

Implications of cytochrome *b* sequence variation for biogeography and conservation of the northern flying squirrels (*Glaucomys sabrinus*) of the Alexander Archipelago, Alaska

John R. Demboski, Brandy K. Jacobsen, and Joseph A. Cook

Abstract: The Alexander Archipelago of southeast Alaska is a highly fragmented landscape that is suspected to support a relatively large number of endemic mammals. At least two subspecies of northern flying squirrels (*Glaucomys sabrinus*) have been recognized from the region, the endemic Prince of Wales Island flying squirrel, *Glaucomys sabrinus griseifrons*, and the Alaska Coast flying squirrel, *G. s. zaphaeus*. We examined 56 northern flying squirrels from Alaska, Washington State, and Yukon Territory, using the DNA sequence from the mitochondrial cytochrome *b* gene to assess geographic variation. Flying squirrels from Washington were highly divergent (7.3%) from those of Alaska and Yukon Territory. Variation among Alaska and Yukon Territory populations was minimal, but five haplotypes were found. One predominantly “mainland” haplotype was widespread throughout Alaska, one island haplotype was confined to nine islands in southeast Alaska (“Prince of Wales complex”), and three haplotypes were unique. Flying squirrels of the Prince of Wales complex appear to be neoendemics and descended from a single founder population. Mitochondrial variation, although minimal, is consistent with the continued recognition of *G. s. griseifrons*. Our results, in light of increased habitat fragmentation in southeast Alaska, suggest that molecular data can provide important base-line information for effective management of insular populations.

Résumé : L’archipel d’Alexander, dans le sud-est de l’Alaska, représente un paysage fortement fragmenté que l’on croit supporter un nombre relativement élevé de mammifères endémiques. Au moins deux sous-espèces du Grand Polatouche (*Glaucomys sabrinus*) ont été reconnues dans la région, les sous-espèces endémiques de l’île du Prince-de-Galles, *Glaucomys sabrinus griseifrons*, et de la côte d’Alaska, *G. s. zaphaeus*. Nous avons examiné les séquences d’ADN du gène mitochondrial cytochrome *b* pour évaluer la variation géographique chez 56 Grands Polatouches de l’Alaska, du Washington et du Yukon. Les polatouches du Washington sont très différents (divergence 7,3%) de ceux de l’Alaska et du Yukon. La variation entre les populations de l’Alaska et du Yukon est minimale, mais cinq haplotypes ont été reconnus. Un haplotype surtout « continental » est bien répandu dans toute l’Alaska, un haplotype insulaire est confiné à neuf îles du sud-est de l’Alaska (« complexe Prince-de-Galles ») et trois haplotypes sont isolés. Les polatouches du complexe Prince-de-Galles semblent néo-endémiques et dérivés d’une seule population fondatrice. La variation mitochondriale, quoique minime, justifie la reconnaissance de *G. s. griseifrons* comme un taxon valide. Nos résultats, à la lumière de la fragmentation progressive de l’habitat dans le sud-est de l’Alaska, permettent de croire que les données moléculaires peuvent fournir une base d’information très utile pour l’aménagement efficace des populations insulaires.

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Introduction

The relatively high number of endemic mammal taxa of the Alexander Archipelago in southeast Alaska is related to the region’s biogeographical complexity. Two endemic species, the Glacier Bay water shrew (*Sorex alaskanus*) and

Coronation Island vole (*Microtus coronarius*), and 25 subspecies of mammals are currently recognized from the region (MacDonald and Cook 1996). Determining whether these taxa might be paleoendemics that persisted in coastal refugia during Pleistocene glacial advances (Heaton et al. 1996; Byun et al. 1997), neoendemics that have colonized

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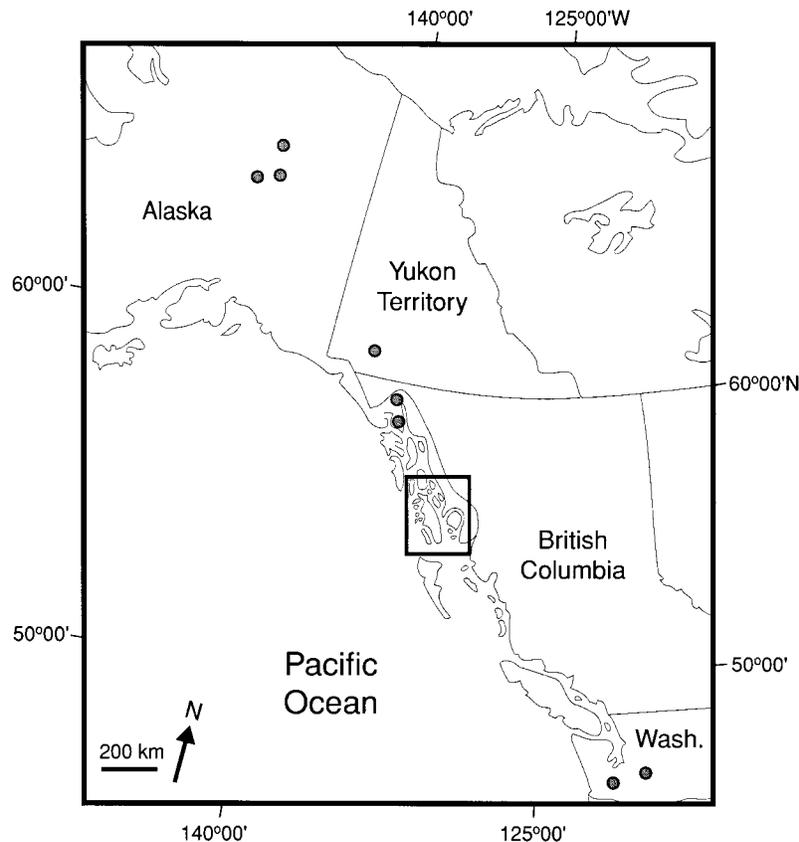
J.R. Demboski.¹ Biochemistry and Molecular Biology Program, Department of Chemistry, University of Alaska, Fairbanks, AK 99775-6160, U.S.A., and University of Alaska Museum, Fairbanks, AK 99775-6960, U.S.A.

B.K. Jacobsen. Institute of Arctic Biology, University of Alaska, Fairbanks, AK 99775-7000, U.S.A.

J.A. Cook. Biochemistry and Molecular Biology Program, Department of Chemistry, University of Alaska, Fairbanks, AK 99775-6160, U.S.A., University of Alaska Museum, Fairbanks, AK 99775-6960, U.S.A., and Institute of Arctic Biology, University of Alaska, Fairbanks, AK 99775-7000, U.S.A.

¹Author to whom all correspondence should be sent at the Mammalogy Department, University of Alaska Museum, 907 Yukon Drive, Fairbanks, AK 99775-6960, U.S.A. (e-mail: ftjrd@aurora.alaska.edu).

Fig. 1. Map of northwestern North America showing selected sampling localities (●) described in Table 1. The boxed area in southeast Alaska is shown in Fig. 2.



since the last glacial advance (Klein 1965; Conroy et al. 1998), or simply the result of poor taxonomic decisions (e.g., taxonomic “splitting”) is important to the management of wildlife in this complex archipelago (MacDonald and Cook 1996). In most cases, knowledge of these mammals has changed little since the initial taxonomic descriptions, which were often based on morphologic characters from a few specimens representing a limited number of islands. Management decisions in southeast Alaska (United States Department of Agriculture 1997) have been based on this weakly substantiated taxonomic framework; however, a significant series of new specimens provides an opportunity to reevaluate geographic variation within taxa of the region (MacDonald and Cook 1996).

Molecular methods have been used successfully to address questions related to historical biogeography and the validity of endemic taxa (e.g., Malhotra et al. 1996; Wayne 1996). In a preliminary effort to examine genetic variation among northern flying squirrels (*Glaucomys sabrinus*) in southeast Alaska, we analyzed the mitochondrial cytochrome *b* gene. This gene has proved to be informative and appropriate for studies aimed at intraspecific and interspecific variation across a variety of mammals (Patton et al. 1996; Talbot and Shields 1996; Ruedi et al. 1997; Lessa and Cook 1998), sciurids in particular (Thomas and Martin 1993; Wettstein et al. 1995). Northern flying squirrels were sampled from previously identified biogeographic subregions (MacDonald and Cook 1996) including mainland, middle/southern inner islands, and southern outer is-

lands of southeast Alaska as well as interior Alaska, Yukon Territory, and Washington State (Fig. 1).

Materials and methods

Fifty-six northern flying squirrels, deposited in the University of Alaska Museum and representing five subspecies (Hall 1981), were examined (Table 1). Specimens from Heceta, Orr, and Suemez represent new island records of this species for southeast Alaska. DNA was extracted from frozen heart or liver, amplified, and sequenced following methods outlined in Lessa and Cook (1998) and Halanych et al. (1998). The primer pairs MVZ04/05, MVZ16/37, and MVZ14/23 were used for both polymerase chain reaction (PCR) amplification and cycle sequencing (Smith and Patton 1993). PCR products were sequenced in both directions. Cytochrome *b* sequences were translated and aligned with Sequence Navigator version 1.01 (ABI).

Initially, the complete cytochrome *b* gene was amplified and sequenced for 18 individuals (Table 1). All nucleotide differences (the two Washington specimens excluded) occurred within a 792 base pair (bp) region (cytochrome *b* positions 348–1140). Only this region of the gene was subsequently examined for an additional 38 northern flying squirrels. All sequences have been deposited with the GenBank Data Library under accession Nos. AF011738–AF011742 and AF030389–AF030394.

Results

The complete cytochrome *b* gene of *G. sabrinus* was the same length (1140 bp) as reported for many other mammals (Irwin et al. 1991), including other sciurids (Thomas and

Table 1. Subspecific designations, collection locations, and voucher numbers for *Glaucomys sabrinus* specimens.

Subspecies	Locality	Alaska Frozen Tissue Collection No. (AF)
<i>fuliginosus</i> <i>griseifrons</i>	Washington, Kittitas County (47°06' N, 121°00' W)	5451 ^a
	Alaska, POW Island (55°41' N, 132°27' W)	1786, 1787
	Alaska, POW Island (55°20' N, 132°27' W)	16788, 16806
	Alaska, POW Island (55°31' N, 132°59' W)	16791, 16792, 16793
	Alaska, POW Island (55°21' N, 132°50' W)	16797
	Alaska, POW Island (55°53' N, 133°14' W)	12466
	Alaska, POW Island (55°48' N, 133°07' W)	5268, ^a 5676 ^a
	Alaska, POW Island (55°20' N, 132°31' W)	16485 ^a
<i>oregonensis</i> <i>yukonensis</i>	Washington, Lewis County (47°N, 122°W)	15854 ^a
	Alaska, Lone Mountain (66°34' N, 148°46' W)	14089, 14090
<i>zaphaeus</i>	Alaska, Ester (64°50' N, 148°01' W)	11201 ^a
	Alaska, Nenana area (64°42' N, 148°36' W)	6587 ^a
	Yukon Territory, Kluane (61°01' N, 138°31' W)	20286 ^a
	Alaska, Chilkat Peninsula (58°34' N, 135°09' W)	10306, 14108 ^a
	Alaska, Cleveland Peninsula (55°45' N, 132°00' W)	5188, 14103, 14104, 14105, 14106, 14107
No designation	Alaska, Haines (59°15' N, 135°33' W)	12539 ^a
	Alaska, Barrier Islands, Middle Island (54°48' N, 132°26' W)	10346
	Alaska, Barrier Islands, unnamed island southeast of Middle Island (54°47' N, 132°24' W)	10932, 10933, 10934
	Alaska, Barrier Islands, unnamed island east of Middle Island (54°48' N, 132°26' W)	10912, 10913, 10914, 10915, 10922, 10923, 10927, 10930
	Alaska, El Capitan Island (55°57' N, 133°19' W)	10411, 12463, 12467
	Alaska, Heceta Island (55°45' N, 133°30' W)	16874, ^a 16879, ^a 16894 ^a
	Alaska, Mitkof Island (56°31' N, 132°42' W)	14099, 14100, 14102, 19881, ^a 19882 ^a
	Alaska, Orr Island (55°57' N, 133°24' W)	16251, ^a 16243 ^a
	Alaska, Revillagigedo Island (55°20' N, 131°38' W)	5235
	Alaska, Suemez Island (55°16' N, 133°21' W)	16873 ^a
Alaska, Tuxekan Island (55°51' N, 133°25' W)	12498	

Note: Subspecific designations follow Hall (1981).

^aComplete cytochrome *b* sequences were obtained for these individuals (all others were 792 bp).

Martin 1993; Wettstein et al. 1995). All sequences followed the patterns of compositional bias expected for a functional mitochondrial cytochrome *b* in mammals (Ma et al. 1993). This included an overall deficit of guanine nucleotides (12%) across codon positions when the complete gene was examined ($n = 18$). This deficit was most pronounced at third-position codon sites (1.2%).

A high level of sequence divergence (7.3%) was found between Washington specimens and all other populations examined. Levels of genetic differentiation among northern flying squirrels from Alaska and Yukon Territory were relatively low (<0.3%). Five haplotypes, two common and three unique, were found among 54 northern flying squirrels from Alaska and Yukon Territory. The most widespread, the "mainland" haplotype, included individuals ($n = 17$) from central Alaska south to mainland southeast Alaska and two nearshore islands (Mitkof and Revillagigedo). Three individuals within this geographic area possessed unique haplotypes identified on the basis of a single base pair difference (Table 2). The other common haplotype, the "Prince of Wales (POW) complex," occurred in northern flying squirrels ($n = 34$) from POW Island and eight islands west of POW Island (El Capitan, Heceta, Orr, Suemez, Tuxekan, and three islands of the Barrier group; Fig. 2). All those in-

dividuals shared two distinctive mutations; neither resulted in an amino acid replacement (Table 2).

Discussion

Our analyses of five subspecies of *G. sabrinus* in northwestern North America corroborate recent molecular work which suggested that populations from Washington and Alaska represent two cryptic species (Arbogast 1996). The sequence difference of cytochrome *b* between the populations (7.3%) is similar to that found between sister species of other rodents (Thomas and Martin 1993; Lessa and Cook 1998). This deep divergence indicates distinct evolutionary histories, possibly as a consequence of vicariant events (e.g., glacial activity) in the Pleistocene Epoch or even earlier (Klicka and Zink 1997). Contact areas between these lineages may exist in southern British Columbia or Washington and should be characterized. The minimal level of mitochondrial differentiation among northern populations of *G. sabrinus* suggests that it may be a recent colonizer of Alaska and Yukon Territory (Hewitt 1996; MacDonald and Cook 1996; Conroy et al. 1998). This late colonization is consistent with the establishment of boreal and temperate

Fig. 2. Map of the southern region of the Alexander Archipelago in southeast Alaska depicting the distribution of northern flying squirrels on the mainland and 12 islands (bold outline). The two cytochrome *b* haplotypes identified in this region are mapped as differentially shaded areas (see the text for details). Type localities for *Glaucomys sabrinus griseifrons* (▼) and *G. s. zaphaeus* (◆) are also shown.

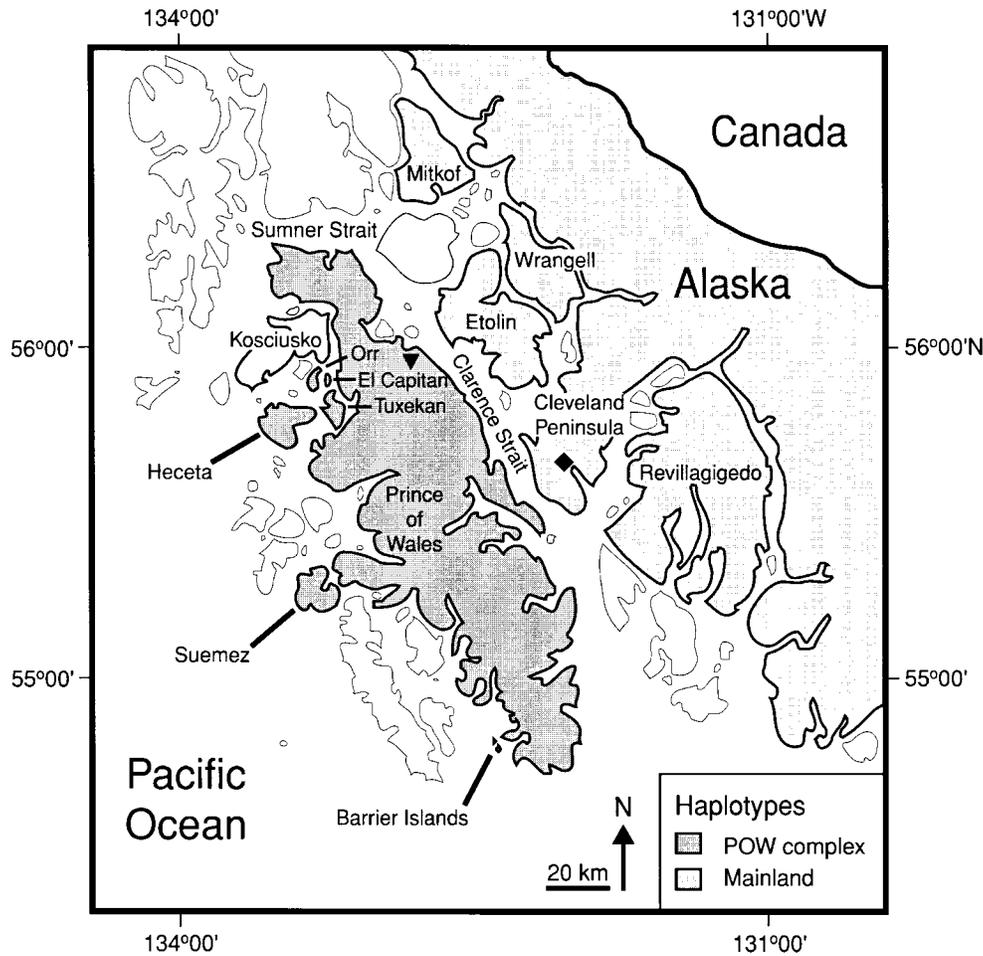


Table 2. Cytochrome *b* haplotypes and nucleotide positions of substitutions.

Haplotype	Cytochrome <i>b</i> position and type of base pair substitution				
	468 (14606)	480 (14618)	574 (14712)	903 (15041)	1131 (15269)
Mainland (<i>n</i> = 17)	C	T	C	T	C
POW complex (<i>n</i> = 34)	—	—	T	—	A ^a
Alaska, Haines (AF 12539)	T	—	—	—	—
Alaska, Chilkat Range (AF 14108)	—	C	—	—	—
Yukon Territory, Kluane (AF 20286)	—	—	—	C	—

rain forests in central and southeast Alaska ca. 5000–4000 B.P. (Mann and Hamilton 1995; Hu et al. 1996).

Within southeast Alaska, at least two subspecies of northern flying squirrels are found throughout the mainland and on only 15 southern islands (MacDonald and Cook 1996; this paper). One of these, the endemic POW Island flying squirrel, *Glaucomys sabrinus griseifrons* (Howell 1934), has been listed as a species of concern (Demboski et al. 1998). This subspecies was described on the basis of the pelage,

which was distinctively darker than that of the Alaska Coast flying squirrel, *Glaucomys sabrinus zaphaeus* (Osgood 1905). Because the original description was based on a small sample (*n* = 2), the status of *G. s. griseifrons* has been controversial (MacDonald and Cook 1996; West 1993). Although this study is limited to a single gene, the results are consistent with the continued recognition of *G. s. griseifrons* and suggest that it occurs on at least eight additional islands. In contrast, specimens representing the subspecies

Glaucomys sabrinus yukonensis and *G. s. zaphaeus* showed little variation in cytochrome *b* sequence across an extensive geographic range.

The genetic similarity of northern flying squirrels of the POW complex may be indicative of a recent founder event on POW Island. Subsequently, descendants of that founder population may have colonized the islands west of POW Island (Fig. 2). The distinctive POW complex haplotype indicates that these are neoendemics and supports the previous recognition of the southern outer islands as a separate biogeographic subregion (Swarth 1936; MacDonald and Cook 1996). Clarence Strait may be an effective barrier to flying squirrel movement, whereas the mainland haplotype is found on the nearshore islands of Mitkof and Revillagigedo (Fig. 2). Other mammals (e.g., southern red-backed vole, *Clethrionomys gapperi*) are found on the mainland and nearshore islands, but not on the southern outer islands (MacDonald and Cook 1996). Additional genetic markers and analysis of other taxa may shed light on the validity of these biogeographic subregions and the role of oceanic channels as barriers to gene flow within the archipelago.

Implications for conservation

The close association of *G. sabrinus* with old growth is well documented (Weigl 1978; Witt 1992; Carey 1995, 1996; but see Rosenberg and Anthony 1992). The species has also been the focus of studies related to the impacts of deforestation on vertebrate populations (Weigl et al. 1992; Carey 1995). Northern flying squirrels use large snags for nests and may disperse mycorrhizal fungi (Maser et al. 1978, 1986), which can aid in regeneration of forests following disturbance (Mowrey and Zasada 1984). However, extrapolating directly from studies in Washington and Oregon (Rosenberg and Anthony 1992; Witt 1992; Carey 1995) to southeast Alaska populations may be premature, given their distinctive evolutionary histories and thus potentially different ecological histories.

Unfortunately, no analyses have focused on life-history, habitat, and population characteristics of *G. sabrinus* in southeast Alaska or coastal British Columbia. Although Howell (1934) stated that flying squirrels were scarce on POW Island, this observation has not been verified. The impact of habitat fragmentation (e.g., potential for extinction) on island and island-like systems is well documented (Weddell 1991; Burkey 1995). Only recently, the insular nature of the region, and thus the increased potential for endemism, was recognized by the land-management plan for the Tongass National Forest (United States Department of Agriculture 1997). Long-term timber sales contracts (United States Department of Agriculture 1997) and an extensive road system (United States Department of Agriculture 1987) have fragmented the old-growth forests of POW Island and surrounding islands. Approximately 21% of the old-growth forest has been harvested on northern POW Island (DeGange 1996). Many of the remaining old-growth stands are interspersed with clear-cut and closed-canopy stands of second growth that lack large snags. Logging of old-growth forests has been suspected to have impacted species on POW Island such as the Alexander Archipelago wolf (*Canis lupus ligoni*), Sitka black-tailed deer (*Odocoileus*

hemionus sitkensis), river otter (*Lutra canadensis*), and bats (*Myotis* spp.) (Yeo and Peek 1992; Parker et al. 1996; Persson et al. 1996; Kohira and Røxstad 1997). The effects of fragmentation on populations of *G. sabrinus* in southeast Alaska are not known, but logging practices have been detrimental to other isolated populations of northern flying squirrels in the Appalachian Mountains (Payne et al. 1989; Weigl et al. 1992; Demboski et al. 1998).

Systematics should play a central role in conservation biology (O'Brien and Mayr 1991; Vane-Wright et al. 1991; Rojas 1992), yet failure to recognize the limitations of existing classifications has resulted in serious management mistakes (Avice and Nelson 1989; Daugherty et al. 1990; May 1990). Recent technological, analytical, and theoretical advances (Moritz 1994; Hillis et al. 1996) have enhanced the ability to describe variation and delineate taxonomic boundaries. A taxonomic framework should reflect evolutionary history and be viewed as a set of hypotheses that require further refinement and testing. Reevaluation of this framework is particularly critical when (i) the original taxonomic description is suspect, (ii) a taxon has a limited distribution (e.g., is restricted to an island), and (iii) habitat modification has potentially impacted the organism's viability. These circumstances describe the current situation for *G. s. griseifrons* in the Alexander Archipelago. Additional morphological and molecular characters should be examined with expanded geographic sampling. Maintenance of viable populations of endemic taxa (particularly insular populations) will require a more complete knowledge of the distribution, taxonomy, ecology, and biogeographic history of southeast Alaska's fauna and flora (MacDonald and Cook 1996). Review of potentially distinctive populations such as *G. s. griseifrons* is a preliminary step toward the goal of effective management of wildlife and forest resources in this complex region.

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