Refugium or crossroads? Alpine biogeography in the Wrangell-St. Elias region

Introduction

Since the concept of Beringia was first advanced (Hultén 1937), it has been recognized as one of the most important biogeographic features in the northern hemisphere. Increasing fossil, morphological, genetic, and parasite data across a wide range of taxa have supported the theory that Pleistocene glaciations isolated this northern region and strongly influenced the species that survived therein (Cook et al. 2005). A model of post-Pleistocene range expansion from Beringia has been supported in many species (Hewitt 2000) but is being continually refined, particularly with respect to growing evidence of additional nearby refugia, located along coastal areas in southeast Alaska (e.g., Leonard et al. 2005) and the Canadian Arctic (e.g., Fedorov and Stenseth 2002). In addition to being identified through fossil and paleobiological evidence, Pleistocene refugia are diagnosed based on the presence of genetically divergent lineages endemic to a particular region (Hewitt 2000). The observation of endemic genetic lineages in several species from one geographic region, especially one separated from the main Beringian refugium by glaciation, may indicate a separate refugium. Preliminary work suggests this may be the case for the Wrangell-St. Elias region of Alaska and Canada. I am requesting funds to collect collared pika samples to test the hypothesis that this region was a separate Pleistocene refugium for alpine-adapted mammals against the alternate hypothesis that this region may instead represent an area of contact between mammals from two or more different refugia.

Wrangell-St. Elias is home to four small-bodied species of alpine mammals: the collared pika (*Ochotona collaris*), the hoary marmot (*Marmota caligata*), the singing vole (*Microtus miurus*), and the arctic ground squirrel (*Spermophilus parryii*). Fossil and/or mitochondrial DNA (mtDNA) evidence suggests a broader Pleistocene distribution for most of these species (e.g., Harington 1978, Gunderson 2007, Weksler and Olson 2007, Zazula et al. 2007). Post-Pleistocene interglacial warming may have both exposed more available habitat and driven these species upslope to seek shelter from the rising treeline (e.g., Krajick 2004). If there had been a second refugium for alpine species in the Canadian Arctic or south of the ice sheets, post-glacial recolonization may have united populations in a geographically intermediate "suture zone," a region of secondary contact between genetically distinct lineages of the same species (Fig. 1; Remington 1968). The Wrangell-St. Elias region has already been suggested to represent a suture zone for lemmings, and this pattern might extend to other species (Fedorov et al, 2003).

Alternatively, this region may represent a separate refugium, isolated from Beringia as traditionally recognized. None of the published phylogeographic analyses that have incorporated samples from the Wrangell-St. Elias region have included alpine taxa. Given the differences in their ecology, habitat preferences, and dispersal abilities, their historical biogeography is likely to be significantly different from that observed in lowland species. Genetic analyses of singing voles and pikas have revealed highly divergent and unique mtDNA haplotypes from specimens collected in Wrangell-St. Elias, suggesting that this region may represent a heretofore unrecognized refugium, at least for alpine taxa (Fig. 2; Lanier and Olson 2006; Weksler and Olson 2007). These analyses require larger datasets to be resolved. The verified presence of another separate refugium for alpine species would revise the currently accepted view that the Wrangell-St. Elias fauna is largely composed of recent immigrant species (Cook and MacDonald 2003) and would enrich and expand our knowledge of the Quaternary biogeography of this region.

The fieldwork described herein is motivated by findings from several larger projects investigating phylogeographic patterns in alpine mammals (pikas, marmots, and singing voles) from Alaska.

This study is designed to complement our lab's ongoing alpine mammal research in other areas of Alaska. Samples resulting from this fieldwork will be integrated with existing datasets to address questions relating to the molecular and morphological uniqueness of alpine mammals in the Wrangell-St. Elias region.

Proposed Activities and Sampling Strategy

I am requesting funds to conduct field work with another member of our lab at three sites within Wrangell-St. Elias National Park. I will collect specimens of alpine mammals, particularly *O. collaris, Marmota caligata, Microtus miurus*, and *S. parryii*. We will hike from a central base camp in the alpine and survey the surrounding area for approximately four days per site, at three sites (Fig. 3). Our goal is to obtain voucher specimens of these taxa, broadly representative of the population but at demographically sustainable levels, in a repeatable manner conducive to future resampling by other scientists.

Upon the discovery of any pika, marmot, or singing vole population and prior to collecting any specimens, we will first determine the basic characteristics of that population. The general range of the population, including elevation, will be determined by walking transects through talus until that habitat ends and/or animals are no longer observed (seen or heard). Vocalizations, presence of haypiles, latrine sites, and grazing near talus will be used to determine the extent and abundance of pika and singing vole populations. Collecting will be done using small-caliber rifles and shotguns for pikas, marmots, and ground squirrels. Singing vole trap lines will consist of Museum Special snap traps set out in alpine areas, with an emphasis on vole colonies. While this trapping effort will target singing voles, co-distributed small mammals will also be collected and vouchered.

All specimens (including skin, skull, skeleton, tissues, embryos, and parasites) will be archived in the Mammal Collection at the University of Alaska Museum (UAM). All collecting will be conducted under UAM's scientific permit issued by the Alaska Department of Fish and Game's Division of Wildlife Conservation and in accordance with the American Society of Mammalogists' Animal Care and Use Guidelines and UAM's IACUC assurance. All data associated with the specimens collected will be freely available on the University of Alaska Museum's online database (http://arctos.database.museum) and linked to the genetic sequences deposited in GenBank, and results will be published in the peer-reviewed literature.

Analyses

Molecular analyses will be conducted in L. Olson's molecular lab in the West Ridge Research Building to determine genetic uniqueness of specimens collected with this study, and specimens will be examined in the context of our existing datasets to determine the presence of a refugium in the Wrangell-St. Elias vicinity. We will test the suture and refugium hypotheses using the distribution of mitochondrial DNA haplotypes. Areas that have been recently colonized, e.g., those that were previously glaciated, are expected to show relatively low genetic diversity when compared to those that served as Pleistocene refugia or have a long history of occupation (Hewitt 2000). If this region is a suture zone, we expect to find high genetic diversity locally due to admixture between two or more separate populations (e.g., Petit et al. 2003). Under this scenario, individuals within the park should share lineages with individuals from two or more external refugia. Support for the refugial hypothesis will be determined based on the presence of unique, deeply divergent, closely-related haplotypes in the Wrangell-St. Elias region. The results of my study will significantly enhance our understanding of the role this region may have played during the Quaternary in shaping present levels of genetic diversity in poorly-studied but iconic alpine mammals.

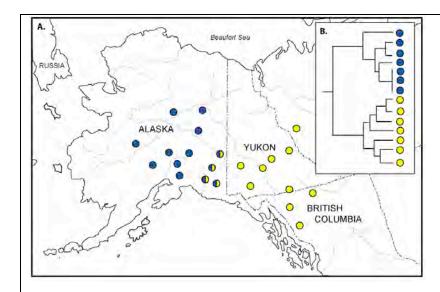


Fig 1– A.) Idealized distribution of mtDNA haplotypes on the landscape under the suture hypothesis. Individuals sampled in the suture zone possess haplotypes from one of two colonizing clades. Suture zone is genetically diverse, but not geographically unique. B.) Idealized phylogenetic tree showing deep divergence between clades but no clades unique to region of interest.

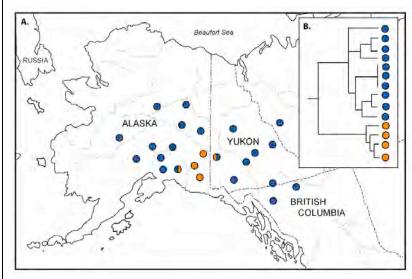


Fig 2– A.) Idealized distribution of mtDNA haplotypes on the landscape under the refugium hypothesis. Individuals sampled from the former refugium are divergent from individuals sampled elsewhere. Region of interest is genetically and geographically distinct, with some admixture along the boundaries. B.) Idealized phylogenetic tree showing deep divergence between main clade and isolated clade.

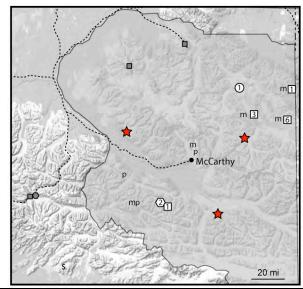


Fig. 3 – Pikas (squares, p), singing voles (circles, s), and marmots (hexagons, m) observed or collected in Wrangell-St. Elias National Park. Numbers indicate specimens collected by Cook et al. (2003) in 2001–2003 survey. Dashed lines indicate road access. Proposed sampling sites indicated by red stars.



Literature Cited

Cook, J.A., and S.O. MacDonald. 2003. Mammal Inventory of Alaska's National Parks and Preserves: Wrangell St. Elias National Park and Preserve. Annual Report 2001–2002. 34 pp.

Cook, J.A., E.P. Hoberg, A. Koehler, H. Henttonen, L. Wickström, V. Haukisalmi, K. Galbreath, F. Chernyavski, N. Dokuchaev, A. Lahzuhtkin, S.O. MacDonald, A. Hope, E. Waltari, A. Runck, A. Veitch, R. Popko, E. Jenkins, S. Kutz, and R. Eckerlin. 2005. Beringia: Intercontinental exchange and diversification of high latitude mammals and their parasites during the Pliocene and Quaternary. *Mammal Study* 30:S33–S34.

Fedorov V.B., A.V. Goropashnaya, M. Jaarola, and J.A. Cook. 2003. Phylogeography of lemmings (*Lemmus*): no evidence for postglacial colonization of Arctic from the Beringian refugium. *Molecular Ecology* 12:725–731.

Fedorov, V.B., and N.C. Stenseth. 2002. Multiple glacial refugia in the North American Arctic: inference from phylogeography of the collared lemming (*Dicrostonyx groenlandicus*). *Proceedings of the Royal Society of London Series B* 269:2071–2077.

Gunderson, A.G. 2007. The Distribution and Phylogeography of the Alaska Marmot (*Marmota broweri*). Master's thesis, University of Alaska Fairbanks.

Harington, C.R. 1978. Quaternary vertebrate faunas of Canada and Alaska and their suggested chronological sequence. *Syllogeus* 15:1–105.

Krajick, K. 2004. All downhill from here? Science 303:1600–1602.

Lanier, H.C. and L.E. Olson. 2006. Pikas, peaks, and post-glacial colonization: Phylogeography of an alpine lagomorph, *Ochotona collaris*. *Oral presentation given at the annual meeting of The American Society of Mammalogists, Amherst, MA*.

Petit et, R.J., I. Aguinaglade, J. de Beauliu, C. Bittkau, S. Brewer, R. Cheddadi, R. Ennos, S. Fineschi, D. Grivet, M. Lascoux, A. Mohanty, G. Müller-Starck, B. Demesure-Musch, A. Palmé, J.P. Martín, S. Rendell, and G.G. Vendramin. 2003. Glacial refugia: Hotspots but not melting pots of genetic diversity. *Science* 300:1563–1565.

Remington, C.L. 1968. Suture-zones of hybrid interaction between recently joined biotas. *Evolutionary Biology* 2:321–428.

Weksler, M. and L.E. Olson. 2007. Unraveling phylogeographic patterns and population genetic processes in Alaskan singing voles (Cricetidae: *Microtus*). *Oral presentation given at the Alaska Chapter of the Wildlife Society, Juneau, AK*.

Zazula, G.D., D.G. Froese, S.A. Elias, S. Kuzmina, and R.W. Mathewes. 2007. Arctic ground squirrels of the mammoth steppe: paleoecology of Late Pleistocene middens (~24 000–29 450 ¹⁴C yr BP), Yukon Territory, Canada. *Quaternary Science Review* 26:979–1003.

Please include an itemized budget and budget justification being as detailed as possible		
(add or delete rows as needed):		
Description	Amount	Source of Funding
Travel		
Fuel (Fairbanks to McCarthy)	135	ASM Grants in Aid
Charter flight to Goat Trail	550	ASM Grants in Aid
Charter flight to Iceberg Lake	740	ASM Grants in Aid
Charter flight to Kuskalana Pass	1360	AQC
Supplies and Equipment		
Field supplies (dry ice, liquid nitrogen, ammo, salt, etc.)	100	Provided by UAM
		Mammalogy Dept.
Food	140	AQC
Extraction, PCR and sequencing costs (50 individuals,	605	NSF DDIG
double stranded sequence, + 10% failure rate)		
Equipment		
Field equipment (prepping equipment, cooking supplies,	Already	Provided by UAM
prep tent, liquid nitrogen dewar, etc.)	purchased	Mammalogy Dept.
Amount requested from AQC (max \$1500)	1500	
TOTAL Project:	5,130	

Budget Justification (use as much space as needed):

Some limited trapping was conducted along the road-system in the center of the park last summer, with minimal success due to accessibility issues. We concluded that targeted fly-in trips to areas with reliable population sightings would the most efficient option. Flight costs calculated on the basis of a two-person crew (McCarthy to field site), requiring one flight provided by Wrangell Mountain Air. Fuel costs are figured on the basis of 740 miles (round trip by road from Fairbanks to McCarthy) getting an average of 20 mpg x \$3.5 per gallon. A departmental vehicle or personal vehicle will be used. Estimated food costs is minimized by purchasing food in bulk for several summer trips supported on other grants.

This funds requested from the AQC are intended to augment my ongoing PhD research on the phylogeography and evolution of the collared pika. Much of the fieldwork and sequencing of samples from surrounding areas (necessary to answer the questions put forth in this project) has already been accomplished. All data resulting from this fieldwork conducted in Wrangell-St. Elias National Park and Preserve will appear in my dissertation, on the UAM database, and in peer-reviewed scientific publications. Laboratory analysis costs will be covered under an NSF Doctoral Dissertation Improvement Grant that has been awarded.