Molecular genetic investigations of mammals were conducted on selected species in our laboratories or elsewhere. Those investigations focused on species that vary considerably in body size, life history traits, ecology, and evolutionary history, but used comparable sampling design and similar molecular markers (Table 1). A mitochondrial gene (usually cytochrome *b*) was sequenced for all. In several cases, nuclear genes were examined to test the validity of the mitochondrial perspective. Herein, we summarize the common themes related to conservation that have emerged across those analyses.

Morphological analyses provided the taxonomic framework that guided our molecular studies across the Alexander Archipelago. Subsequent molecular analyses refined our knowledge of how to manage the archipelago based on two key concepts in island conservation: endemism and connectivity. First, we discuss the historical assembly of the mammal fauna of the Alexander Archipelago; a history based on differential invasion of the region through multiple colonization corridors (Fig. 2) during the Quaternary and divergent evolution leading to endemism within the archipelago. Second, we address contemporary issues facing the biota of the archipelago based on this underlying dynamic history, and the heavy human imprint now evident throughout the system.

2.3. Deeper history: development of a regional fauna

Within North America, Southeast Alaska was recognized as a distinctive biogeographic unit over 100 years ago when Nelson (1887) coined the term "Sitkan District." Subsequent investigators (Swarth, 1911, 1936) followed this lead. These early explorers provided a baseline for understanding biotic diversity in the region, which is largely isolated from the remainder of continental North America by the coastal mountains. That physiographic barrier, transected by relatively few large rivers, apparently played a large role in structuring diversity.

The geologic history of the North Pacific Coast has been dynamic and principally dominated over the past two million years by large-scale climatic oscillations (Mann and Hamilton, 1995). During the Pleistocene, Southeast Alaska repeatedly was covered by glaciers (Mann and Hamilton, 1995; Carrara et al., 2003), and glacial dynamics shaped species assemblages (Klein, 1965; Heaton et al., 1996; Conroy et al., 1999). The massive Cordilleran Ice Sheet blanketed most of the region until about 12,000 years ago when ice retreated eastward into the Coast Range (Mann, 1986; Mann and

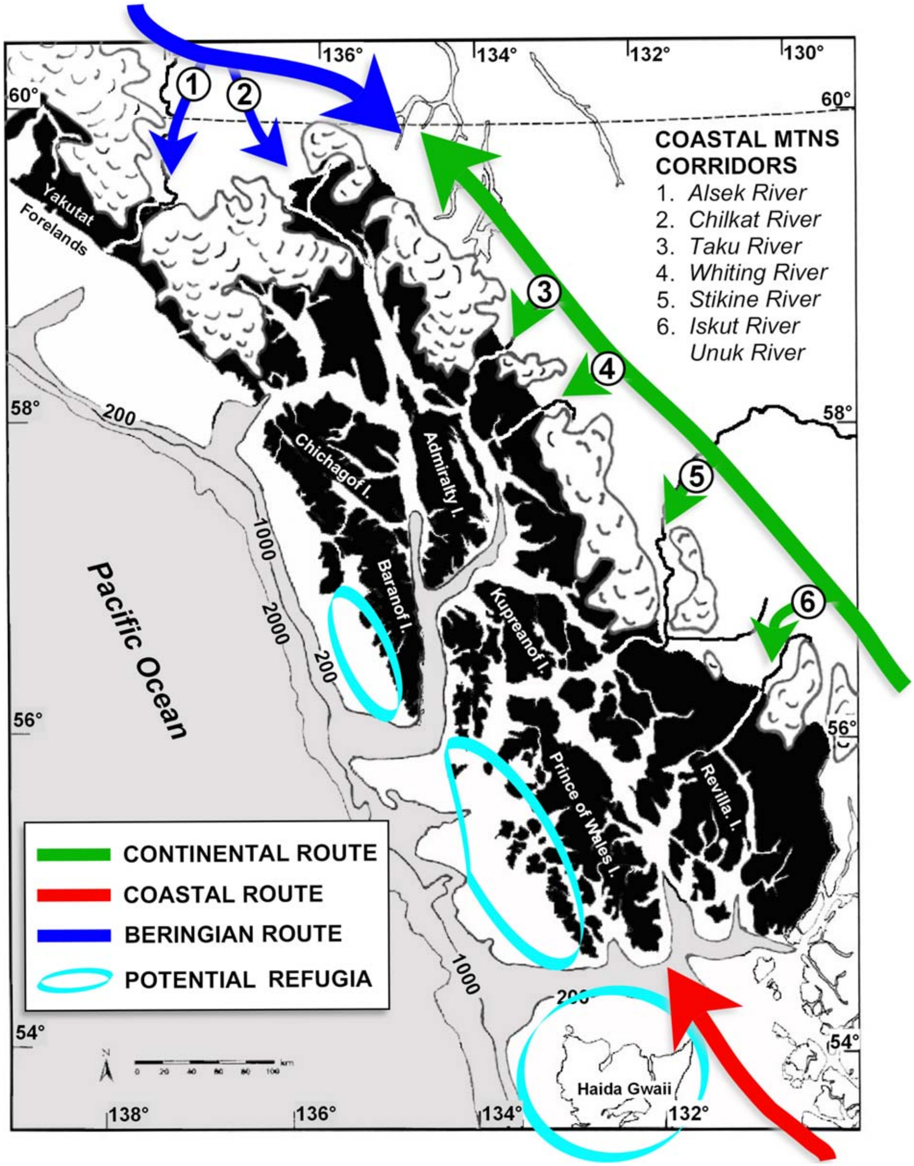

Fig. 2 – Map indicating the possible recolonization routes into Southeast Alaska following deglaciation of the Late Wisconsin advance (based on phylogeographic studies in Table 1). Locations of possible refugia are based on presence of paleoendemic lineages (e.g., Fleming and Cook, 2002) or glacial ice (Carrara et al., 2003).

Hamilton, 1995). Because this essentially created a “ *tabula rasa*” situation, most extant species have recolonized the region during the Holocene. It may appear, then, that the Holocene sets the temporal stage for interpreting evolutionary change, endemism and the development of ecological communities within the terrestrial biota of Southeast Alaska. Molecular genetic studies and a growing fossil record suggest, however, that evolutionary changes also have accumulated and persisted over a series of glacial advances and retreats, thus producing a much deeper time frame for development of a divergent and highly endemic fauna.

Molecular studies of Southeast Alaska mammals generally fall into two broad categories (Cook et al., 2001) based on whether a particular “species” is represented in the region by a single deep (i.e., reciprocally monophyletic) lineage or by multiple deep lineages (Table 1). A single lineage plausibly indicates that this species colonized coastal Southeast Alaska from a single source, while species with multiple lineages originated from multiple locations.

2.3.1. *Single lineage species*

A suite of species (Table 1) apparently recolonized or expanded (Lessa et al., 2003) into the region from a single refugium, originating from the north (i.e., the Beringian Refugium with species such as wolverine *Gulo gulo*, northern red-backed vole *Myodes rutilus*, tundra vole *Microtus oeconomus*, arctic ground squirrel *Spermophilus parryii*), the south (i.e., southern coastal refugium; cinereus shrew *Sorex cinereus*, Keen’s mouse *Peromyscus keeni*, wolf *Canis lupus*) or the east (i.e., southern continental refugium; northern flying squirrel *Glaucomys sabrinus*, moose *Alces alces*, southern red-backed vole *Myodes gapperi*).

2.3.2. *Multiple lineage species*

Other species are represented in the region by more than one lineage (Table 1). These presumably reflect multiple episodes of independent colonization that originated from multiple source populations or refugia. Those lineages, in some cases, are evolutionarily significant units (Moritz, 1994) or incipient species that likely began to diverge in distinct refugia located outside of this glaciated region before recolonizing. In several cases, the depth of genetic divergence between the lineages suggest that they began diverging in the mid-Pleistocene and have accumulated differences through repeated cycles of glacial advance (and presumably repeated recolonizations). Most of these species (marten *Martes americana*, montane shrew *Sorex monticolus*, long-tailed vole *Microtus longicaudus*, black bear *Ursus americanus*) are represented by lineages from southern coastal (termed Coastal) and southern continental (Continental) refugia. Following deglaciation, these "multiple lineage" species moved into the region along more than one route with individuals representing each of the distinctive lineages recolonizing Southeast Alaska independently. Brown bear (*Ursus arctos*) and ermine (*Mustela erminea*) also have multiple distinctive lineages, but they are special cases as each has a very old lineage (paleoendemic) that apparently is now restricted only to this region of the North Pacific Coast.

2.3.3. *Endemics or tabula not so "rasula"*

Brown bear and ermine are considered paleoendemics because these distinctive lineages likely arose in situ and have not spread, or at least persisted, elsewhere. The hypothesis that a North Pacific Coastal refugium (or series of refugia) existed has been supported in the last decade (Heaton et al., 1996; Fleming and Cook, 2002). A series of papers focused on the fauna and flora of the Haida Gwaii (Queen Charlotte Islands) also have supported the Coastal Refugium hypothesis (e.g., Byun et al., 1999; Burg et al., 2005; but see Demboski et al., 1999). The existence of refugia along the coast has significant implications for a "coastal route" of exchange of organisms (including humans) between Far East Asia and the lower latitudes of western North America (Rogers et al., 1991; Dalton, 2005). New fossil discoveries (Heaton and Grady, 2003) and distinctive molecular genetic signatures that are endemic to the region (e.g., ermine; Fleming and Cook, 2002) are consistent with the Coastal Refugium hypothesis. These paleoendemics push our temporal perspective of the diversification of this fauna much deeper than the Holocene (*contra* Klein, 1965) and suggest that glaciation did not wipe the slate clean for all species.

Summaries of species richness and endemism based on taxonomy concluded that the North Pacific Coast is one of the regions of highest taxonomic endemism for mammals in North America (Cook and MacDonald, 2001). For example, traditionally four island and one mainland subspecies of ermine were described as endemic to Southeast Alaska. Variation among DNA sequences of ermine from across North America and Eurasia partitioned into three distinct lineages of ermine worldwide. All three occur in Southeast Alaska (Fig. 3), but they do not strictly correspond to the previously described endemic subspecies. One lineage has a very limited distribution along the North Pacific Coast and is found only on the Prince of Wales Island (POW) complex in Southeast Alaska (two subspecies) and nearby Haida Gwaii (another subspecies). The federal government of Canada has listed the Queen Charlotte ermine (*M.e. haidarum*; a member of this endemic island lineage) as threatened (COSEWIC, 2005), but there is no legal protection for this taxon in the United States. The restricted distribution of this lineage and its level of divergence from others suggest that these island populations may be derived from relicts that persisted in a refugium on the North Pacific Coast during the Wisconsin Glaciation. Further work is needed to carefully reconcile the differences between the subspecies classifications, based on morphologic studies, and the distinctive genetic lineages uncovered by DNA studies. The Prince of Wales complex of islands supports a large number of other endemic vertebrates including divergent forms of Keen's mouse, northern flying squirrel (Bidlack and Cook, 2002), spruce grouse (*Falcipennis canadensis isleibi*; Dickerman and Gustafson, 1996), and chum salmon (*Oncorhynchus keta*; Kondzela et al., 1994). This complex also hosts highly disjunct populations of subalpine fir (*Abies lasiocarpa*; Carrara et al., 2003).

About 23% of the 107 mammalian species or subspecies known from Southeast Alaska are endemic to the region (MacDonald and Cook, 1996). Molecular analyses are providing an opportunity to assess the depth of divergence, spatial extent, and taxonomic validity of these endemics, thereby building a foundation for understanding impacts, such as deforestation, on insular forms. Because endemism is highly likely in classes of organisms other than mammals, there is an elevated potential for extinction or extirpation of a variety of plants and animals. Hence, molecular studies now limited principally to mammals should be expanded to other taxa.

2.3.4. *Differential arrival in the region*

Progressive eastward retreat of ice during the Holocene is mirrored in the molecular genetic structure of the colonizing lineages. Recolonization routes northward along the Pacific Coast (presumably including areas of continental shelf now submerged) would have been available earlier than routes that crossed the Coast Range. Corridors from the east apparently were obstructed by the relatively late recession of the Cordilleran Ice Sheet in the Coast Range (Small et al., 2003). Coastal access into the region from the northwest remains largely blocked by tidewater glaciers to this day. Hence, representatives of coastal lineages apparently arrived in the region much earlier than the continental lineages. Coastal lineages consistently show deeper divergence when compared with nearby continental populations and coastal lineages typically are found on islands. In contrast, continental lineages are minimally diverged, appear to have recently colonized the region (likely through one of the large river corridors or mountain passes that transect the Coast Range), and generally are found along the mainland and a few nearshore islands (e.g., continental lineage of *Martes americana*). Wolverine, tundra voles, northern red-backed voles, and the Beringian lineage of ermine colonized from the north and generally show very low levels of diversification likely reflecting their late arrival into the region. Klein (1965) and Darimont et al. (2005) indicated that moose entered Southeast Alaska and coastal British Columbia within the last 100 years. Southeast Alaska populations may be

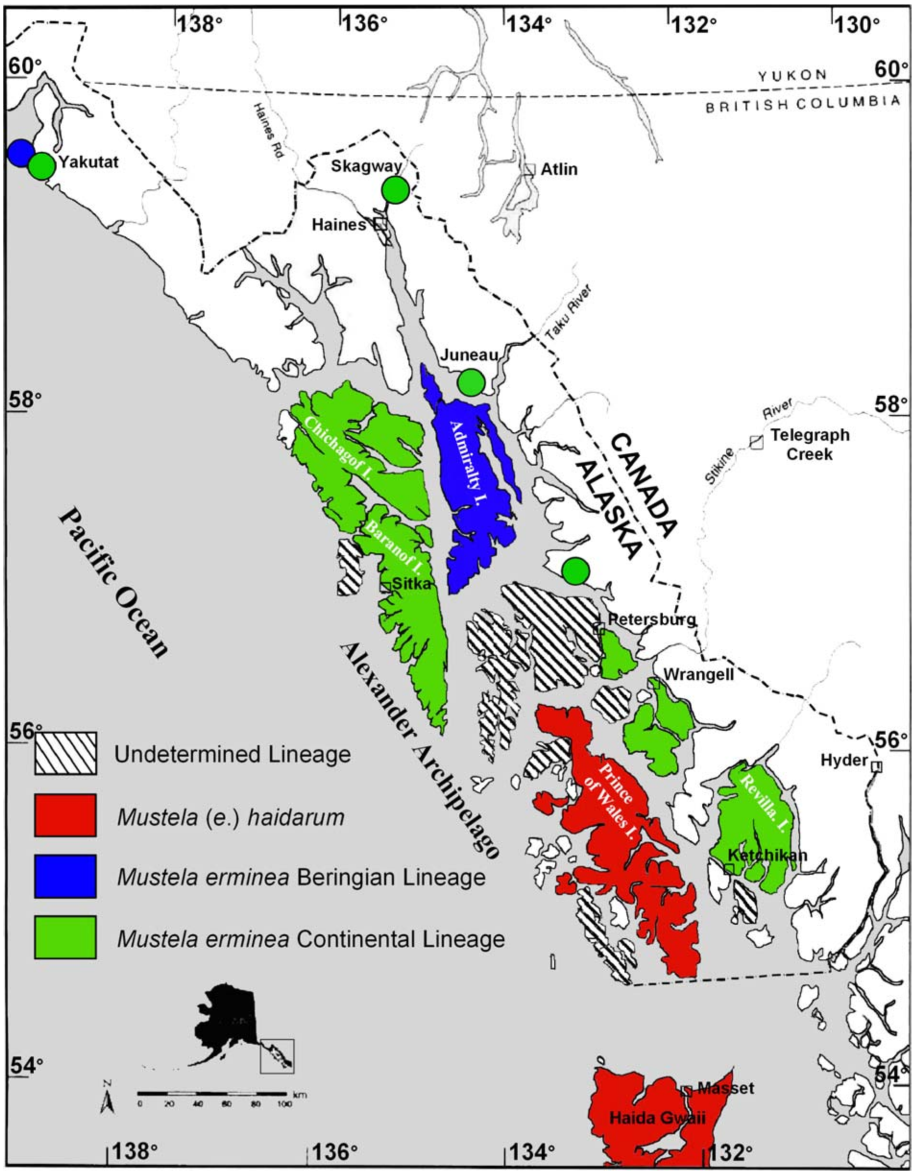

Fig. 3 – Three ermine clades are known worldwide and all three occur in Southeast Alaska. One lineage is endemic to only the POW island complex and the nearby Haida Gwaii islands of British Columbia (Fleming and Cook, 2002; Dawson unpublished data). Undetermined island records are those ermine specimens that have not been sequenced, so their lineage identity has not been determined yet. The mainland distribution is poorly documented, so only sites where lineages have been identified are shown.

the result of two immigrations, one from populations in nearby British Columbia and the other from northerly (Beringian) sources (Hundertmark et al., in press).

2.3.5. *Post-Pleistocene contact*

In several instances, distinctive lineages have come into secondary contact (contact zones) in Southeast Alaska (black bears, Peacock, 2004 and Stone and Cook, 2000; red-backed voles, Runck and Cook, 2005; marten, Small et al., 2003). Careful analysis of the dynamics of these zones has not been completed but may provide insight into the processes of diversification, reinforcement, and ultimately speciation. For example, we suspect that the two lineages of marten found in Southeast Alaska actually represent two distinct species, *Martes americana* and *M. caurina*, as previously proposed by Merriam (1890) based on morphological differences. If so, *M. caurina* has an extremely limited distribution in Southeast Alaska (Kuiu and Admiralty islands) and globally (northern California to Admiralty Island). Genetic analysis of marten shows deep phylogeographic subdivision that likely reflects incipient speciation. Using a suite of microsatellite markers and sequences of the mitochondrial cytochrome *b* gene, Stone and collaborators (Stone and Cook, 2000; Stone et al., 2002; Small et al., 2003) confirmed significant genetic divergence between *caurina* and *americana*. Hybridization between *caurina* and *americana* individuals was documented in two regions of sympatry (Kuiu Island in Southeast Alaska and southern Montana).

In summary, a number of species along the North Pacific Coast are comprised of multiple distinctive lineages that likely reflect a history of multiple colonization events from diverse geographic sources. In some cases, populations that we previously considered to represent a single species (e.g. montane shrew, Demboski and Cook, 2001) are instead composites of two species with very distinctive evolutionary histories. Both species should be recognized. In addition, populations of other species (although represented by a single lineage in Southeast Alaska) may be distinct from populations outside the region. Weckworth et al. (2005, submitted) documented unique genetic diversity in coastal wolves and concluded that these populations had colonized early in the Holocene from the south (southern source populations have since been extirpated) and subsequently were isolated from other North American populations. Limited dispersal eastward into interior British Columbia may be occurring, but there is no indication of gene flow into Southeast Alaska at this time. Knowledge of these historic routes of colonization may provide a framework for future restoration of some populations and species.

2.4. *Contemporary perspective: islands influence local diversity*

Elevated levels of intraspecific diversity due to the dynamic colonization history of the region described above are now heavily influenced or structured by the contemporary insular landscape. Some managers in Southeast Alaska have asked: Do we need to consider the special attributes that are associated with an "island lifestyle" given that the archipelago is likely less than 10,000 years old? The inventory of insular mammals stimulated a series of analyses aimed at addressing this question; analyses that were initiated at scales ranging from ecological communities down to molecular variability within populations.

2.4.1. *Island communities*

Consistent with classic island biogeography theory (MacArthur and Wilson, 1967), size and distance from the mainland have played a prominent role in shaping diversity across the Alexander Archipelago (Table 2). Larger islands (e.g., Revillagigedo) close to the mainland have higher species richness, while small distant islands (e.g., Forrester) have lower species richness (MacDonald and Cook, 1996). Conroy et al. (1999) used species lists for each island to explore factors responsible for community assembly of mammals across the archipelago. They demonstrated that mammalian communities on smaller islands were nested within communities on larger islands. Conroy et al. (1999) concluded that, across all species, colonization ability (not extinction probability) has been the most important determinant of current community composition on islands. That study, however, was unable to consider the hidden diversity (i.e., multiple lineages) that has since been documented for a number of these species. Reanalysis based on a more accurate depiction of richness uncovered by the molecular genetic studies (unpublished manuscript) indicates that lineages that are endemic to islands are not nested; those older forms instead appear to be structured by extinction processes.

Despite the overall nested pattern found in the archipelago (Conroy et al., 1999), species assemblages vary spatially (i.e., from island to island) and temporally (Heaton and Grady, 2003). For example, *M. longicaudus* is widespread among islands throughout the archipelago, while other species of *Microtus* have very limited distributions (e.g., *Microtus pennsylvanicus* on Admiralty Island). Historically, brown and black bears coexisted on Prince of Wales Island, but in the last 10,000 years brown bears have ceased to occupy this island (Heaton and Grady, 2003). Now, black bears occupy islands south of Frederick Sound, while brown bears occur on northern islands and the two species are sympatric only on the mainland.

2.4.2. *Linkages among islands*

Attempting to manage 2000 independent islands is an overwhelming task, but this complex landscape should not be managed as a single continuous unit. Substructure within the archipelago may exist, allowing the identification of groups of islands that are tightly connected (now or in the past, >10,000 ybp when sea levels were lower). MacDonald and Cook (1996) refined earlier attempts (e.g., Swarth, 1936) to simplify this complexity by proposing five biogeographic subregions based on the presence of endemics and unique combinations of native species. These subregions are bounded by significant biogeographic barriers and generally parallel Swarth's original review of the region (1911, 1936). We have attempted to refine these subregions using molecular phylogeography (Fig. 1). The challenge is to delineate areas with high levels of connectivity as these could form the basis for management units grounded in biology. Molecular studies

Table 2 – Island size and mammalian species richness varies across major islands of the Alexander Archipelago (MacDonald and Cook, 1996, unpublished data)

Island	Area (km^2)	Species richness
Prince of Wales	6675	15
Chichagof	5388	11
Admiralty	4362	14
Baranof	4064	10
Revillagigedo	2965	24
Kupreanof	2813	19
Kuiu	1962	16
Etolin	870	17
Dall	655	12
Wrangell	560	24
Mitkof	546	22
Zarembo	478	11
Kosciusko	437	12
Kruzof	435	7
Annette	392	7
Heceta	181	10
Sukkwan	167	8
Suemez	153	10
Duke	149	6
Long	115	9
Baker	115	3
Noyes	97	3
San Fernando	89	5
Lulu	78	3

are well suited to testing the significance of these barriers and validity of subregions. Indeed our very preliminary studies have revealed common genetic signatures (or linkages) across island groups for a variety of taxa. The endemic Prince of Wales flying squirrel, for example, has diverged from mainland squirrels (Demboski et al., 1998; Bidlack and Cook, 2001), but little to no differentiation was found among island populations within the Prince of Wales Complex (e.g., Prince of Wales and islands to the west like Heceta, Suemez, Dall). Such a pattern suggests high historic or contemporary levels of connectivity among these islands. Other species that share this close connectivity across the POW islands include Keen's mouse (Lucid and Cook, 2004) and ermine (Fleming and Cook, 2002).

A number of factors should be assessed with regard to connectivity. The role of purported linkages in facilitating gene exchange has varied considerably through time, so signals of contemporary and historic gene flow must be teased apart. Differences in life history characteristics among species and between sexes within a species also should be recognized when assessing probability of movement among islands (e.g., Paetkau et al., 1998). Large carnivores and herbivores are more vagile and likely moving among islands much more often (populations are more highly connected) than smaller mammals such as shrews and mice. Preliminary molecular perspectives (Table 1) are consistent with this trend. Differential connectivity across these groups provides a more precise view of the severity of particular barriers. With regard to assessing barriers throughout the archipelago, nearly ubiquitous species such as Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) or Keen's mouse are good candidates for identifying levels of connectivity across the entire archipelago, but species with more limited distributions are also informative. A solid understanding of the relative timing of arrival into the region is also essential to interpreting connectivity for particular species. That is, wolverine or moose might be capable of dispersing to all islands in the archipelago, but because of their relatively recent arrival in the region they are still limited primarily to the mainland and nearshore islands (Tomasik and Cook, 2005; Hundertmark et al., in press) or islands tightly linked to the mainland such as Mitkof, Kupreanof and Kuiu.

Furthermore, faunal exchange among islands may not be symmetrical, with some islands acting as source populations while others act as sink populations. Kuiu Island has one of the highest black bear densities worldwide (e.g., 1.5 bear/km^2) and a larger number of migrants per generation move from Kuiu to Kupreanof Island than vice versa (Peacock, 2004). Unequal rates of immigration illustrate the distinctive microevolutionary dynamics that populations in close proximity, but on different islands, may be experiencing. In addition, Peacock (2004) noted little exchange between Kuiu and Prince of Wales islands, with each appearing to be discrete populations. Given the increased harvest pressures on black bears in Southeast Alaska (and in particular on these two islands), these new perspectives on connectivity should guide future management decisions related to potentially unsustainable harvests.

2.4.3. *Islands and genetic variability*

Lucid and Cook (2004) assessed levels of genetic variability across 23 island populations of the widespread Keen's mouse. Populations of this ubiquitous species showed highest levels of variability on the mainland and larger islands while lowest variability was recorded on the smallest and most distant islands. Other island endemics show extremely low levels of variability (Prince of Wales flying squirrel and *caurina* marten). Hence, insularization reduced species richness on these islands and also left a characteristic signature of lower genetic variability on the few species examined (Table 1). The generality of this finding to other Alexander Archipelago organisms should be explored. Lower genetic variability decreases the likelihood that a species will be able to respond to novel environmental challenges and thereby increases the probability of local extirpation (Frankham, 1995). Nonetheless, there is much we have to learn with regard to the relationship between genetic variability and the process of extinction (Aguilar et al., 2004). Considerable interest also is building in the new fields of landscape and community genetics (Whitham et al., 2003).

Islands have sculpted diversity at levels scaling from molecular variability through ecological structure and community composition in the Alexander Archipelago. It is precisely this "island effect" on diversity that may be profoundly impacted by humans in the coming decades as has been documented in other archipelagos worldwide (Quammen, 1996). Much more detailed sampling of the islands will allow the development of comprehensive archives of specimens that will help establish baseline (or historic conditions) for assessing change across the archipelago. When inventories are followed by molecular studies, new perspectives on the status of wildlife populations will emerge that are likely to contribute to a variety of future management questions across the Alexander Archipelago.

2.5. *Threats to island systems*

Habitat conversion, mining, increasing human settlement, tourism, sport and subsistence hunting and trapping, and species introductions should be more stringently monitored and regulated with respect to impact on island endemics. In addition, climate warming is predicted to substantially increase extinction risk for populations and species with limited ability to disperse (Thomas et al., 2004), such as those found on islands. A growing number of management plans have been established for archipelagos worldwide and these threats are the subject of numerous scientific papers, books, and action plans (e.g., Golumbia, 2000; Sherley, 2000; McNeely et al., 2001; Wittenberg and Cock, 2001).

2.5.1. *Differential impacts across islands*

The relatively few morphological (Eger, 1990; Dickerman and Gustafson, 1996) and molecular studies (Table 1) completed on Alexander Archipelago organisms in the past few decades have tagged the POW island complex as an important center of endemism (Fig. 4b). Perturbations on these islands need to be carefully regulated and monitored, yet it is unfortunate that most of these islands (e.g., Prince of Wales, Heceta, Suemez, Long, Tuxekan) already have been (or are projected to be) heavily roaded and deforested (Fig. 4a,c). Prince of Wales Island, in particular, is likely to experience large increases in human occupation (and associated impacts) in the coming

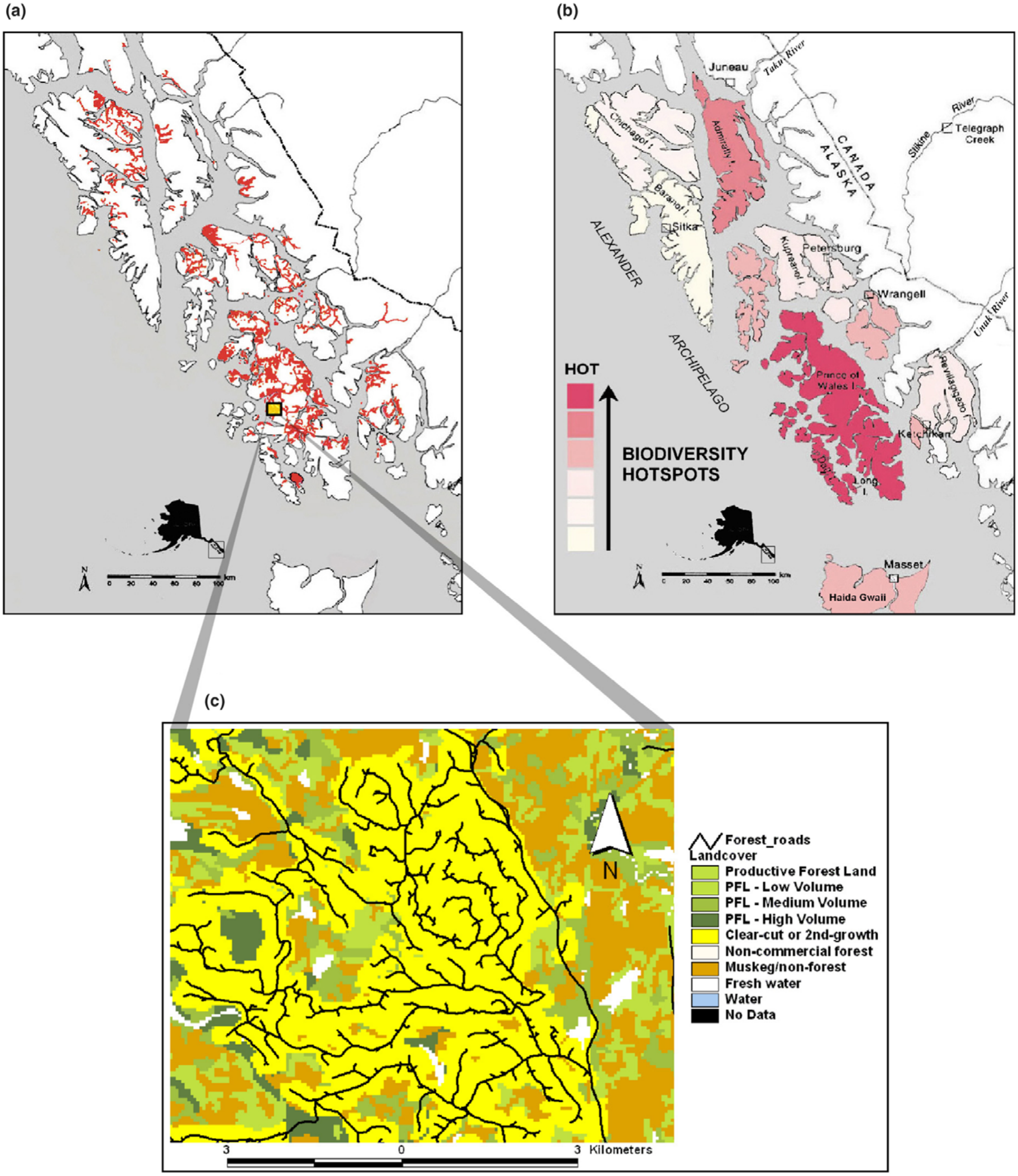

Fig. 4 – (a) Areas of concentrated clear-cut logging (now secondary-growth vegetation) and roads in Southeast Alaska since 1950 are highlighted in red (*Source*. www.inforain.org/tongass). (b) Areas of greatest conservation concern (diversity hotspots) in the Alexander Archipelago, Southeast Alaska, based on the distribution of eight endemic mammal lineages. Note the correspondence between most heavily impacted areas and highest concentration of endemics (e.g. POW island complex). (c) Clear-cut logging practices in Southeast Alaska result in a high density of roads and highly fragmented forests.

decade due in part to increased access across the island. Prince of Wales Island now has over 3000 km of roads, nearly half of all timber-associated roads within the Tongass National Forest. Roads can severely fragment populations and increase human access to remote areas, thus increasing the probability of over exploitation of some species (Person et al., 1996). New ferry terminals on northern Prince of Wales Island (Coffman Cove) and southern Mitkof Island (Blind

Slough) are opening in 2006 and will stimulate additional traffic and development across these islands.

2.5.2. *Invasive and exotic species decimate insular faunas*

A significant threat to island ecosystems worldwide is the introduction of nonnative species (Golumbia, 2000). For example, steep declines in diversity have been documented on tropical islands of the Pacific, such as Guam, other Mariana Islands, and the Hawaiian Archipelago (Fritts and Rodda, 1998). Introduction of exotic species such as rats, mongooses, and brown tree snakes is the prime cause of the demise of these faunas, and these ill-fated events have led to severe restrictions on commerce and development on these islands. Although tropical islands are routinely cited as the classic examples of highly threatened insular biotas, North Pacific archipelagos have also experienced significant reductions in diversity and loss of ecosystem function. Nearly 50 years ago, Murie (1959) noted the devastation experienced by nesting waterfowl on the Aleutian Islands after foxes and rats were introduced. In the last decade, the US Fish and Wildlife Service has instituted an aggressive (and expensive) campaign to eradicate those exotics from over 30 islands (S. Ebbert, pers. comm.). The Alaska Maritime Refuge also helped coordinate proactive efforts on St. George and St. Paul (Pribilof Islands) in 1993 to stymie the possibility that rats (*Rattus* ssp.) might establish populations on these productive islands. Closer to the Alexander Archipelago, the introduction of rats (*Rattus norvegicus*, *R. rattus*), raccoons (*Procyon lotor*) and red squirrels (*Tamiasciurus hudsonicus*) to Haida Gwaii (Queen Charlotte Islands) has had a profound impact on seabirds, songbirds, and other native species (Bertram and Nagorsen, 1995; Hartman and Eastman, 1999; Golumbia, 2000; Martin et al., 2001).

Of the two distinctive forms of marten on the Alexander Archipelago, molecular signatures suggest that *caurina* is the original island form (now only on Kuiu and Admiralty). These northern insular populations of *caurina* exhibited higher differentiation and lower variability relative to northern populations of *americana*. Greater divergence among *caurina* populations may reflect longer isolation and persistence in coastal forest habitat that was fragmented by rising sea level in the early Holocene. The endemic *caurina* lineage apparently has been displaced by the *americana* form, a more recent colonizer of the coast. Indeed, we suspect that *americana* has naturally colonized just a few near-shore islands, but the ongoing displacement (or genetic swamping) of *caurina* by *americana* has likely been hastened through human-mediated introduction of *americana* to Chichagof, Baranof, Prince of Wales and a number of other islands in the last century. Unfortunately, we have too few museum records from these islands to accurately determine the historic range of *caurina* or *americana* across the archipelago. Specimens from several key islands (e.g., Dall, Annette, Heceta, Tuxekan, Zarembo) have not yet been characterized. The impact of industrial logging, fur trapping, and translocations on marten and especially the insular populations of *M. caurina* should be carefully monitored.

There are examples of introductions of 18 other mammal species and three amphibians to Southeast Alaska (unpublished data) and these include exotics like raccoons to islands in Sea Otter Sound and Baranof Island, elk introduced onto Etolin Island (and now spread to Zarembo, Prince of Wales, and other nearby islands and surrounding mainland), and foxes to numerous islands (Bailey, 1993). Increasing human populations and associated pets will negatively impact wildlife populations, such as the transmission of pathogens to wild carnivores (Thorne and Williams, 1988). All of these species have devastated natural systems and cost millions of dollars in control efforts elsewhere when they have been introduced to islands (Bailey, 1993; Martin and Daufresne, 1999; Golumbia, 2000; Burbridge and Manley, 2002; Blackburn et al., 2004).

Over 20 species of exotic plants have been identified as invasive within southeast Alaska (Huette and Bella (in press)) and most thrive in disturbed habitat. Prince of Wales Island is experiencing an influx of domestic exotic plants (e.g., Scotch Broom *Cytisus scoparius*), that have rapidly invaded the island along roads. A comprehensive species introduction task force should be constituted to establish more effective regulations and ensure their implementation. The Alexander Archipelago has already experienced a number of intentional and unintentional introductions (unpublished data). The easiest and cheapest way to avoid significant impacts from invasive species is prevention.

2.5.3. *Maintaining connectivity among islands*

MacDonald and Cook (1999, manuscript) proposed several areas within Southeast Alaska that may function as linkages, but a comprehensive GIS review that takes into account factors such as oceanic currents and spatial reconstructions of past sea level fluctuation and its impact on connectivity needs to be completed. Management plans should prioritize the protection of sites that may facilitate connectivity among islands (not just within islands) by establishing logging (and other disturbance) buffers for suspected linkages and wildlife corridors for natural movement of organisms between islands.

2.6. *Maintaining the ecological integrity of the Alexander Archipelago*

The Alexander Archipelago is a thriving and productive north temperate island system undergoing significant environmental change. Limited information on island endemic mammals (morphological descriptions and molecular phylogeography) portends comparable or perhaps higher levels of divergence in other organisms. Inventory programs coupled with molecular perspectives of selected species have been used across the globe in the restoration and conservation of important managed landscapes. One example is helping managers choose appropriate source populations for efforts to supplement declining population (Florida panther *Puma concolor coryi*; Maehr and Lacy, 2002). Molecular techniques have allowed managers to supplement declining populations based on knowledge of evolutionary histories, and hence ensure genetic integrity of species (Matthee and Robinson, 1999). Such a molecular framework would have demonstrated the folly of the introduction of mainland *americana* marten onto several islands in the Alexander Archipelago. Active management of marten and marten habitat over the last 50 years has likely hastened the extirpation of *caurina* marten in the region, but the overall impact is unknown (MacDonald and Cook, 1996). In addition, few studies have addressed basic ecological attributes of these insular forms, but seminal ecological studies of coastal and insular mammals should help guide future management and restoration efforts (e.g., McCabe and Cowan, 1945; Darimont et al., 2004). Still, managers cannot reproduce the process of natural selection that has been shaping these coastal populations since their arrival, so it is critical that key components of this endemic fauna are not lost.

2.7. Management recommendations and research needs

Sophisticated technologies have significantly enhanced wildlife management over the past few decades. Given the complexity of issues facing resource managers along Alaska's southeastern coast and particularly on this vast archipelago, a diverse set of approaches is needed to effectively administer wildlife management plans and monitor potential threats to these native biotas. Several steps can be taken immediately that will lessen costs associated with impacts and facilitate swift responses to these perturbations in the future.

First, a serious discussion by state and federal management agencies, Native American and other local communities, politicians, NGOs, and other interested groups should focus on establishing a comprehensive management plan aimed at preserving the endemic biota and natural ecosystems of the Alexander Archipelago. Other regions of the planet are grappling with similar issues and are developing guiding principles for management of island systems.

Second, there is a pressing need to continue inventorying the biotic diversity of these islands, but inventories should be specimen based and include more than just vertebrates. Building spatially and temporally deep archives of insular wild populations on the Tongass is critical to many kinds of investigations that will form the basis for careful management (Chapman, 2005) and broad, integrated investigations (Cook et al., 2005; Thompson, 2005). In many situations worldwide, the lack of available baseline materials has become the primary limitation to effective application of new technologies.

Finally, inventories should be followed with surveys of molecular diversity and analyses of morphological variation so that centers of endemism and important sites for sustaining connectivity can be identified. Historical geologic events, combined with the insular nature of the region have contributed to the development of a highly structured, diverse, and endemic biota. Hence, islands are distinct based not only on their geographic isolation, but also due to the dynamic interplay between glacial advance, isostatic rebound and sea level recalibration. Molecular perspectives are powerful allies in our quest to understand island systems as they provide the bridge between deeper history and contemporary population dynamics and conservation biology (Riddle, 1996). This integrated approach is elucidating the region's rich historical complexity, highlighting contemporary insularity, and charting a course for addressing imminent conservation concerns on the Tongass and on other archipelagos worldwide.

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REFERENCES

Aguilar, A., Roemer, G., Debenham, S., Binns, M., Garcelon, D., Wayne, R.K., 2004. High MHC diversity maintained by balancing selection in an otherwise genetically monomorphic mammal. Proceedings of the National Academy of Sciences of the United States of America 101, 3490–3494.

Alaback, P.B., 1995. Biodiversity in relation to climate: the coastal temperate rainforests of North America. In: Lawford, R.G., Alaback, P.B., Fuentes, E. (Eds.), High-latitude rainforests and associated ecosystems of the west coast of the Americas: climate, hydrology, ecology and conservation, Ecological Studies, vol. 113. Springer-Verlag, Berlin, pp. 105–133.

Bailey, E.P., 1993. Introduction of foxes to Alaskan islands: history, effects on avifauna, and eradication. United States Fish and Wildlife Service, Technical Report Series 193, pp. 1–53.

Barnes, I., Matheus, P., Shapiro, B., Jensen, D., Cooper, A., 2002. Dynamics of Pleistocene population extinctions in Beringian brown bears. Science 295, 2267–2270.

Bertram, D.F., Nagorsen, D.W., 1995. Introduced rats, *Rattus* spp., on the Queen Charlotte Islands: implications for seabird conservation. Canadian Field-Naturalist 109, 6–10.

Bidlack, A., Cook, J.A., 2001. Reduced genetic variation in insular northern flying squirrels (*Glaucomys sabrinus*) along the North Pacific Coast. Animal Conservation 4, 283–290.

Bidlack, A.L., Cook, J.A., 2002. A nuclear perspective on endemism in northern flying squirrels (*Glaucomys sabrinus*) of the Alexander Archipelago, Alaska. Conservation Genetics 3, 247–259.

Blackburn, T.M., Cassey, P., Duncan, R.P., Evans, K.L., Gaston, K.J., 2004. Avian extinction and mammalian introductions on oceanic islands. Science 305, 1955–1958.

Burbridge, A.A., Manley, B.F.J., 2002. Mammal extinctions on Australian islands: causes and conservation implications. Journal of Biogeography 29, 465–473.

Burg, T.M., Gaston, A.J., Winker, K., Friesen, V.L., 2005. Rapid divergence and postglacial colonization in western North American Steller's jays (*Cyanocitta stelleri*). Molecular Ecology 14, 3745–3755.

Burkey, T.V., 1995. Extinction rates in archipelagos: implications for populations in fragmented habitats. Conservation Biology 9, 527–541.

Byun, S.A., Koop, B.F., Reimchen, T.E., 1997. North American black bear mtDNA phylogeography: implications for morphology and the Haida Gwaii glacial refugium controversy. Evolution 51, 1647–1653.

Byun, S.A., Koop, B.F., Reimchen, T.E., 1999. Coastal refugia and postglacial colonization routes: A reply to Demboski, Stone, and Cook. Evolution 53, 2013–2015.

Carrara, P., Ager, T.A., Baichtal, J.F., VanSistine, D.P., 2003. Map of glacial limits and possible refugia in the southern Alexander Archipelago, Alaska, during the Late Wisconsin Glaciation. US Department of the Interior, US Geological Survey, Miscellaneous Field Studies Map MF-2424:1-13 (+ map).

Case, T.J., Bolger, D.L., Richman, A.D., 1992. Reptilian extinctions: the last ten thousand years. In: Fielder, P.L., Jain, S.K. (Eds.), Conservation Biology: The Theory and Practice of Nature Conservation, Preservation, and Management. Chapman and Hall, New York, pp. 91–125.

Chapman, A.D., 2005. Uses of Primary Species–Occurrence Data, version 1.0. Report for the Global Biodiversity Information Facility, Copenhagen.

Conroy, C.J., Cook, J.A., 2000. Phylogeography of a post-glacial colonizer: *Microtus longicaudus* (Muridae: Rodentia). Molecular Ecology 9, 165–175.

Conroy, C.J., Demboski, J.R., Cook, J.A., 1999. Mammalian biogeography of the Alexander Archipelago of Southeast Alaska: a north temperate nested fauna. Journal of Biogeography 26, 343–352.

Cook, J.A., Bidlack, A.L., Conroy, C.J., Demboski, J.R., Fleming, M.A., Runck, A.M., Stone, K.D., MacDonald, S.O., 2001. A phylogeographic perspective on endemism in the Alexander Archipelago of the North Pacific. Biological Conservation 97, 215–227.

Cook, J.A., Hoberg, E.P., Koehler, A., Henttonen, H., Wickstrom, L., Haukisalmi, V., Galbreath, K., Chernyavski, F., Dokuchaev, N., Lahzuhtkin, A., MacDonald, S.O., Hope, A., Waltari, E., Runck, A., Veitch, A., Popko, R., Jenkins, E., Kutz, S., Eckerlin, R., 2005. Beringia: intercontinental exchange and diversification of high latitude mammals and their parasites during the Pliocene and Quaternary. Mammal Science 30, S33–S44.

Cook, J.A., MacDonald, S.O., 2001. Should endemism be a focus of conservation efforts along the North Pacific Coast of North America? Biological Conservation 97, 207–213.

Cook, J.A., Runck, A., Conroy, C.J., 2004. Historical biogeography at the crossroads of the northern continents: molecular phylogenetics of red-backed voles (Rodentia: Arvicolinae). Molecular Phylogenetics and Evolution 30, 767–777.

COSEWIC, 2005. Committee on the Status of Endangered Wildlife in Canada. Available from: <www.cosewic.gc.ca>.

Dalton, R., 2005. Caveman DNA hints at map of migration. Nature 436, 162.

Darimont, C.T., Paquet, P.C., Reimchen, T.E., Crichton, V., 2005. Range expansion by moose into coastal temperate rainforests of British Columbia, Canada. Diversity and Distributions 11, 235–239.

Darimont, C.T., Price, M.H.H., Winchester, N.N., Gordon-Walker, J., Paquet, P.C., 2004. Predators in natural fragments: foraging ecology of wolves in British Columbia's Central and North Coast Archipelago. Journal of Biogeography 31, 1867–1877.

Demboski, J., Cook, J., 2001. Phylogeography of the dusky shrew, *Sorex monticolus* (Insectivora, Soricidae): insight into deep and shallow history in northwestern North America. Molecular Ecology 10, 1227–1240.

Demboski, J.R., Cook, J.A., 2003. Phylogenetic diversification within the *Sorex cinereus* complex (Insectivora: Soricidae). Journal of Mammalogy 84, 144–158.

Demboski, J.R., Jacobsen, B.K., Cook, J.A., 1998. Endemism in the Alexander Archipelago, Southeast Alaska: an assessment of genetic variation in flying squirrels (Rodentia: *Glaucomys sabrinus*). Canadian Journal of Zoology 76, 1–7.

Demboski, J.R., Stone, K.D., Cook, J.A., 1999. Further perspectives on the Haida Gwaii glacial refugium hypothesis. Evolution 53, 2008–2012.

Diamond, J.M., 1989. The present, past and future of human-caused extinctions. Philosophical Transactions of the Royal Society of London B 325, 469–477.

Dickerman, R.W., Gustafson, J., 1996. The Prince of Wales Spruce Grouse: a new subspecies from Southeastern Alaska. Western Birds 27, 41–47.

Eger, J.L., 1990. Patterns of geographic variation in the skull of Nearctic ermine (*Mustela erminea*). Canadian Journal of Zoology 68, 1241–1249.

Fleming, M.A., Cook, J.A., 2002. Phylogeography of endemic ermine (*Mustela erminea*) in southeast Alaska. Molecular Ecology 11, 795–808.

Frankham, R., 1995. Inbreeding and extinction – a threshold effect. Conservation Biology 9, 792–799.

Fritts, T.H., Rodda, G.H., 1998. The role of introduced species in the degradation of island ecosystems: a case history of Guam. Annual Review of Ecology and Systematics 29, 113–140.

Galbreath, K., Cook, J., 2004. Genetic consequences of Pleistocene glaciations for the tundra vole (*Microtus oeconomus*) in Beringia. Molecular Ecology 13, 135–148.

Golumbia, T.E., 2000. Introduced species management in Haida Gwaii (Queen Charlotte Islands). In: Darling, L.M. (Ed.), Proceedings of a Conference on the Biology and Management of Species and Habitats at Risk, vol. 1. Kamloops, BC, pp. 327–332.

Hartman, L.H., Eastman, D.S., 1999. Distribution of introduced raccoons *Procyon lotor* on the Queen Charlotte Islands: implications for burrow-nesting seabirds. Biological Conservation 88, 1–13.

Heaton, T.H., Grady, F., 2003. The Late Wisconsin vertebrate history of Prince of Wales Island, southeast Alaska. In: Schubert, B.W., Mead, J.I., Graham, R.W. (Eds.), Ice Age Cave Faunas of North America. Indiana University Press, pp. 17–53.

Heaton, T.H., Talbot, S.L., Shields, G.F., 1996. An Ice Age refugium of large mammals in the Alexander Archipelago, southeastern Alaska. Quaternary Research 46, 186–192.

Huette, T., Bella, E. Invasive and exotic weeds of Southeast Alaska. USDA, Forest Service Technical Publication. Available from: <http://www.fs.fed.us/r10/spf/fhp/> (in press).

Hundertmark, K.J., Bowyer, R.T., Shields, G.F., Schwartz, C.C., Smith, M.H. Colonization history and taxonomy of moose *Alces alces* in southeastern Alaska inferred from mtDNA variation. Wildlife Biology (in press).

Klein, D.R., 1965. Postglacial distribution patterns of mammals in the southern coastal regions of Alaska. Journal of the Arctic Institute of North America 18, 7–20.

Kondzela, C.M., Guthrie, C.M., Hawkins, S.L., Russell, C.D., Helle, J.H., Gharrett, A.J., 1994. Genetic relationships among chum salmon populations in southeast Alaska and northern British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 51, 50–64.

Lessa, E.P., Cook, J.A., Patton, J.L., 2003. Genetic footprints of demographic expansion in North America, but not Amazonia, following the Late Pleistocene. Proceedings of the National Academy of Sciences, USA 100, 10331–10334.

Lucid, M., Cook, J., 2004. Phylogeography of Keen's mouse (*Peromyscus keeni*) in a naturally fragmented landscape. Journal of Mammalogy 85, 1149–1159.

MacArthur, R.H., Wilson, E.O., 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, NJ. 203pp.

MacDonald, S.O., Cook, J.A., 1996. The land mammal fauna of Southeast Alaska. Canadian Field-Naturalist 110, 571–598.

MacDonald, S.O., Cook, J.A., 1999. The mammal fauna of Southeast Alaska. University of Alaska Museum, Fairbanks. 141pp.

MacDonald, S.O., Runck, A.M., Cook, J.A., 2004. The heather vole (genus *Phenacomys*) in Alaska. Canadian Field-Naturalist 118.

Maehr, D.S., Lacy, R.C., 2002. Avoiding the lurking pitfalls in Florida panther recovery. Wildlife Society Bulletin 30, 9710978.

Mann, D., 1986. Wisconsin and Holocene glaciation of Southeast Alaska. In: Hamilton, T.D., Reed, K.M., Thorson, R.M. (Eds.), Glaciation in Alaska. Alaska Geologic Society Report, pp. 237–265, 265pp.

Mann, D., Hamilton, T.D., 1995. Late Pleisticene and Holocene paleoenvironments of the North Pacific Coast. Quaternary Science Reviews 14, 449–471.

Martin, J.L., Daufresne, T., 1999. Introduced species and their impacts on the forest ecosystem of Haida Gwaii. In: Wiggins, G. (Ed.), Proceedings of the Cedar Symposium. Canada–British Columbia South Moresby Forest Replacement Account, Vic., Canada. pp. 69–89.

Martin, J.L., Joron, M., Gaston, A.J., 2001. The squirrel connection: influence of squirrels as songbird nest predators in Laskeek Bay. In: Gaston, A.J. (Ed.), Laskeek Research, vol. 8. Laskeek Conservation Society, Queen Charlotte City, BC, pp. 43–61.

Matthee, C.A., Robinson, T.J., 1999. Mitochondrial DNA population structure of roan and sable antelope: implications for the translocation and conservation of the species. Molecular Ecology 8, 227–238.

McCabe, T.T., Cowan, I.M., 1945. *Peromyscus maniculatus macrorhinus* and the problem of insularity. Transactions of the Royal Canadian Institute 25, 117–216.

McNeely, J.A., Mooney, H.A., Neville, L.E., Schei, P.J., Waage, J.K., 2001. A Global Strategy on Invasive Alien Species: IUCN, Gland, Switzerland and Cambridge, UK in collaboration with the Global Invasive Species Programme.

Merriam, C.H., 1890. Descriptions of twenty-six new species of North American mammals. North American Fauna 4, 1–55.

Moritz, C., 1994. Applications of mitochondrial DNA analysis in conservation: a critical review. Molecular Ecology 3, 401–411.

Murie, O.J., 1959. Fauna of the Aleutian Islands and Alaska Peninsula. North American Fauna 61, 1–364.

Nagorsen, D., 1994. Endangered mammals in British Columbia. In: Harding, L.E., McCullum, E. (Eds.), Biodiversity in British Columbia: Our Changing Environment. Environment Canada, Canadian Wildlife Service, pp. 143–151.

Nagorsen, D.W., 2004. Canada's endemic mammals at risk: recent taxonomic advances and priorities for conservation. In: Hooper, T.D. (Ed.), Proceedings of the Species at Risk 2004 Pathways to Recovery Conference. 1 March 2–6, 2004, Victoria, BC. Species at Risk 2004 Pathways to Recovery Conference Organizing Committee, Victoria, BC, pp. 1–2.

Nelson, E.W., 1887. Report upon natural history collections made in Alaska between the years 1877 and 1881. Arctic Series of Publications, US Signal Service, III. 337pp.

Olson, S.L., 1989. Extinction on islands: man as a catastrophe. In: Western, D., Pearl, M. (Eds.), Conservation for the Twenty-First Century. Oxford University Press, Oxford, pp. 50–53.

Paetkau, D., Shields, G.F., Strobeck, C., 1998. Gene flow between insular, coastal and interior populations of brown bears in Alaska. Molecular Ecology 7, 1283–1292.

Paquet, P.C., Darimont, C.T., Nelson, R.J., Bennett, K., 2004. A critical assessment of protection for key wildlife and salmon habitats under the proposed British Columbia Central Coast Land and Resource Management Plan. Rainforest Conservation Society. Available from: <www.raincoast.org>.

Peacock, E., 2004. Population, genetic, and behavioral studies of black bears *Ursus americanus* in Southeast Alaska. Doctoral Dissertation, University of Nevada, Reno. 230pp.

Person, D.K., Kirchhoff, M., Van Ballenberghe, V., Iverson, G.C., Grossman, E., 1996. The Alexander Archipelago wolf: a conservation assessment. Forest Service General Technical Report PNW-GTR-384.

Quammen, D., 1996. The Song of the Dodo. Touchstone Books. 702pp.

Reid, W.V., Miller, K.R., 1989. Keeping Options Alive: The Scientific Basis for Conserving Biodiversity. World Resources Institute, Washington, DC.

Riddle, B.R., 1996. The molecular phylogeographic bridge between deep and shallow history in continental biotas. Trends in Ecology and Evolution 11, 207–211.

Rogers, R.A., Rogers, L.A., Hoffmann, R.S., Martin, A., 1991. Native American biological diversity and the biographic influence of ice age refugia. Journal of Biogeography 18, 623–630.

Runck, A.M., 2001. Molecular and morphological perspectives on post-glacial colonization of Clethrionomys rutilus and Clethrionomys gapperi in Southeast Alaska. Master's thesis. University of Alaska Fairbanks. 89pp, unpublished.

Runck, A., Cook, J., 2005. Post-glacial expansion of the southern red-backed vole (*Clethrionomys gapperi*) in North America. Molecular Ecology.

Shank, C.C., 1999. The committee on the status of endangered wildlife in Canada (COSEWIC): a 21 year retrospective. Canadian Field-Naturalist 113, 318–341.

Sherley, G., 2000. Invasive species in the Pacific: A technical review and draft regional strategy. Apia, Samoa: South Pacific Regional Environmental Programme with funding assistance from the Government of Australia.

Small, M.P., Stone, K.D., Cook, J.A., 2003. American marten (*Martes americana*) population structure across a landscape fragmented in time and space. Molecular Ecology 12, 89–103.

Steadman, D.W., 1995. Prehistoric extinctions of Pacific Island birds: biodiversity meets zooarchaeology. Science 267, 1123–1131.

Stone, K.D., Cook, J.A., 2000. Phylogeography of black bears (*Ursus americanus*) from the Pacific Northwest. Canadian Journal of Zoology 78, 1–6.

Stone, K., Cook, J., 2002. Molecular evolution of the Holarctic genus *Martes*. Molecular Phylogenetics and Evolution 24, 169–179.

Stone, K., Flynn, R., Cook, J., 2002. Post-glacial colonization of northwestern North America by the forest associated American marten (*Martes americana*). Molecular Ecology 11, 2049–2064.

Swarth, H.S., 1911. Birds and mammals of the 1909 Alexander Expedition. University of California, Publication in Zoology 7, pp. 9–172.

Swarth, H.S., 1936. Origins of the fauna of the Sitkan District, Alaska. Proceedings of the California Academy Science 223, 59–78.

Talbot, S., Shields, G.F., 1996. Phylogeography of the brown bears (*Ursus arctos*) of Alaska and paraphyly within the Ursidae. Molecular Phylogenetics and Evolution 5, 477–494.

Thomas, C.D., Cameron, A., Green, R.E., et al, 2004. Extinction risk from climate change. Nature 427, 145–148.

Thompson, J.N., 2005. The Geographic Mosaic of Coevolution. University of Chicago Press.

Thorne, E.T., Williams, E.S., 1988. Disease and endangered species: The black-footed ferret as a recent example. Conservation Biology 2, 66–94.

Tomasik, E., Cook, J., 2005. Mitochondrial phylogeography and conservation genetics of wolverine (*Gulo gulo*) in Northwestern North America. Journal of Mammalogy 86, 386–396.

Tongass Land Management Plan, 1997. United States Department of Agriculture, Forest Service Tongass National Forest, Land and Resource Plan R10-MB-338dd, Juneau, Alaska.

Vitousek, P.M., Loope, L., Adsersen, H. (Eds.), 1995. Islands: Biological Diversity and Ecosystem Function. Springer-Verlag, Berling.

Weckworth, B., Talbot, S., Sage, G., Person, D., Cook, J., 2005. A signal for independent coastal and continental histories for North American wolves. Molecular Ecology 14, 917–931.

Whitham, T.G., Young, W.P., Martinsen, G.D., Gehring, C.A., Schweitzer, J.A., Shuster, S.M., Wimp, G.M., Fischer, D.G., Bailey, Lindroth, R.L., Woolbright, S., Kuske, C.R., . Community and ecosystem genetics: a consequence of the extended phenotype. Ecology 84, 559–573.

Wittenberg, R., Cock, M.J.W., 2001Invasive Alien Species: A Toolkit of Best Prevention and Management Practices, vol. 228. CAB International, Wallingford, Oxon, UK.