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Evolutionary diversity and ecology of endemic small mammals of southeastern Alaska with implications for land management planning

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Abstract

The dynamic geological history and naturally fragmented landscapes of southeastern Alaska create an environment with a high potential for endemism. The temperate rainforest of the region regenerates and develops slowly, and old-forest characteristics do not appear until ≥300 years following disturbance. The challenges of managing forest resources are intensified in island archipelagos because of the increased sensitivity of indigenous biota to disturbance and higher rates of extinction, especially among endemic organisms. Early expeditions of the large islands of the Alexander Archipelago (≈1% of all named islands) documented 27 endemic mammalian taxa. More recent studies with modern techniques found that some reputed endemics showed nominal levels of genetic divergence from other conspecific populations, but more divergence existed among several taxa than was reflected in the current taxonomy. Furthermore, the mammal fauna of southeastern Alaska has a nested structure with complex phylogeographic patterns suggesting multiple colonization events. Of eight taxa examined through phylogeographic analyses, five species showed acute genetic variation and divergence in mitochondrial sequences. Four species were comprised of coastal and continental clades (i.e. populations of recent common descent), whereas the fifth species showed a third clade. Conversely, the northern flying squirrel (*Glaucomys sabrinus*) and southern red-backed vole (*Clethrionomys gapperi*) were represented by relatively shallow divergent lineages. Still, *G. sabrinus* showed a distinct mitochondrial lineage on 11 islands (Prince of Wales Island complex), which exhibited severely reduced genetic variation. Moreover, flying squirrels in southeastern Alaska are genetically distinct from populations in the Pacific Northwest; as different as each is from the southern flying squirrel (*G. volans*).

Recent ecological studies of endemic populations of the northern flying squirrel and the southern red-backed vole (reputed old-growth associates) suggest that risk of extirpation in managed landscapes is likely less than was presumed during recent land management planning in the region because: (1) abundant noncommercial forests apparently contribute to breeding populations of northern flying squirrels, which appear to have a more general lifestyle than populations in the Pacific Northwest; and (2) red-backed vole populations may be able to exist in managed young-growth stands that originated from clearcut logging. Still, there are essential questions for both species regarding the influence of annual population fluctuations on habitat distribution

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and population demography, stand and landscape features that restrict dispersal, and vegetative and structural characteristics of second-growth stands that will sustain breeding populations of both species.
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1. Endemic mammals, population viability, and the revision of the 1997 Tongass land management plan

The Alaska Region of the USDA Forest Service recently completed a revision of the land management plan for the Tongass National Forest (USDA Forest Service, 1997). The Tongass National Forest encompasses the Alexander Archipelago and narrow mainland regions of southeastern Alaska, which extends from Dixon Entrance (54°30′N latitude) to the Malaspina Glacier (59°45′N latitude; Fig. 1). The Tongass is unique among national forests in several ways (Everest et al., 1997; Everest, this issue) including naturally fragmented and isolated landscapes, dynamic geological history, and environmental complexity (MacDonald and Cook, 1996; Cook and MacDonald, 2001; Cook et al., 2001). Cumulative habitat disturbance is especially problematic for archipelagos where habitat is already naturally fragmented among oceanic islands, average population size is smaller than in mainland habitats (MacArthur and Wilson, 1967; Soulé and Wilcox, 1980; Cook et al., 2001), source populations are isolated (Burkey, 1995), and demographic stochasticity and inbreeding depression increase risk of extinction, especially among endemic taxa (Frankham, 1998; Cook and MacDonald, 2001). Smaller populations are more severely impacted by habitat disturbance, and the likelihood of rescue following extirpation is influenced greatly by the number and proximity of source populations (MacArthur and Wilson, 1967; MacArthur, 1972; Soulé and Wilcox, 1980; Laurance, 1991, 1995; Burkey, 1995). Indeed, most vertebrate extinctions during the last 400 years were island endemics (Cook and MacDonald, 2001).

Not surprisingly, a focal issue during the revision of the Tongass land management plan (TLMP) was viability of wildlife populations (Everest et al., 1997; Hanley et al., this issue). Risk assessment panels were established to evaluate an array of forest plan alternatives relative to the impact that each would impose on selected wildlife species (Shaw, 1999). Numerous indigenous mammals were grouped into the category 'Endemic Small Mammals' and evaluated collectively by a panel of experts. Taxa in this group were subspecies with restricted ranges, many of which were limited to one or a few islands in the Alexander Archipelago (MacDonald and Cook, 1996). The high potential for endemism, increasing evidence of undocumented evolutionary diversity, and the acknowledged dearth of information regarding the natural history of endemic populations in southeastern Alaska (Cook and MacDonald, 2001) heightened awareness and elevated concerns over viability of isolated populations of old-growth associated small mammals (Everest et al., 1997; Hanley et al., this issue).

Endemic small mammals received the lowest score (i.e. highest viability risk) during initial effects analyses of a range of forest planning scenarios and during a subsequent risk assessment of the proposed preferred alternative (Shaw, 1999). These low scores reflected uncertainty on the part of panel experts regarding distributional and taxonomic status of indigenous wildlife taxa (Cook and Kirkland, 1998; Demboski et al., 1998a, 1998b), particularly the extent of undocumented endemism in southeastern Alaska (Cook and MacDonald, 2001; Cook et al., 2001), and the risk to extinction of some endemic taxa because of extensive clearcut logging throughout the region. The Prince of Wales flying squirrel (*Glaucomys sabrinus griseifrons*) and island populations of the red-backed vole (*Clethrionomys gapperi*) were endemic subspecies that were specifically acknowledged because of a reputed association with old-growth forests and clearcut logging of significant portions of their geographic ranges.

The Prince of Wales flying squirrel is known only from the "Southern Outer Islands" Biogeographic Subregion (MacDonald and Cook, 1996; Demboski et al.,

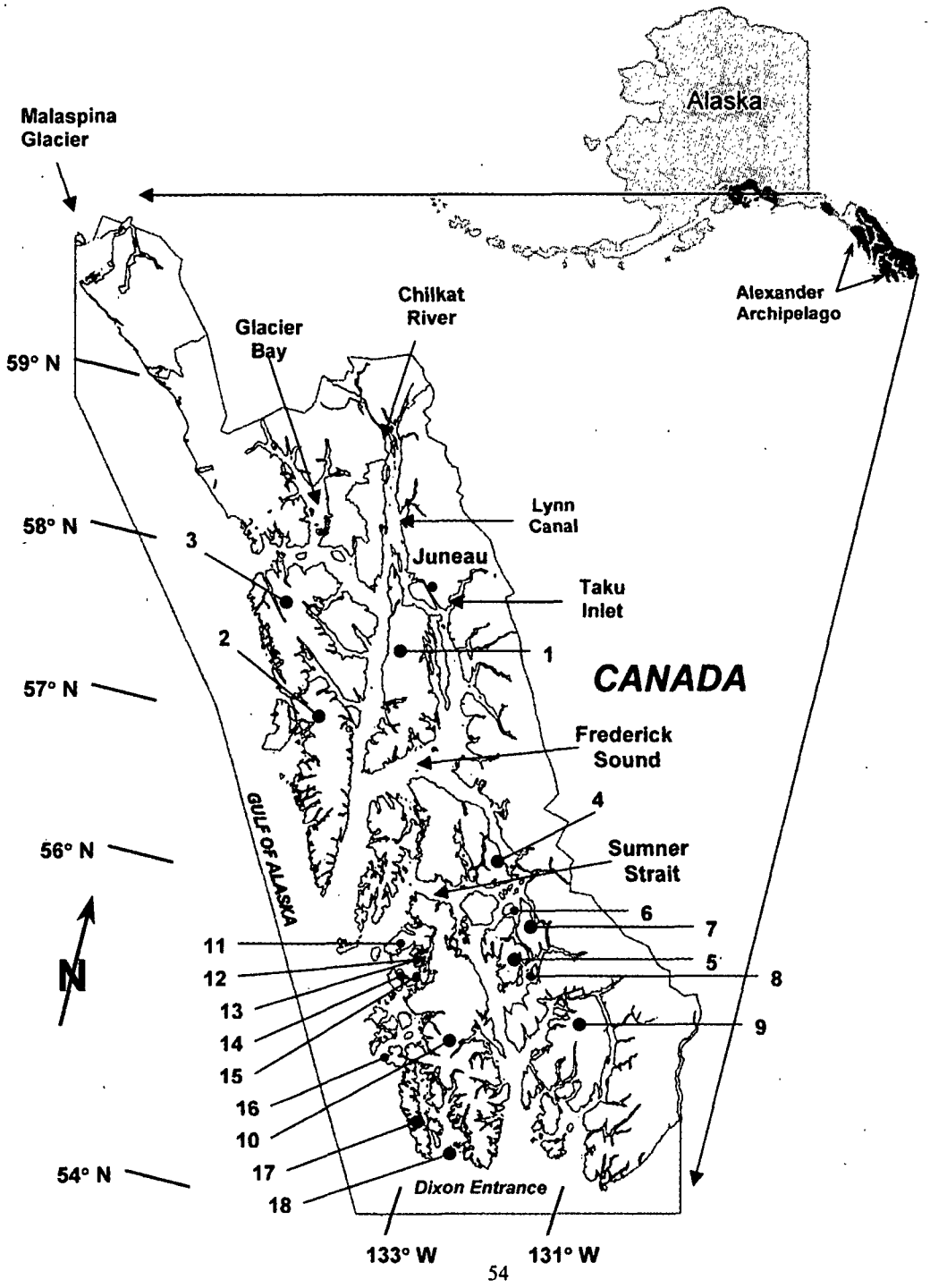

Fig. 1. Alexander Archipelago and narrow mainland panhandle region of southeastern Alaska, noting the following islands: (1) Admiralty, (2) Baranof, (3) Chichagof, (4) Mitkof, (5) Etolin, (6) Woronkofski, (7) Wrangell, (8) Deer, (9) Revillagigedo, (10) Prince of Wales, (11) Kosciusko, (12) Orr, (13) El Capitan, (14) Heceta, (15) Tuxecan, (16) Suemez, (17) Dall, and (18) Barrier Islands.

1998a; Bidlack and Cook, 2002), extensive portions of which were clearcut between 1954 and 1995 (USDA Forest Service, 1997). Furthermore, a substantial portion of its habitat was not under federal stewardship but was largely Native corporation or other private land, of which 80% has or will likely experience clearcut logging in the near future. The Prince of Wales flying squirrel is listed as "endangered" in the recent status survey of North American rodents (Demboski et al., 1998b, p. 38). Ecological information on *G. sabrinus* in southeastern Alaska is limited with only one quantitative study of demography (Smith and Nichols, 2003) and habitat relations (Smith et al., 2004; in press) of the Prince of Wales flying squirrel.

The southern red-backed vole occurs as four endemic subspecies in southeastern Alaska (MacDonald and Cook, 1996). Two subspecies occur on islands and have limited geographic ranges. Ecological information on *C. gapperi* is scarce with only one quantitative study (*C. g. wrangeli* populations on Wrangell Island) of demography (Smith and Nichols, 2004) and habitat relations (W.P. Smith et al., submitted for publication). *C. g. solus* remains listed as "data deficient" in the recent status survey of North American rodents (Cook and Kirkland, 1998, p. 87). Neither Wrangell Island nor Revillagigedo Island has been clearcut logged to the relative extent of the Southern Outer Islands, but Wrangell and Revillagigedo are an order of magnitude smaller than Prince of Wales and therefore are subject to the vagaries typical of small populations (MacArthur and Wilson, 1967; MacArthur, 1972; Soulé and Wilcox, 1980; Burkey, 1995; Frankham, 1998).

2. Taxonomy and distribution of endemic mammals in southeastern Alaska

2.1. Faunal composition and distribution

Much of the knowledge regarding composition and distribution of southeastern Alaska's vertebrate fauna came from collections by the United Sates Biological Survey and Alexander Alaska expeditions of the late 19th and early 20th century. Until recently, taxonomy of the terrestrial mammal fauna of southeastern Alaska was solely developed from morphologic analyses of this biological material, which came from a minute fraction of the total area of 22 of >2000 named islands (MacDonald and Cook, 1996). The dynamic geological history of the region and extent of documented in situ differentiation offer persuasive evidence that the diversity of evolutionary significant units likely exceeds what have been established with relatively few inventories (Cook et al., 2001). Because taxonomy shapes the perceptions of how nature is organized (Avise, 1994), a taxonomic framework that adequately embodies the geographic structure of genetic variation is fundamental to any land management paradigm that seeks to maintain the biological diversity of southeastern Alaska (Cook and MacDonald, 2001). Indeed, it is impossible to sustainably manage forests without a thorough inventory of unique resources that exist within the planning area (Cook and MacDonald, 2001; Cook et al., 2001).

Southeastern Alaska has 48 extant, native land mammal species (MacDonald and Cook, 1996). The highest number of species occurs in the upper Lynn Canal area (Fig. 1), whereas the highest absolute number of endemics occurs in the Mainland Subregion of southeastern Alaska (MacDonald and Cook, 1996). The Alexander Archipelago has a terrestrial mammalian fauna with a nested structure that apparently resulted from differential colonization following glacial retreat (Conroy et al., 1999). This pattern distinguishes the Alexander Archipelago from most mainland and landbridge archipelagos, which are typically structured by differential extinction (Patterson, 1990). In southeastern Alaska, variation in mammalian species richness was more closely associated with island isolation than island area, although both variables were significant and highly correlated with one another (Conroy et al., 1999). Despite features typical of landbridge archipelagos (i.e. shallower ocean depth among islands; Lawlor, 1986), some patterns of species diversity (e.g. depauperate fauna) in the Alexander Archipelago were more typical of oceanic archipelagos than landbridge or mainland archipelagos (Conroy et al., 1999). Still, some aspects of faunal composition (e.g. highly nested structure) were idiosyncratic of mainland and low-latitude landbridge archipelagos (Patterson, 1990).

Although Conroy et al. (1999) demonstrated a highly significant relationship between island isolation and species richness, there were likely other factors that contributed to the composition and distribution of the extant mammal fauna in the Alexander Archipelago (Patterson, 1990). Heusser (1989) proposed that some

taxa persisted in glacial refugia. The presence of glacial refugia would be consistent with the unusually large number of endemic mammals among outer islands of the Alexander Archipelago (MacDonald and Cook, 1996). Also, the presence of subalpine fir (*Abies lasiocarpa*) on Dall Island and Prince of Wales Island suggests a glacial refugium from the Late Wisconsin period (Heusser, 1989). In addition, proximate ecological factors such as habitat complexity (which is directly related to island area), competition, predation, and symbiotic relationships influence extinction probabilities and faunal relaxation, a primary cause of nested structure in vertebrate fauna (Patterson, 1990). The distribution of the three largest carnivores (i.e. *Ursus arctus*, *U. americanus*, and *Canis lupus*) across the Alexander Archipelago differs from mainland northwestern North America where the three species are commonly syntopic. Similarly, the two most common shrews in southeastern Alaska (*Sorex cinereus* and *S. monticolus*) co-occur on the mainland and near-shore islands, but not on the outer large islands such as Prince of Wales (only *S. monticolus*) or Admiralty (only *S. cinereus*) (MacDonald and Cook, 1996). The disjunct distributions of species of similar body size and ecology among the islands suggest that competition may have played a role in their current distributions (Conroy et al., 1999). Regardless of the primary mechanism producing a nested fauna, more habitat loss and fragmentation will likely reduce the diversity of mammalian taxa in southeastern Alaska through increasing extinction probabilities (Patterson, 1990; Burkey, 1995; Frankham, 1998).

2.2. Phylogeography and taxonomy

MacDonald and Cook (1996) presented an overview of the land mammal fauna of southeastern Alaska. In their synopsis, they provided an annotated list of species with taxonomy and distributions based on previously published accounts and additional distributional records obtained from fieldwork conducted through the University of Alaska Museum where specimens are deposited. Nomenclature followed Wilson and Reeder (1993) with the exception of *Peromyscus*, which reflected the recent revision by Hogan et al. (1993). They reported on 48 native mammal species and included brief accounts (i.e. type locality and known distribution) of subspecies (Hall, 1981) of polytypic forms. Much of the taxonomy of endemic taxa presented in MacDonald and Cook (1996) was developed from specimens collected from 22 islands during early expeditions to the region. Cook et al. (2001) listed 24 mammals endemic to southeastern Alaska. Small (<10 kg) mammals ($n=66$) included 21 endemic taxa (Table 1); the other three endemics were beaver (*Castor canadensis phaeus*), Alexander Archipelago wolf (*Canis lupus ligoni*), and black bear (*U. a. pugnax*) (MacDonald and Cook, 1996). Also, they documented three new species for the region since Hall (1981): collared pika (*Ochotona collaris*), fisher (*Martes pennanti*), and mountain lion (*Puma concolor*). Three unconfirmed (i.e. without voucher specimens) species from the region were least weasel (*Mustela nivalis*), caribou (*Rangifer tarandus*), and Dall sheep (*Ovis dalli*).

More recently, Cook et al. (2001) detailed results of phylogeographic analyses of eight mammal species in southeastern Alaska to provide an independent assessment of endemism in the region. Whereas some reputed endemics showed insignificant levels of genetic divergence from other conspecific populations, Cook et al. (2001) found more divergence among some taxa than was reflected in the current taxonomy. Of the taxa examined, five species showed acute genetic variation and divergence in the mitochondrial sequence of the cytochrome b gene (Cook et al., 2001). Four species were comprised of coastal and continental clades (i.e. populations of recent common descent), whereas the fifth showed a third clade.

Variation between Alaska and Yukon Territory populations of the northern flying squirrel was minimal (Demboski et al., 1998a), clearly showing affinity with a widespread eastern lineage (Arbogast, 1999) and distinct from a western lineage comprised of populations in Washington, Oregon, and western California (Demboski et al., 1998a; Arbogast, 1999). Flying squirrels in southeastern Alaska are as genetically distinct from populations in the Pacific Northwest as each is from the southern flying squirrel (*G. volans*). In Alaska, the northern flying squirrel was represented by two slightly divergent lineages as compared to other taxa with multiple lineages in the region. Still, mitochondrial DNA sequences revealed a distinct mitochondrial lineage on 11 islands (Prince of Wales Island complex) as compared to mainland and near-shore island populations (Bidlack and Cook, 2001, 2002). Flying squirrels of the Prince of Wales complex appear to be de-

Table 1
Indigenous small[a] mammal taxa of southeastern Alaska (MacDonald and Cook, 1999)

Common name	Taxon	Type locality[b]	Distribution[c]
Common shrew	*Sorex cinereus cinereus*	Fort Severn, Ontario	Widely
Common shrew	*S. c. streatori*	Yakutat, AK	Widely
Dusky shrew	*Sorex monticolus alascensis*	Yakutat, AK	Confined
Dusky shrew	*S. m. elassodon*	Clew, Queen Charlotte Islands, BC	Confined
Dusky shrew	*S. m. longicaudus*	Wrangell, AK	Confined
Dusky shrew	*S. m. malitiosus*	Warren Island AK	Endemic
Dusky shrew	*S. m. obscurus*	Leadore, ID	Widely
Glacier Bay water shrew	*Sorex alaskanus*	Point Gustavus, AK	Endemic
Water shrew	*Sorex palustris navigator*	Yakima River, WA	Widely
Little brown myotis	*Myotis lucifugus alascensis*	Sitka, AK	Unknown
Little brown myotis	*M. l. pernox*	n/a	Unknown
Keen's myotis	*Myotis keeni*	Massett, Queen Charlotte Islands, BC	Unknown
Long-legged myotis	*Myotis volans longicrus*	Puget Sound, WA	Widely
California myotis	*Myotis californicus caurinus*	Massett, BC	Widely
Silver-haired bat	*Lasionycteris noctivagans*	n/a	Widely
Big brown bat	*Eptesicus fuscus*	n/a	Widely
Collared pika	*Ochotona collaris*	Tanana River, AK	Widely
Snowshoe hare	*Lepus americanus dalli*	Nulato, AK	Widely
Hoary marmot	*Marmota caligata caligata*	Bristol Bay, AK	Widely
Hoary marmot	*M. c. vigilis*	Glacier Bay, AK	Endemic
Arctic ground squirrel	*Spermophilus parryi plesius*	Lake Bennett, BC	Widely
Red squirrel	*Tamiasciurus hudsonicus picatus*	Kupreanof Island, AK	Endemic
Red squirrel	*T. h. petulans*	White Pass, AK	Widely
Northern flying squirrel	*Glaucomys sabrinus alpinus*	Jasper House, Alberta	Widely
Northern flying squirrel	*G. s. zaphaeus*	Helm Bay, Cleveland Peninsula, AK	Confined
Northern flying squirrel	*G. s. griseifrons*	Lake Bay, Prince of Wales Island, AK	Endemic
Keen's mouse	*Peromyscus keeni algidus*	Lake Bennett, BC	Confined
Keen's mouse	*P. k. macrorhinus*	Skeena River, BC	Confined
Keen's mouse	*P. k. hylaeus*	Hollis, AK	Endemic
Keen's mouse	*P. k. oceanicus*	Forrester Island, AK	Endemic
Keen's mouse	*P. k. sitkensis*	Sitka, AK	Endemic
Bushy-tailed woodrat	*Neotoma cinerea occidentalis*	Willapa Bay, WA	Widely
Northern red-backed vole	*Clethrionomys rutilus glacialis*	Glacier Bay, AK	Endemic
Northern red-backed vole	*C. r. dawsoni*	Finlayson River, Yukon	Widely
Southern red-backed vole	*Clethrionomys gapperi phaeus*	Boca de Quadra, AK	Confined
Southern red-backed vole	*C. g. wrangeli*	Wrangell Island, AK	Endemic
Southern red-backed vole	*C. g. saturatus*	Upper Portland Canal, AK	Widely
Southern red-backed vole	*C. g. solus*	Loring, Revillagigedo Island, AK	Endemic
Southern red-backed vole	*C. g. stikinensis*	Stikine River (south of Flood Glacier), AK	Endemic
Meadow vole	*Microtus pennsylvanicus admiraltiae*	Windfall Harbor, Admiralty Island, AK	Endemic
Meadow vole	*M. p. alcorni*	Kluane, Yukon	Widely
Meadow vole	*M. p. rubidus*	Sawmill Lake, BC	Widely
Tundra vole	*Microtus oeconomus littoralis*	n/a	Widely
Tundra vole	*M. o sitkensis*	Sitka, AK	Endemic
Tundra vole	*M. o yakutatensis*	Yakutat Bay, AK	Confined
Long-tailed vole	*Microtus longicaudus littoralis*	Prince of Wales Island, AK	Confined
Long-tailed vole	*M. l. vellerosus*	Upper Liard River, BC	Widely
Coronation Island vole	*M. l. coronarius*	Egg Harbor, AK	Endemic
Muskrat	*Ondatra zibethicus spatulatus*	Lake Marsh, Yukon	Widely
Northern bog lemming	*Synaptomys borealis truei*	Wrangell, AK	Confined
Meadow jumping mouse	*Zapus hudsonicus alascensis*	Yakutat Bay, AK	Widely
Western jumping mouse	*Zapus princeps saltator*	Telegraph Creek, BC	Widely
American marten	*Martes americana kenaiensis*	Kenai Peninsula, AK	Widely

Table 1 (*Continued*)

Common name	Taxon	Type locality[b]	Distribution[c]
American marten	*M. a. actuosa*	Fort Yukon, AK	Widely
American marten	*M. a. caurina*	Grays Harbor, WA	Widely
American marten	*M. a. nesophila*	Massett, Queen Charlotte Islands, BC	Confined
Ermine	*Mustela erminea arctica*	Point Barrow, AK	Widely
Ermine	*M. e. alascensis*	Juneau, AK	Endemic
Ermine	*M. e. initis*	Saook Bay, Baranof Island, AK	Endemic
Ermine	*M. e. salva*	Mole Harbor, Admiralty Island, AK	Endemic
Ermine	*M. e. celenda*	Kasaan Bay, Prince of Wales Island, AK	Endemic
Ermine	*M. e. seclusa*	Port Santa Cruz, Suemez Island, AK	Endemic
Least weasel	*Mustela nivalis eskimo*	Point Barrow, AK	Widely
Mink	*Mustela vison energumenos*	Sumas, BC	Widely
Mink	*M. v. nesolestes*	Windfall Harbor, Admiralty Island, AK	Endemic

[a] Small: mean body mass <10 kg.

[b] From Hall (1981); n/a: information is not available or relevant for southeastern Alaska.

[c] Endemic: distribution is limited to southeastern Alaska; confined: distribution is confined to the region surrounding southeastern Alaska; widely: distribution includes portions of North America beyond the region surrounding southeastern Alaska (MacDonald and Cook, 1999); unknown: insufficient data for southeastern Alaska or surrounding region.

scended from a single founder population (Demboski et al., 1998a) that subsequently remained isolated from mainland or near-shore island populations (Bidlack and Cook, 2001, 2002). Analyses of micro-satellite loci revealed lower heterozygosity and allelic diversity than mainland populations (Bidlack and Cook, 2001). Together, the results of the mitochondrial and nuclear DNA analyses provide compelling evidence that the Prince of Wales complex lineage exhibits severely reduced genetic variation.

Populations of northern red-backed voles (*Clethrionomys rutilus*) in southeastern Alaska also showed minimal levels of intraspecific genetic divergence. Southern red-backed voles, however, exhibited higher levels of intraspecific divergence (than *C. rutilus*), which was indicative of an earlier colonization of the region and was consistent with the current subspecific taxonomy. Specimens from a zone of contact identified morphologically as *C. gapperi* showed cytochrome *b* haplotypes characteristic of *C. rutilus* (Cook et al., 2001). The current ranges depicted for the two species in southeastern Alaska (MacDonald and Cook, 1999) are misleading and need revision (Runck, 2001). Smith et al. (2001) captured *C. rutilus* on the mainland ≥100 km south of the published southern distributional limit of this species.

Phylogeographic analyses of several species (Demboski et al., 1998a; Arbogast, 1999; Stone and Cook, 2000; Cook et al., 2001) provided further understanding of the evolutionary diversity, subspecific taxonomy, and underlying processes associated with the extant mammal fauna in southeastern Alaska, all of which are fundamental to the conservation of biological diversity across the Tongass National Forest (MacDonald and Cook, 1996; Stone and Cook, 2000; Cook and MacDonald, 2001). For species like *C. rutilus*, which showed low levels of genetic divergence relative to conspecific populations elsewhere, the evidence suggested recent (i.e. Holocene), post-glacial colonization of southeastern Alaska. Similarly, *G. s. griseifrons* and the four endemic subspecies of *C. gapperi* are likely part of a group of neoendemics that colonized the region during the Holocene, perhaps even using similar dispersal routes during interglacial periods (Demboski et al., 1998a; Stone and Cook, 2000). Although these neoendemics showed relatively low levels of intraspecific divergence, genetic differentiation was diagnostic and consistent with corresponding subspecific delineations (Cook et al., 2001). In most circumstances (e.g. *G. s. griseifrons*), the original subspecific descriptions based on morphology were corroborated by genetic analyses (Demboski et al., 1998a).

In contrast, the more divergent lineages of several species (e.g. American marten, *Martes americana*) suggest a much longer period of isolation from conspecific populations (Stone and Cook, 2000; Cook et al., 2001; Demboski and Cook, 2001). These taxa may represent paleoendemics; that is, relic populations that persisted in refugia during periods of glacial maxima (Cook et al., 2001). Moreover, the presence of

multiple lineages within several species indicates that geography and evolution were paramount in shaping the community dynamics of mammal assemblages in southeastern Alaska (Stone and Cook, 2000). Nevertheless, the levels of genetic variation exhibited by these species suggest that the current taxonomy may underestimate the diversity of some mammalian taxa in southeastern Alaska.

Conservation of biological diversity requires maintaining the evolutionary diversity of organisms indigenous to a region (Cook and MacDonald, 2001) as well as its ecological elements, processes, and functions. A solid evolutionary framework founded in phylogeography is fundamental to documenting endemism throughout southeastern Alaska and managing the Tongass National Forest to sustain its endemic mammal taxa (Demboski et al., 1998a; Stone and Cook, 2000; Cook and MacDonald, 2001; Cook et al., 2001). Emerging patterns of genetic variation and divergence have immediate, direct implications for the management of endemics in southeastern Alaska. The Tongass National Forest in its recent revision of the land management plan included standards and guidelines that stipulate additional survey and analyses among small (≥20,000 ha) islands where viability risks for endemics are high before significantly modifying vegetation (USDA Forest Service, 1997). Cook et al. (2001) suggested managing distinctive regions of southeastern Alaska independently.

More work is needed in southeastern Alaska because of the complexity of the questions and the dynamic geological history of the region, because of shortcomings of techniques used to characterize zoogeography, and because the available evidence suggests that the mammal fauna of southeastern Alaska is comprised of multiple elements with discontinuities and different histories representing distinct regional assemblages (Cook et al., 2001). At a minimum, all recognized endemic taxa of the region would benefit from examination with molecular techniques (Cook and MacDonald, 2001). Furthermore, comprehensive sampling and rigorous analyses of specimens from smaller islands (especially near-shore islands) throughout the Alexander Archipelago are needed to confirm the geographic range and review the taxonomy of documented taxa and to determine if endemic taxa remain undocumented (Cook and MacDonald, 2001; Cook et al., 2001).

3. Ecology of endemic arboreal and forest-floor mammals

3.1. Prince of Wales flying squirrel

3.1.1. Geographic and habitat distribution

In southeastern Alaska, northern flying squirrels occur on the mainland east of Glacier Bay National Park and south of the Chilkat River (MacDonald and Cook, 1996, 1999). In the Alexander Archipelago, they have not been documented on Etolin Island or Woronkofski Island, the islands north of Sumner Strait (except Mitkof Island), and the islands south of Revillagigedo Island (MacDonald and Cook, 1999). The known distribution of the Prince of Wales flying squirrel (*G. s. griseifrons*) includes the following islands (Bidlack and Cook, 2002): Dall, El Capitan, Heceta, Kosciusko, Orr, Suemez, Tuxecan, Prince of Wales, and Barrier Islands southwest of Prince of Wales (Fig. 1).

In the Pacific Northwest, the northern flying squirrel (hereafter flying squirrel) is considered an old-growth associate (but see Rosenberg and Anthony, 1992) because its highest densities occur in late-seral coniferous forests (Carey, 1995; Carey et al., 1992). Also, it has been implicated as a keystone species of coniferous forest ecosystems of the Pacific Northwest because of its roles in the dissemination of mycorrhizal fungi and as primary prey of the spotted owl and several small carnivores (Maser et al., 1978, 1985, 1986; Forsman et al., 1984; Maser and Maser, 1988; Carey, 1995; Carey et al., 1999). Flying squirrels are more abundant in late-seral and complex young forest (Carey, 2000a, 2000b) than in conventionally managed stands in a variety of coniferous forest types in the Pacific Northwest (Carey et al., 1992; Witt, 1992; Carey, 1995; Waters and Zabel, 1995). Important forest habitat attributes associated with higher densities of flying squirrels include complex forest canopy structure, higher decadence, large live and dead trees (standing and down), and a well-developed understory of ericaceous shrubs (Carey et al., 1999).

In southeastern Alaska, Smith and Nichols (2003) observed the Prince of Wales flying squirrel in unmanaged landscapes of old-growth peatland-scrub/mixed-conifer and western hemlock (*Tsuga heterophylla*)–Sitka spruce (*Picea sitchensis*) forests. Their study provided the first evidence of flying squirrel populations in peatland-scrub/mixed-conifer forests

Table 2
Abundances of northern flying squirrels (*G. sabrinus*) among forested habitats of western North America (Smith et al., 2003)

Forest type	Age/disturbance history	Season	Densities (ha)		Reference
			Mean	Range	
Douglas-fir	Young growth, clearcut	Spring	1.1	0.7–1.6	Carey et al. (1992)
Douglas-fir	Young growth, clearcut	Fall	0.5	0.3–0.7	Carey et al. (1992)
Douglas-fir	Young growth, clearcut	Fall	1.9	1.1–2.5	Rosenberg and Anthony (1992)
Douglas-fir	Old growth, natural	Spring	1.8	1.1–2.2	Carey et al. (1992)
Douglas-fir	Old-growth, natural	Fall	1.9	1.8–2.2	Carey et al. (1992)
Douglas-fir	Old-growth, natural	Fall	2.3	1.4–3.3	Rosenberg and Anthony (1992)
Douglas-fir	Old-growth, natural	Annual	1.0	0.5–1.8	Witt (1992)
Douglas-fir	Second growth, clearcut	Annual	0.1	0–0.2	Witt (1992)
W. hemlock/Sitka spruce	Young growth, clearcut	Fall	0.2	n/a	Carey et al. (1992)
W. hemlock/Sitka spruce	Old-growth, natural	Fall	0.5	n/a	Carey et al. (1992)
Peatland-scrub/mixed-conifer	Old-growth, natural	Fall	1.7	1.5–1.9	Smith and Nichols (2003)
W. hemlock/Sitka spruce	Old-growth, natural	Fall	3.2	2.2–4.0	Smith and Nichols (2003)
Mixed-conifer	Old-growth, natural	Spring	1.7	0.9–3.2	Carey et al. (1992)
White fir/red fir	Mature, fire replacement	Summer	2.3	2.2–2.4	Waters and Zabel (1995)
White fir/red fir	Old-growth, natural	Summer	3.3	2.8–3.5	Waters and Zabel (1995)
White fir/red fir	Old-growth, shelterwood cut	Summer	0.4	0.2–0.6	Waters and Zabel (1995)

and the first quantitative estimates of flying squirrel abundance in southeastern Alaska. In interior Alaska, flying squirrel populations apparently thrive in open-canopied white spruce (*Picea glauca*) forest (Mowrey and Zasada, 1984), which seem similar in stand structure to some peatland-scrub/mixed-conifer sites of southeastern Alaska (Smith and Nichols, 2003).

3.1.2. Abundance and demography

Flying squirrel abundance in western coniferous forests differs considerably (Table 2) depending on forest type, seral stage, and management history (Smith et al., 2003). In southeastern Alaska, flying squirrel densities were among the highest reported anywhere in North America and were nearly 2× higher in western hemlock–Sitka spruce forests than in peatland-scrub/mixed-conifer (Smith and Nichols, 2003). Still, peatland-scrub/mixed-conifer, which is mostly non-commercial forest because of the prominence of muskegs and wet, shallow, organic soils (DeMeo et al., 1992; Julin and Caouette, 1997), supported flying squirrel densities that were comparable to some old-growth Douglas-fir (*Pseudotsuga menziesii*) stands in Washington (Table 2; Carey et al., 1992).

Possible factors contributing to variation in flying squirrel densities among regions, especially between Oregon and Washington and southeastern Alaska, include predation (Rosenberg and Anthony, 1992), competitive release (Carey et al., 1992), diet (Pyare et al., 2002), and habitat relations (Smith et al., 2004, in press). Unlike in Oregon and Washington, where flying squirrels are primary prey of northern spotted owls (*Strix occidentalis occidentalis*), there is no known specialized predator of *G. sabrinus* in southeastern Alaska. Also, southeastern Alaska has a relatively depauperate mammal fauna with only one other arboreal rodent (i.e. red squirrel, *Tamiasciurus hudsonicus*), which is absent from Prince of Wales Island (MacDonald and Cook, 1996). In contrast, the arboreal rodent community of western Oregon and Washington is comprised of many species, some of which overlap in use of important forest resources (Carey, 1991). Diet (or food habits) also has been implicated as a factor influencing squirrel abundance in the Pacific Northwest (Carey et al., 1999; Pyare and Longland, 2002). Diet of flying squirrels in the Pacific Northwest (e.g. Pyare and Longland, 2001) differs substantially from diet of flying squirrels in southeastern Alaska, where frequency of truffles was lower and frequency of mushrooms, lichens, and vascular vegetation was higher than reported elsewhere (Pyare et al., 2002). Habitat relations also differed between regions, as variation in micro-habitat use and density in southeastern Alaska was attributable to a few key habitat variables rather than multi-variate habitat factors (Smith et al., 2004, in press). The less specialized diet and less complex habitat relations of northern

flying squirrels in southeastern Alaska may reflect a more general lifestyle, including opportunities to use a broader range of rainforest habitats because of less interspecific competition (Carey, 1991, 1996, 2000a, 2001; Carey et al., 1999).

Age and sex composition, mean body weight of flying squirrels, and juvenile recruitment in southeastern Alaska generally were independent of habitat (Smith and Nichols, 2003). The only exception was that sex ratios consistently favored males, with a larger bias in peatland-scrub/mixed-conifer than western hemlock–Sitka spruce forests (Smith and Nichols, 2003). This pattern contrasted with slightly female-biased sex ratios elsewhere in the Pacific Northwest (Carey, 1995; Villa et al., 1999). Also, juvenile recruitment was substantially lower in southeastern Alaska than elsewhere in the Pacific Northwest (Smith and Nichols, 2003), which may have been related to density-dependent influences on natality or survivorship (Villa et al., 1999). Summer survivorship of flying squirrels in southeastern Alaska was higher in western hemlock–Sitka spruce forests than in peatland-scrub/mixed-conifer, whereas overwinter survival and longevity were similar between habitats (Smith and Nichols, 2003). Mean number of reproductive females was significantly higher in western hemlock–Sitka spruce forests than in peatland-scrub/mixed-conifer, but the percentage of reproductive females in the population did not differ between habitats. Thus, the disparity in density between habitats likely was related to differences in spatial heterogeneity, which influenced number of macro-habitats (sensu Morris, 1987a, 1987b) and micro-habitat variation in preferred resources, especially distribution of large trees and snags (Smith et al., 2004).

3.1.3. Habitat relations

Northern flying squirrel populations become more abundant with increasing forest complexity in the Pacific Northwest (Carey, 2001; Carey et al., 1999) and elsewhere (Weigl et al., 1992). Abundance of northern flying squirrels has been correlated with micro- and macro-habitat features that are common among forest types across several locations in the Pacific Northwest (Carey et al., 1999; Waters and Zabel, 1995; Witt, 1992), including midstory cover, understory vegetation, coarse woody debris, prevalence of ericaceous shrubs, and frequency of hypogeous sporocarps (Waters and Zabel, 1995; Carey et al., 1999). However, no single habitat variable or group of habitat attributes thoroughly explained variation in habitat use or abundance across regions (Carey et al., 1999), and at least one study reported that flying squirrel densities in second-growth and old-growth forests were not correlated with habitat characteristics (Rosenberg and Anthony, 1992).

Rather, the relationship between habitat and flying squirrel abundance in the Pacific Northwest has been characterized as multi-factorial; that is, a consequence of increasing synergism among habitat elements as forests develop and additional key habitat features coincide at spatial scales that facilitate integration within individual home ranges (Carey et al., 1999; Carey, 2000b). Habitat conditions that consistently explained variation in abundance among stands or foraging activity within stands were multi-variate factors of forest condition such as decadence. For this reason, flying squirrels have been proposed as a management indicator species of old-growth coniferous forest condition in the Pacific Northwest and southeastern Alaska (Carey et al., 1999; Carey, 2000a).

In temperate rainforest of southeastern Alaska, Smith et al. (2004) modeled the relationships of habitat variables (e.g. density of snags, large trees) with micro-habitat use by flying squirrels in western hemlock–Sitka spruce forests and peatland-scrub/mixed-conifer forests. They reported that large (>74 cm diameter-at-breast height [dbh]) trees and understory cover of *Vaccinium* were positively correlated with flying squirrel captures during both seasons in peatland-scrub/mixed-conifer. A projected increase in density of large trees of 10 stems/ha increased the odds of capture by a factor of 2.7 and 16.9 during spring and autumn, respectively. Similarly, an increase of 10% understory cover of *Vaccinium* increased the odds of capturing flying squirrels by a factor of 1.9 during spring and 2.7 during autumn. The ecological significance of large trees and *Vaccinium* in peatland-scrub/mixed-conifer (Smith et al., 2004) was corroborated by analyses of multivariate factors (Smith et al., in press). In contrast, patterns of micro-habitat use in western hemlock–Sitka spruce forests were less obvious and insightful. Captures were inversely related to percentage cover of surface water during spring and percentage cover of herbs and density of saplings during autumn (Smith et al., 2004, in press). Micro-habitat use during

autumn was positively correlated with density of large (50–74 cm dbh) and small (10–49 cm dbh) snags. The performance of models developed from habitat features were similar in predicting habitat use in both habitats during both seasons and comparable to that reported for habitat models in the Pacific Northwest (Carey et al., 1999). Furthermore, individual habitat features were as effective as multivariate factors in explaining habitat use (Smith et al., in press), suggesting that the northern flying squirrel in southeastern Alaska differs ecologically in important ways from populations in the Pacific Northwest that may diminish its value as a management indicator species (Smith et al., in press).

Smith et al. (2004) also examined flying squirrel density relative to average habitat features among stands; 23 of 26 measured habitat variables differed between habitats. Density of large (>74 cm) live trees explained 65% of the variation in autumn population density among stands. Density of trees 5–10 cm dbh (which were inversely correlated with density of large trees) explained 72% of the variation in flying squirrel density during autumn. In the spring, percentage cover of moss and amount of decayed downed wood were positively correlated with flying squirrel density, explaining 70 and 77% (decay class 3) of the variation in flying squirrel density among stands, respectively (Smith et al., 2004). Despite its apparent ecological importance in influencing micro-habitat use in peatland-scrub/mixed-conifer, mean percentage cover of *Vaccinium* explained little variation in flying squirrel density between habitats.

3.2. *Wrangell Island red-backed vole*

3.2.1. *Geographic and habitat distribution*

In southeastern Alaska, the southern red-backed vole (hereafter vole) occurs on the mainland south of Taku Inlet and on near-shore islands near the southern end of the Alexander Archipelago (MacDonald and Cook, 1996, 1999). Four subspecies are recognized in this region (Hall and Cockrum, 1952); two taxa (*C. g. stikinensis* and *C. g. phaeus*) occur on the mainland, whereas the remaining two are island endemics. *C. g. wrangeli* occurs on Wrangell and Sergief islands, whereas *C. g. solus* is known only from Revillagigedo Island (Fig. 1). Recent efforts to detect voles on nearby islands (Deer, Woronkofski, Etolin; Fig. 1) were unsuccessful (USDA Forest Service, unpublished data, on file with Wrangell Ranger District). Several factors complicated attempts to document vole presence, not the least of which is the potential for dramatic annual fluctuations in population levels (e.g. Fuller, 1977; Smith and Nichols, 2004). In addition, there is no estimate of probability of detection or standardized protocol for surveying voles that allows statistical inference about absence. Nonetheless, a fundamental aspect of managing forests to sustain biological diversity is completing rigorous surveys on smaller islands to thoroughly document the geographic range of previously documented endemic mammal populations and to determine if additional unique mammalian taxa exist (Cook and MacDonald, 2001; Cook et al., 2001).

Little is known about the natural history, habitat distribution, or population ecology of *C. gapperi* in southeastern Alaska (Runck, 2001; Smith et al., 2001). Of particular interest is their reputed association with old-growth coniferous forests (Jerry, 1984; Nordyke and Buskirk, 1988; Aubry et al., 1991; West, 1991). Old-growth forests apparently represent optimal habitat for voles in the Pacific Northwest (Jerry, 1984; but see Taylor, 1999). Vole densities in old-growth forests were 2× that observed in younger (55–75-year-old) second-growth stands (Aubry et al., 1991) and about 4–5× more abundant in old-growth forest than young (17-year-old) growth (Sullivan et al., 2000) or recent (3–9-year-old) clearcuts (Sullivan et al., 1999), respectively. Moreover, voles may show acute sensitivity to habitat fragmentation (Bayne and Hobson, 1998; Bowman et al., 2001; Mech and Hallett, 2001).

In southeastern Alaska, there have been few studies of vole demography or habitat relations (Smith and Nichols, 2004). Similar to the vast majority of studies in the Pacific Northwest, Smith and Nichols (2004) found that *C. gapperi* populations showed consistently high densities in late-seral coniferous forests. They also reported that peatland-scrub/mixed-conifer (peatland-scrub/mixed-conifer) was marginal habitat for voles; whereas, recently thinned young (20–25-year-old) growth may be suitable for supporting breeding populations, at least in years when vole population levels are relatively high.

3.2.2. *Abundance and demography*

Vole densities reported for the Pacific Northwest differ substantially according to region, forest type, land use, and methodology (Table 3). Regrettably, densi-

Table 3
Mean abundance and coefficient of variation (CV) of southern red-backed vole (*C. gapperi*) populations among forested habitats of western North America

Forest type	Age/disturbance history	Method	Densities (ha)		Reference
			Mean	CV (%)	
Spruce/fir	Old-growth	Jolly-Seber	7.04	101	Sullivan et al. (1999)
Spruce/fir	Young clearcut	Jolly-Seber	1.10	61	Sullivan et al. (1999)
Spruce/fir	Young clearcut, burned	Jolly-Seber	0.04	173	Sullivan et al. (1999)
Douglas-fir/pine	Old-growth	Jolly-Seber	13.78	81	Sullivan et al. (2000)
Douglas-fir/pine	Thinned seed tree	Jolly-Seber	3.41	90	Sullivan et al. (2000)
Douglas-fir/pine	Thinned clearcut	Jolly-Seber	2.72	52	Sullivan et al. (2000)
Douglas-fir	Old-growth	Lincoln-Petersen	3.41	41	Medin (1986)
Douglas-fir	Old-growth	Lincoln-Petersen	0.74	20	Medin (1986)
Douglas-fir	Young diameter-limit harvest	Lincoln-Petersen	0	0	Medin (1986)
W. hemlock/Sitka spruce	Old-growth (gap-phase)	Lincoln-Petersen	6.17	52	Smith and Nichols (2004)
W. hemlock/Sitka spruce	Old-growth (multi-cohort)	Lincoln-Petersen	8.73	105	Smith and Nichols (2004)
Peatland-scrub/mixed-conifer	Unmanaged	Lincoln-Petersen	0.71	<1	Smith and Nichols (2004)
W. hemlock/Sitka spruce	Thinned clearcut	Lincoln-Petersen	10.77	119	Smith and Nichols (2004)

ties from the Pacific Northwest did not include estimates of effective area sampled (Swift and Steinhorst, 1976) and therefore are not directly comparable to densities reported for southeastern Alaska (Smith and Nichols, 2004). Effective area sampled often is substantially larger than corresponding sampling grids and may approach an order of magnitude greater in size (Van Horne, 1982; Smith and Nichols, 2004). Consequently, many density estimates reported for the Pacific Northwest were inflated because the area encompassed by the sampled population was underestimated (Swift and Steinhorst, 1976; Van Horne, 1982). Still, a striking contrast in vole density is apparent between young-growth forests of southeastern Alaska and the Pacific Northwest where differences in mean population density approached an order of magnitude (Table 3). Though not directly comparable, the higher vole density in thinned, young-growth forests of southeastern Alaska is likely ecologically meaningful, especially considering that estimates from the Pacific Northwest were likely inflated (Smith and Nichols, 2004).

In southeastern Alaska, old-growth forests and peatland-scrub/mixed-conifer were the highest and lowest ranked habitats according to a suite of vole demographic parameters, respectively (Smith and Nichols, 2004). Vole densities reported for old-growth and managed hemlock–spruce forests were significantly higher than densities in largely noncommercial forests of peatland-scrub/mixed-conifer, which remained low throughout the study (Table 3). Scrub-peatland/mixed-conifer forests of southeastern Alaska probably do not support breeding populations of *C. gapperi* (Smith and Nichols, 2004). Mean body mass, minimum summer and overwinter survival, age and sex composition, and percentage of reproductive females did not differ among gap-phase (GP), multi-cohort (MC), and young (20–25-year-old) growth habitats.

3.2.3. Habitat relations

There has been only one study of the habitat relations of *C. gapperi* in southeastern Alaska, in which correlates of micro-habitat use and population density were quantified within and among four common habitats, respectively (W.P. Smith et al., submitted for publication). Not surprisingly, habitat use differed among seasons and years and reflected temporal variation in population levels (Smith and Nichols, 2004). Total number of trap stations where voles were captured corresponded directly with population density, whereas unique number of stations where voles were captured increased as populations of voles and Keen's mouse (*Peromyscus keeni*) declined. Few voles were captured in Peatland-scrub/mixed-conifer and it is unlikely that this habitat supports breeding populations of *C. gapperi*. Relatively few mice were captured in Peatland-scrub/mixed-conifer during this study, but it is unclear what the ecological value of this forest type is to Keen's mouse populations in southeastern Alaska as Smith et al. (2001) reported capturing *P. keeni* in similar habitat

among several Research Natural Areas of the Tongass National Forest.

During spring, vole captures were correlated with density of stumps in thinned young growth and percentage cover of deciduous shrubs in MC. However, vole micro-habitat use was most influenced by percentage cover of deciduous shrubs in the vertical stratum between the forest floor and 0.3 m, especially in GP during autumn. Volume of highly decayed down wood also was positively correlated with vole micro-habitat use in GP during autumn, whereas vole captures were lower at sites with a higher density of saplings (trees 5–10 cm dbh) and more deciduous shrub cover in the vertical stratum between 0.5 and 1.5 m. In MC, density of small (10–49 cm dbh) snags was directly related to vole captures. Multi-variate habitat factors (i.e. linear combinations of single variables; Cody and Smith, 1997) explained little additional variation in micro-habitat use, and only during autumn, when vole captures in GP were positively correlated with a multi-variate factor that mostly reflected the percentage cover of *Vaccinium* (e.g. blueberry) in the understory. In contrast, vole micro-habitat use in young growth was indirectly correlated with a similar habitat factor, except that percentage cover of moss contributed the largest portion of variation to this multi-variate correlate.

Several stand-level features were correlated with population density, explaining 50–87 and 52–84% of the variation in vole population levels during spring and autumn, respectively (W.P. Smith et al., submitted for publication). Population density during both seasons was most positively influenced (according to amount of variation explained) by the amount of highly decayed down wood among habitats. Other habitat features positively correlated with vole density included amount of moderately decayed wood during spring and autumn and percentage cover of surface water during spring. Density of small (10–49 cm dbh) snags and percentage cover of conifer seedlings between 0.30 and 1.5 m (Conif1.5) above the forest floor had the greatest negative effect on population density during spring and autumn, respectively. Vole densities also were negatively correlated with Conif1.5 and percentage cover of moss during spring and percentage cover of conifer seedlings within 0.3 m of the forest floor and density of small snags during autumn (W.P. Smith et al., submitted for publication).

Elsewhere in western coniferous forests, voles favored mesic habitats (Merritt, 1981; Ramirez and Hornocker, 1981; but see West, 1991) and moist micro-environments (Odum, 1944; Getz, 1968). *C. gapperi* has high water requirements and little resistance to drought (Getz, 1962, 1968; McManus, 1974). Gunderson (1959) and Odum (1944) suggested that a high water requirement was a limiting factor in habitat selection. Butsch (1954) proposed that the local distribution of *C. gapperi* was influenced more by the availability of free water than food. Voles prefer sites with abundant stumps and coarse woody debris, especially rotting logs and exposed roots within a loose forest litter (Gunderson, 1959; Merritt, 1981; Orrock et al., 2000; Moses and Boutin, 2001); habitat use has been correlated with the amount of coarse woody debris in the understory (Merritt, 1981; Scrivner and Smith, 1984; Ucitel et al., 2003). Vole abundance also has been linked to vegetative cover in the understory, which likely influences micro-habitat moisture and provides important foods and escape cover (Nordyke and Buskirk, 1991; Keinath and Hayward, 2003).

The role of competition in the habitat relations or population dynamics of voles in southeastern Alaska is unknown. Causal factors underlying the interspecific dynamic of small mammal populations can be determined only through manipulative ecological experiments (Morris, 1987b). However, attempts to understand the interspecific relationships of voles and other species in temperate rainforest communities likely will provide valuable insights for future conservation efforts, especially the restoration of habitat through active second-growth stand management. In southeastern Alaska, *C. gapperi* is sympatric with Keen's mouse (*P. keeni*; MacDonald and Cook, 1996), often occurring in the same habitats and using the same micro-habitats (W.P. Smith et al., submitted for publication). Throughout most of its range (particularly western North America), *C. gapperi* has been characterized as a specialist of late-seral forest condition (Merritt, 1981; Ramirez and Hornocker, 1981; Scrivner and Smith, 1984; Keinath and Hayward, 2003), whereas *Peromyscus* populations have been characterized as habitat generalists. Habitat specialization can facilitate the coexistence of species with similar resource needs, but in southeastern Alaska (and elsewhere), this model of vole and mouse habitat relations likely is an oversimplification because of the influence of spatial scale on habitat use (Morris, 1987a,

1987b; Orrock et al., 2000). This was true of both red-backed voles and Keen's mouse in southeastern Alaska.

In addition, *C. gapperi* and *P. keeni* showed density-dependent habitat responses at two spatial scales (W.P. Smith et al., submitted for publication), indicating that both were exhibiting micro-habitat and macro-habitat selection (Morris, 1996). However, density-dependent responses of *P. keeni* were not as striking as *C. gapperi*, implying that mice generally were less selective than voles. Voles and mice achieved their highest densities in different macro-habitats, but there was overlap in habitat conditions to which they responded similarly. However, there was evidence of micro-habitat segregation, as vole and mouse captures were correlated with different habitat variables and factors. Still, in some habitats (MC and GP) the likelihood of capturing mice among micro-habitats was positively correlated with the capture rate of voles. As has been shown elsewhere (Morris, 1996), the habitat relations of voles and mice in southeastern Alaska differed according to habitat types. More importantly, the correlation between species in their use of old-growth habitats suggests that scramble or interference competition from Keen's mouse populations potentially could make it more difficult for locally extirpated vole populations to colonize older, second-growth stands that became suitable habitat (Morris, 1996).

4. Implications for forest management

Implications for forest management are significant and include two fundamental elements. The first element relates to fully documenting potential consequences of land management and requires a thorough inventory of the mammal fauna in southeastern Alaska. Without detailed knowledge of the variety of organisms that occur in a region, it is impossible to evaluate the success of land management in maintaining biological diversity across a planning area. The second element is related to understanding autecology and community ecology of organisms that are impacted by land management. In southeastern Alaska, this requires knowledge of biogeography as well as life history traits and habitat needs. The interplay of these two aspects creates unique challenges for sustainable multiple use of forest values because of the unique setting of this biome and because of life history attributes of organisms adapted to living in late-seral forest habitat.

4.1. Endemism and evolutionary diversity

There has been an unprecedented effort to document the composition and distribution of land mammals in this region. As with most good research, however, many more questions have been generated than answers. The good news is that we are beginning to understand the historical events and processes that were likely responsible for structuring the region's extant mammal fauna. Unfortunately, along with this understanding comes the recognition that the potential for endemism and taxonomic diversity is greater than previously thought. With few exceptions, our knowledge regarding the evolutionary diversity of mammals in southeastern Alaska is rudimentary (MacDonald and Cook, 1996).

Early expeditions sampled a minute fraction (<1%) of the islands in the Alexander Archipelago (MacDonald and Cook, 1996). Surveys included the larger islands, but only a small portion of the total area of each island has been sampled, and in many instances, only once. More recent surveys substantially increased the number of specimens that now include representatives from 87 islands. Still, except for islands with a good road system, most surveys were conducted within 2 km of the shoreline, leaving much of the island interior undocumented. That multiple unique taxa of species may evolve within large contiguous land areas has been clearly illustrated in the Mainland Subregion, where the highest number of endemics in southeastern Alaska occurs (MacDonald and Cook, 1996).

The 1997 TLMP incorporated standard and guidelines to reduce the risk of extinction of endemic small mammals on islands (USDA Forest Service, 1997). Unfortunately, these guidelines are applied to small ($\leq$20,000 ha) islands, only when there is evidence of endemic taxa present and when proposed management actions are perceived as substantially increasing the risk of population viability. Without continued efforts to verify the composition and distribution of mammals in southeastern Alaska, the likelihood of modifying habitat of undocumented unique small mammal populations remains reasonably high (Cook and

MacDonald, 2001). There are numerous islands in the vicinity of island endemic populations that have not been adequately sampled (MacDonald and Cook, 1996; Cook and MacDonald, 2001). New information obtained from additional surveys likely will have direct consequences for future land management of southeastern Alaska. As more islands are inventoried, the likelihood of extending the known ranges of endemic mammals increases. Furthermore, any new knowledge that increases the range or number of populations of endemic taxa reduces the risk of extinction (Burkey, 1995; Frankham, 1998).

4.2. *Ecology of endemic arboreal and forest-floor mammals*

Arboreal rodents have an obvious association with forests, and a dependence on trees predisposes them to being impacted by timber harvests (Carey, 1991, 1995; Smith et al., 2003). For that reason, arboreal rodent populations are a good barometer of forest habitat condition and often are useful as management indicator species (Carey, 2000b; Carey and Harrington, 2001). Among these, the flying squirrel has been viewed as an indicator species of old-forest condition in the Pacific Northwest because many aspects of its life history are linked to old-forest features (Carey, 1991, 1995, 2000a, 2000b, 2001). Forest-floor mammals may not have such an obvious link to old-growth forests, but some species have biological requirements that are met mostly in forests with specific vegetative or structural characteristics. Southern red-backed voles, like flying squirrels, attain their highest densities in late-seral coniferous forests. The reasons are not clear, but some investigators suggested that it might be related to physiological demands of *C. gapperi* for free water (Getz, 1962, 1968) and the cool, wet micro-climatic conditions typical of older coniferous forest (Odum, 1944; Getz, 1968; Smith and Nichols, 2004). Understanding the autecology of flying squirrels and voles in temperate rainforests is basic to evaluating the influence of timber management on their population viability.

4.2.1. *Flying squirrels*

Smith and Nichols (2003) and Smith et al. (2004, in press) provided the first quantitative information on flying squirrel demography and habitat relations in southeastern Alaska. An especially relevant contribution of this work to future land management was their findings in peatland-scrub/mixed-conifer forests. Results of their demographic analyses support the view that western hemlock–Sitka spruce forests are primary habitat for northern flying squirrels in southeastern Alaska (Smith and Nichols, 2003). More important from a perspective of future land management, however, were their findings that flying squirrel densities among noncommercial peatland-scrub/mixed-conifer forests were comparable to densities reported for several unmanaged and managed forest types in the Pacific Northwest. Furthermore, many demographic parameters did not differ between western hemlock–Sitka spruce forests and peatland-scrub/mixed-conifer. These results suggest that flying squirrel populations in southeastern Alaska are not limited to higher volume spruce–hemlock forests. Moreover, peatland-scrub/mixed-conifer forests likely contribute to breeding populations of northern flying squirrels in managed landscapes and likely reduce risk of extirpation (Smith and Nichols, 2003).

Many of the habitat features that influenced flying squirrel micro-habitat use and density in temperate rainforests were similar to those reported for populations in the Pacific Northwest (Carey, 1995, 2000a, 2000b; Carey et al., 1999). Of these, a higher density of large live and dead trees, greater abundance of decaying, down coarse woody debris, and higher percentage cover of moss on the forest floor are features typical of old-growth, coastal coniferous forests (Spies et al., 1988). Another valuable result was that the density of large (>74 cm) trees explained significant variation in micro-habitat use in peatland-scrub/mixed-conifer, but it was not among the variables influencing flying squirrel captures in western hemlock–Sitka spruce forests (Smith et al., 2004, in press). Large live and dead trees probably are more valuable to flying squirrels in peatland-scrub/mixed-conifer (especially as natal dens during spring, Carey, 1995), which has less forest canopy cover than western hemlock–Sitka spruce forests. That micro-habitat use in western hemlock–Sitka spruce forests was not correlated with large trees suggests that large trees were readily available and not limiting to flying squirrels. This result is not surprising, given a more uniform distribution and much higher density of large trees in western hemlock–Sitka spruce forests than in peatland-scrub/mixed-conifer

(Smith et al., 2004, in press). Nonetheless, removing large trees, such as through selective logging, will likely have a disproportionally greater impact on flying squirrel densities in peatland-scrub/mixed-conifer than western hemlock–Sitka spruce forests. Moreover, there are implications for flying squirrel populations of managed landscapes, especially where breeding populations of more productive peatland-scrub/mixed-conifer are a source for recolonizing managed western hemlock–Sitka spruce forests stands that become suitable habitat. Select logging of peatland-scrub/mixed-conifer forest likely will diminish its value in reducing the risk to viability of flying squirrel populations by reducing population density, increasing the likelihood of local extirpations, and decreasing opportunities for recolonization.

4.2.2. *Red-backed voles*

Smith and Nichols (2004) provided the first quantitative estimates of demography and habitat relations of southern red-backed voles in southeastern Alaska. A valuable contribution of their research as it relates to forest management was their findings that red-backed voles consistently occupied thinned young second-growth stands and that abundance was higher than expected because of this species' reputed association with old-growth coniferous forests. Old-growth spruce–hemlock forests were the highest ranked habitat according to several demographic parameters, but pre-commercially thinned second-growth stands supported breeding populations of *C. gapperi*, at least in years when overall population levels were high. Climatic conditions in southeastern Alaska may mitigate the drier understory conditions that often occur in coniferous forests when the canopy is removed. Consequently, red-backed voles in young second-growth stands may be exposed to desiccation less frequently because of the cooler, wetter summers in southeastern Alaska as compared to the Pacific Northwest. Nonetheless, the potential capability of managed second-growth stands to support breeding populations of *C. gapperi* has significant implications for risk to viability. Conversely, peatland-scrub/mixed-conifer forests are marginally suitable habitat for *C. gapperi* and probably would not contribute to breeding populations in managed landscapes (Smith and Nichols, 2004). Their value as corridors of dispersal for maintaining connectivity among sub-populations is unknown.

Despite evidence that red-backed vole populations in temperate rainforest may not be as sensitive to canopy removal as has been suggested elsewhere, there remain many questions that warrant further study (Smith and Nichols, 2004; W.P. Smith et al., submitted for publication). Their study was of short duration and at only one location. Red-backed voles show substantial annual (Fuller, 1977) and geographic variability in population size (Table 3). Smith and Nichols (2004) reported significant annual variation in small mammal abundance during their 2.5-year study with potentially important implications for habitat distribution. It is crucial to understand how habitat distribution and abundance of vole populations differs over time as population levels fluctuate.

In addition, there are important questions about the habitat capability of older second-growth stands, especially the period between canopy closure (following precommercial thinning) and the understory initiation phase. In southeastern Alaska, the benefits to the understory of pre-commercial thinning are relatively short-lived (Alaback, 1998) and the period of stem exclusion can last several decades (Nowacki and Kramer, 1998). Uncertainty regarding the value of older second-growth stands as habitat elevates viability risk for endemic *C. gapperi* populations in intensively managed landscapes. To reduce these risks, future land managers will need to focus on acquiring the knowledge that will facilitate management of second-growth stands to benefit red-backed vole populations.

5. Future management issues and information needs

Future management information needs will likely fall into three general categories: (1) continued documentation of endemism and associated taxonomy of terrestrial mammals of southeastern Alaska; (2) population ecology of endemic forest habitat specialists with a focus on identifying stand and landscape features that restrict dispersal in managed landscapes; and (3) population ecology of late-seral forest habitat specialists in managed second-growth stands. There is an element of category 3 that includes retrospective studies (Hanley et al., this issue) and second-growth management experiments designed for the purpose of effective habitat restoration in watersheds where extensive commercial

clearcut logging has substantially reduced and fragmented old-growth forests. More importantly, there are opportunities for synergism from studying communities of endemic wildlife with similar life histories and resource needs, or with close interspecific relationships (e.g. predator–prey dynamics).

Obvious research under category 1 includes field inventories and genetic analysis of animals to document the composition and distribution of mammals in southeastern Alaska. This effort should focus on near-shore islands, especially in the vicinity of known island endemics; and in remote, interior portions of large islands, especially where land features (e.g. mountains, rivers) may serve as a barrier to free movement of small mammals. A crucial and fundamental information need associated with category 1 includes development of the technical basis of sampling protocols for detecting presence/absence of arboreal and forest-floor mammals. Without rigorous protocols, it is virtually impossible to document that endemic small mammals *do not occur* on islands with any statistical confidence. Knowledge obtained from this work will also contribute valuable information for ecological studies, as it will provide a statistical estimate of detection probability for species of interest.

In addition, there are important assumptions of the TLMP conservation strategy that need to be tested, not the least of which is the assumption of freely interbreeding demes among old-growth reserves. This assumption requires an understanding of factors that affect dispersal of flying squirrels in unmanaged and managed landscapes. It requires studying old-growth forest patches in managed landscapes and documenting successful dispersal through an intervening matrix of different aged second-growth stands. This work can be accomplished in such a way as to gain information about habitat capability of managed and unmanaged second-growth stands and also will be useful in planning habitat restoration efforts.

Another basic element of the conservation strategy is that small (400–500 ha) habitat conservation areas (HCA) will support breeding populations of flying squirrels indefinitely. The findings of Smith and Nichols (2003) provide evidence that high-volume spruce–hemlock forest on Prince of Wales Island support flying squirrel densities that meet the criterion of small HCAs. However, southeastern Alaska spans across a wide latitudinal gradient and has a diverse array of climatic, physical, and biotic conditions, including ecologically significant differences in community composition of potential predators and competitors of flying squirrels (Smith et al., 2003; Smith and Nichols, 2003). Additional investigations of flying squirrel demography stratified across the forest will increase confidence that HCAs throughout southeastern Alaska will support breeding populations of flying squirrels.

For forest-floor mammals, there is a need for longer-term (>5 years) population studies. These investigations can be designed to obtain information about habitat capability of managed second-growth stands, as well as answer crucial questions about patterns of habitat distribution as population levels fluctuate among years. With planning, some studies can be integrated into activities in cooperation with Tongass National Forest personnel to meet objectives that require wildlife surveys.

The priority that each category receives will be influenced by several factors, not the least of which are policies that directly influence the amount, diversity, and distribution of old-growth forests that remain in reserves on the Tongass National Forest (Hanley et al., this issue). If, for example, the Tongass were to remain roadless for the foreseeable future, opportunities to modify old-growth forests likely would diminish substantially. Opportunities for selective logging would exist, but limited surface access (water or road) probably imposes constraints on the amount of helicopter logging that can occur. Policy influences on future management of the Tongass National Forest likely would shift the research priorities of information needs from issues that relate to logging of old-growth forests to questions about managing second-growth stands to achieve vegetative and structural characteristics that would benefit wildlife communities. Nonetheless, the knowledge gained from TLMP follow-on studies represents invaluable baseline information, providing an essential foundation upon which to develop future research; whether it is questions related to the influence of additional regeneration harvests on the persistence of breeding populations or meta-population dynamics in managed landscapes, or identifying silvicultural prescriptions that enhance second-growth forest as habitat for arboreal or forest-floor endemic mammal populations.

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