THE DISTRIBUTION AND PHYLOGEOGRAPHY OF THE

ALASKA MARMOT (*Marmota broweri*)

By

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THE DISTRIBUTION AND PHYLOGEOGRAPHY OF THE ALASKA MARMOT (*Marmota broweri*)

A

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By

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Abstract

The taxonomic and distributional status of the *Marmota broweri* has been the subject of much debate and confusion since it was first described as a subspecies of the hoary marmot (*M. caligata*). Through a review of all museum specimens, published accounts of this species, field surveys, and the identification of previously unidentified marmot specimens we have determined the current distribution of the Alaska marmot to include the Brooks Range, the Ray Mountains, and the Kokrines Hills of northern Alaska. The Yukon River forms the boundary between the peripatric distributions of *M. broweri* and *M. caligata* in Alaska. Since *M. broweri* was a resident of Beringia during the Pleistocene, I expect the phylogeographic structure of Alaska marmots (*M. broweri*) to exhibit the signature of persistence in Beringia and subsequent expansion into glaciated areas. My objective is to investigate the phylogeographic structure of Alaska marmot populations through phylogenetic tree construction, measures of genetic diversity, a mismatch distribution, and nested clade analysis of DNA sequence data from the mitochondrial cytochrome *b* gene. I found significant geographic structure across the range of *M. broweri*. The results of my analyses suggest a recent population expansion from central Alaska (Beringia) into the formerly glaciated Brooks Range.

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General Introduction

This thesis is focused on the Alaska marmot (*Marmota broweri*), a poorly understood mainland Alaska endemic mammal. Alaska marmots were first discovered in the extreme northwestern Brooks Range in the late 1920s. They were originally described in 1934 as a subspecies of the hoary marmot, known from southern Alaska, western Canada, Washington, Idaho, and Montana. For more than thirty years after its discovery the taxonomic status of the Alaska marmot was unsettled. The Alaska marmot had already gone through two name changes when it was recognized as a distinct species in 1965. Unfortunately, its status as a unique species went unnoticed by some authors who continued to lump the Alaska marmots with the hoary marmots. This taxonomic confusion led to the erroneous depiction of the geographic distributions of both species. The Alaska marmot has been shown as occurring throughout the Brooks Range. The hoary marmot has been depicted as inhabiting all alpine areas in Alaska, including both the Alaska Range in the south and Brooks Range in the north, giving the impression that both species can be found in the Brooks Range. In reality, hoary marmots have never been documented north of the Yukon River, and Alaska marmots were known from just 15 localities in the Brooks Range. No focused effort has previously been made to determine the distribution of the Alaska marmot. The objectives of the first portion of my thesis are to correct the confusion surrounding the geographic distributions of hoary and Alaska marmots in Alaska and to establish the current distributional boundaries of the Alaska marmot. Marmots were cited by Krajick (2004) in the journal Science as being at risk for local extirpation or extinction due to the effects climate change is having on alpine ecosystems around the world. A baseline understanding of the current distribution of species is required to study the effects of climate change on distribution and population structure.

The second chapter of my thesis investigates the evolutionary and geographic histories of the Alaska marmot. Due to their isolation in high elevation habitats and assumed limited dispersal ability I expect marmot species to exhibit high levels of population structure, but no phylogeographic studies have been conducted to establish a current measure of population structure or a baseline of genetic diversity for any species of marmot. Many phylogeographic studies have been published investigating the effects of the Pleistocene glacial cycles on the diversity and population structure of species inhabiting Beringia, the ice age refugium of interior Alaska and eastern Siberia. The objectives of chapter two are to test for significant geographic structure of genetic variation in Alaska marmot populations and to determine how their current distribution was determined by Pleistocene glacial cycles.

Literature Cited

KRAJICK, K. 2004. All downhill from here? Science 303:1600-1602.

Chapter 1 The distribution of the Alaska marmot (*Marmota broweri*)[1]

1.1 Abstract

The taxonomic status of the Alaska marmot (*Marmota broweri*) has been the subject of much debate and confusion since it was first described as a subspecies of the hoary marmot (*M. caligata*). As a result of its early association with *M. caligata* and a lack of focused effort to determine its range, our current understanding of the distribution of *M. broweri* is vague at best and completely erroneous at worst. Through a review of all museum specimens and published accounts of this species, field surveys, and the identification of previously unidentified marmot specimens I have determined the current distribution of the Alaska marmot to include the Brooks Range, the Ray Mountains, and the Kokrines Hills of northern Alaska. I report the first records of this species outside of the Brooks Range and a range extension of 250 miles southward. The Yukon River appears to form the boundary between the peripatric distributions of *M. broweri* and *M. caligata* in Alaska.

1.2 Introduction

Alaska marmots (*Marmota broweri*) inhabit boulder fields, talus slopes, and rock outcrops found in alpine tundra of northern Alaska (Bee and Hall 1956). They are locally abundant and generally occur in loose communities (Bee and Hall 1956). *Marmota broweri* was first described by Hall and Gilmore (1934) based on four specimens collected by Charles D. Brower from native residents of Point Lay and Cape Thompson on the northwestern coast of Alaska. Based on morphology data, Hall and Gilmore (1934) concluded those four specimens constituted a new subspecies of the hoary marmot (*M. caligata*) known from southern Alaska,

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[1] Gunderson, A. M. and L. E. Olson. 2008. Journal of Mammalogy. The distribution of the Alaska marmot (Marmota broweri).

western Canada, and alpine areas of Washington, Idaho, and Montana. They named this new subspecies *M. caligata broweri*. Since its description, the taxonomy and distribution of this marmot has been the subject of much debate and confusion. With few voucher specimens available for morphological analyses, the taxonomic status of *M. broweri* was tentative for more than thirty years after its discovery. The distributions of *M. broweri* and *M. caligata* have been published erroneously due to the taxonomic confusion and speculation surrounding *M. broweri*, and those errors have been perpetuated through the literature.

1.2.1 Taxonomic history

> As part of their original description, Hall and Gilmore (1934) stated
>
> "...it might be maintained with some justice that *broweri* should be accorded full specific rank. However, the differences distinguishing the two forms [*Marmota caligata caligata* and *M. c. broweri*] are of much the same nature as those which distinguish other subspecies of the *caligata* group (p. 58)."

Therefore, the new marmot was described as a subspecies of the hoary marmot, *M. c. broweri*. No new *M. broweri* specimens were collected until 1951 when Robert Rausch made an effort to collect marmots from the central Brooks Range. Based on the conclusions of Ognev (1947) and Ellerman and Morrison-Scott (1951) (*M. caligata*, *M. camtschatica* and *M. marmota* constituted a single species) and the morphology of a series of Eurasian and North American marmot skulls, Rausch (1953) concluded that all named subspecies of *M. caligata*, including *broweri*, the Olympic marmot (*M. olympus*), and the Vancouver Island marmot (*M. vancouverensis*) were subspecies of a single marmot species, *M. marmota*, that also included three forms from Europe and Asia. *Marmota marmota broweri* was the new name given to the marmots found in northern Alaska. Bee and Hall (1956) were reluctant to adopt this new name citing a lack of sufficient evidence that the purported subspecies intergraded geographically or could interbreed if in

contact. They maintained the name *M. caligata broweri* in reference to the marmots found in the Brooks Range. The application of karyology settled the taxonomic issues surrounding *Marmota broweri*. Rausch and Rausch (1965) found *M. broweri* to have 2n=36 chromosomes whereas *M. caligata* had 2n=42. They named *Marmota broweri* as a unique species.

Two competing hypotheses have been suggested for the origin of *Marmota broweri*. Rausch and Rausch (1971) considered *M. broweri* "to be probably a relict North American species which became established in the Brooks Range during pre-Wurm time, rather than a late Pleistocene invader of middle Asian derivation...(p. 96)," based on the fact that *M. broweri* shared two species of cestodes with the North American species *M. caligata*, *M. flaviventris*, *M. olympus*, and M. *vancouverensis*. They claimed that the diverse and distinct cestode faunas of the North American and Eurasian marmots were "indicative of a long period of separation of the two groups (p. 96)." Hoffmann and Nadler (1968) and Hoffmann et al. (1979) proposed an alternative origin for *M. broweri* — it dispersed into North America from Asia during the Pleistocene, and is most closely related to the Russian species *M. camtschatica*.

The first molecular study to investigate the relationships among all fourteen marmot species, conducted by Steppan et al. (1999), supported the full species status of *M. broweri* and determined that Alaska marmots are more closely related to all the Asian marmots and the woodchuck (subgenus *Marmota*) than to other North American species (subgenus *Petromarmota*). However, the position of *M. broweri* within the subgenus *Marmota* remained unresolved and the question of its origin unanswered.

1.2.2 Distributional history

Prior to the research presented here, the distribution of the Alaska marmot, *Marmota broweri*, had been described as restricted to the Brooks Range (Anderson 1934, Rausch 1953, Barash 1989). Earlier reports of marmots occurring north of the known range of *M. caligata*

claimed that *M. caligata* was the species observed (Bailey and Hendee 1926, Hall 1929, Howell 1915), and Hall and Gilmore (1934) thought "it probable that [geographic] intergradation will be found to exist between *M. c. broweri* and *M. c. caligata* (p. 58)." Consequently, Anderson (1934) expanded the distribution of hoary marmots to include the Alaska Range, the Brooks Range and much of the area in between (Figure 1). In 1951, after having collected and observed marmots from the central and eastern Brooks Range, Rausch concluded, "it is clear that *M. caligata broweri* is the form found throughout the Brooks Range, probably as far as the Alaska-Canada boundary (p.178)". Rausch (1953) later published a map of this distribution that more accurately displayed the geographic separation between *M. c. broweri* and *M. c. caligata* (Figure 1). Unfortunately, both the map published by Rausch (1953) and the specific distinction of *M. broweri* from Rausch and Rausch (1965) went unnoticed by Hoffmann (1981) in his species account of *M. caligata* in The Mammals of North America (Hall 1981). Hoffmann (1981) published an older version of the distribution of *M. caligata* (Figure 1) and failed to recognize *M. broweri* as a unique species. This error has been perpetuated such that the distribution of *M. broweri* and *M. caligata* have been confused in modern publications (Hoffmann 1999) (Figure 1).

In the original description of *M. broweri* Hall and Gilmore (1934) cite Point Lay as the type locality for this "subspecies." Point Lay is a coastal community, far from suitable marmot habitat. Based on his personal communications with "old Utukamiut, or Kukmiut, Eskimo (p. 117)," Rausch (1953) assumed the likely origin of these specimens, and type locality, to be near the head of the Kukpowruk River, an area frequently traveled by native people. Prior to this study, 85 voucher specimens had been collected to verify the occurrence of Alaska marmots at 15 locations in the Brooks Range (see appendix for a list of all known specimens). Many of those specimens (n = 34) came from the central Brooks Range at Anaktuvuk Pass, 325 miles east of the putative type locality (Rausch 1951, 1953) or were captive animals from Anaktuvuk Pass stock

maintained by Rausch at Barrow, AK. The northern- and eastern-most specimens were collected at Lake Peters, 100 miles west of the Alaska-Yukon border (Bee and Hall 1956, this study). The westernmost *M. broweri* specimens came from the Lisburne Peninsula at the edge of the Brooks Range bordering the Chukchi Sea (Childs Jr. 1969, Hall and Gilmore 1934, Pruitt 1966). Prior to the research presented here, the only locality on the south side of the Brooks Range from which a specimen had been collected is Arctic Village (Rausch 1951). It has often been speculated that *M. broweri* occurs in the British and Richardson Mountains of northern Yukon Territory (Anderson 1946, Rausch 1951, Rausch and Rausch 1971, Youngman 1975) and perhaps as far east as the Northwest Territories (Hoffman et al. 1979). Many observational records can be found in the literature citing *M. broweri* in areas outside their known distribution or from new localities in the Brooks Range, but none has been revisited to verify the presence of marmots (Howell 1915, Bailey and Hendee 1926, Bee and Hall 1956, Juday 1984). Since the work of Robert Rausch, James W. Bee and E. Raymond Hall in the 1950s and '60s, there has been no focused effort to collect new specimens or to determine the distributional limits of this species. The distribution and status of Alaska marmots, therefore, remains poorly understood.

As a consequence of the original description of *Marmota broweri* as a subspecies of *M. caligata*, the distributions of hoary marmots (*M. caligata*) and Alaska marmots (*M. broweri*) are often confused (Figure 1). The distribution of *M. caligata* has frequently been portrayed as including all of the Brooks Range in northern Alaska, the Alaska marmot's (*broweri*) known distribution. In addition, it was previously assumed that marmots of some subspecies of *M. caligata* would be found to inhabit areas between the Alaska Range and the Brooks Range (Hall and Gilmore 1934, Anderson 1934, Anderson 1946), and thus the distribution of *M. caligata* was displayed as including that area (Anderson 1934, ADFG 1978, Hoffmann 1981), though *M. caligata* has never been found north of the Yukon River.

The distribution of the hoary marmot is far more widespread than that of the Alaska marmot. Hoary marmots are found from Washington and Montana in the south through the White Mountains of interior Alaska. The two alpine marmot species are not known to occur in sympatry. Currently, hoary marmots are known only from areas south of the Yukon River while Alaska marmots occur north of the Yukon River.

Two specimens in the University of Alaska Museum indicate the presence of marmots in the Kokrines Hills and Ray Mountains of central Alaska. These two alpine areas lie directly north of and adjacent to the Yukon River, between the Alaska Range and the Brooks Range. A skin and skull were preserved from the Kokrines Hills (UAM 15044). This specimen has been tentatively identified as *Marmota broweri* based on pelage characters. A marmot cranium (with no associated mandible) was collected as part of a broad environmental survey of the Ray Mountains conducted in 1979 (Farquhar and Schubert 1980). These authors reported that marmots were common in alpine areas of the Ray Mountains and assumed them to be *M. broweri* due to their occurrence north of the Yukon River, but could not reliably identify which species (*M. broweri* or *M. caligata*) they were observing. The identity of this specimen has heretofore remained unconfirmed due to a lack of reliable cranial features from which *M. caligata* and *M. broweri* can be distinguished. If these specimens were confirmed to be *M. broweri*, they would represent the only records of this species outside the Brooks Range and a range extension of 250 miles southward. If either of these specimens is determined to be *M. caligata* it would represent the first documented occurrence of hoary marmots north of the Yukon River.

The objectives of this research are to clarify the taxonomy and distribution of the Alaska marmot, *M. broweri*, with a review of all literature and museum records and to establish the current distributional limits of the Alaska marmot through field surveys and the identification of previously unidentified museum specimens via DNA sequencing. The distribution of hoary

marmots is discussed in relation to the Alaska marmot distribution, and a new extralimital record of *M. caligata* is also reported.

1.3 Methods

1.3.1 Field surveys

Field surveys were conducted during the summer months of 2005 - 2007. Figure 2 shows the areas targeted for field surveys. These areas were chosen based on their proximity to known Alaska marmot populations or reported observations of marmots outside the established range of this species. Where marmots were observed, specimens were collected using firearms. Table 1 contains information regarding specific survey efforts. All voucher specimens were deposited at the University of Alaska Museum (see Table 2 for a list of specimens cited herein).

1.3.2 Molecular methods

To verify the species identity of the marmot skin collected from the Kokrines Hills (UAM Mamm 15044) and the cranium collected from the Ray Mountains (UAM Mamm 15043), DNA was extracted and sequenced from each specimen. Extractions were performed in the Ancient DNA Laboratory at the University of Alaska Museum (a PCR-free building), a laboratory designed specifically for procedures with high risks of contamination. A small subsample (approx. 25 mm^2) was removed with flame-sterilized forceps and scissors from the ventral incision of the study skin. The skin subsample was digested in a 1.6 ml tube with 600 µL Cell Lysis Solution (PureGene Genomic DNA Purification Kit, Gentra Systems, Minneapolis, MN), 10 µL proteinase K (20 mg/ml), and 30 µL DTT (100 mM) for 24 hours, shaking at 55°C. Approximately 20 mg of maxilloturbinal bone was removed from the nasal cavity of the cranium specimen as described in Wisely et al. (2004). The bone sample was digested in 600 µL cell lysis solution, 20 µL proteinase K, and 30 µL DTT for 72 hours shaking at 55°C, with the addition of 20 µL proteinase K every 24 hours (60 µL total). After digestion, both extractions proceeded

according to the PureGene Genomic DNA Purification Kit protocol for DNA purification from 5-10 mg fresh or frozen solid tissue with the following modifications: RNAse treatment was omitted and all reagent/solution volumes were doubled (protein precipitation solution, isopropanol, ethanol, DNA hydration solution). Each extraction included a negative control to test for contamination that might result from the extraction procedure. For comparative purposes, DNA was extracted from frozen tissue of four known *Marmota broweri* (UAM Mamm 78513, 35015, 85848, 85226) and five *M. caligata* specimens (UAM Mamm 58241, 49848, 31724, 35130, 38304) in a separate facility using the PureGene Genomic DNA Purification Kit protocol for DNA purification from 5-10 mg fresh or frozen solid tissue. A fifth *M. broweri* sequence was obtained from GenBank (accession number AF143918).

I amplified the first 556 base-pairs of the mitochondrial gene cytochrome *b*. Due to the degraded nature of the DNA extracted from the skin and bone specimens, I amplified and sequenced this segment of cytochrome *b* in three overlapping sections (39 bp and 61 bp of overlap) using the following primer pairs: CB-F1 (5' CTCACCGTTGTTATTCAACTA 3') and CB-R4AG (5' TGTGGGCAACTGATGAGAAA 3'), CB-F4AG (5' ATCCAAATCTTTACCGGACT 3') and CB-R5AG (5' TGACCTCAGGGGAGGACATA 3'), CB-F5AG (5' CTACGGCTCATATACCTACTC 3') and CB-R6AG (5' TAGGGCTGCGATGATAAAGG 3'). I amplified and sequenced the entire length of cytochrome *b* (1140 base-pairs) for the four *Marmota broweri* and five *M. caligata* specimens used for comparison in two overlapping segments (104 bp of overlap) using the primer pairs CB-F1 and CB-AGR1 (5' GGGATTTTGTCTGAGTCAGA 3'), and CB-AGF1 (5' CAAAGCCACTCTAACACGAT 3') and CB-R3AG (5' GGTTTACAAGGCCAGGGTAATG 3'). Volumes and concentrations of reagents used in the amplifications were as follows: 1 μL DNA template, 1 μL each of primers (10 μM), 2.5 μL 10X Promega (Madison, WI) reaction

buffer, 1 μL $MgCl_2$ (25 mM), 0.5 μL dNTPs (10 mM), 0.25 Promega GoTaq polymerase (5 U/μL), and 17.75 μL H_2O for a total reaction volume of 25 μL. The reactions were run on an MJ Research PTC-200 Peltier thermal cycler (Bio-Rad Laboratories, Inc. Hercules, CA) with the following cycling parameters: 94°C for three minutes, then 40 cycles of 94°C for one minute, 55°C for one minute, 72°C for one minute. The extraction negatives were run along with DNA extracts, and each PCR reaction also included a negative control to determine if any contaminating DNA was introduced from the PCR reagents.

Prior to cycle sequencing, PCR products were purified with Exo-SAP-IT (USB, Cleveland, Ohio) according to the manufacturer's protocol. Purified PCR products (1-2 μL) were cycle sequenced in both directions (forward and reverse) using BigDye Terminator (Perkin-Elmer, Boston, MA) (2 μL), 5X reaction buffer (1μL), water (6 μL) and the same PCR primers (1 μL). Sequencing reactions were purified using ethanol/sodium acetate precipitation and electrophoresed on an ABI 3100 (Applied Biosystems, Foster City, CA) sequencer.

1.3.3 Data analysis

DNA sequences were aligned with reference to the *Marmota broweri* sequence obtained from GenBank and checked by eye using Sequencher (ver. 4.7 Gene Codes, Ann Arbor, MI). Maximum likelihood (ML) and maximum parsimony (MP) trees were produced, and average pairwise differences were calculated using PAUP* (ver. 4.0, Swafford 2003). A *Spermophilus parryii* sequence obtained from Genbank (AY427977) was used as an outgroup for rooting trees. Heuristic MP and ML tree searches were conducted using stepwise addition of 100 random addition sequences with the tree bisection-reconnection branch-swapping algorithm. For the ML analysis a model of nucleotide substitution (GTR+I) and associated parameters were estimated using Modeltest 3.7 (Posada and Buckley 2004, Posada and Crandall 1998) under the Akaike Information Criterion.

1.4 Results

1.4.1 Field Surveys

Six previously unknown marmot populations were documented as a result of field surveys. The northernmost Alaska marmots along the Dalton Highway were found at Slope Mountain. I collected three voucher specimens on June 18, 2005 at 3,250 feet in elevation and one specimen on June 27, 2006 at 3,550 ft elevation. Another colony of Alaska marmots was found 25 road miles to the south, near the Galbraith airstrip, on August 24, 2006 from which 3 specimens were collected at 3,350 ft elevation. A single marmot was live trapped from the east side of the Dalton Highway, across from Toolik Field Station, on August 6, 2007. I obtained a tissue (skin) voucher from that individual. Other areas surveyed along the Dalton Highway were the mountains directly west of Galbraith airstrip, Jade Mountain west of Toolik Field Station, Imnavait Mountain, Finger Mountain, and the alpine areas north and west of the Kanuti River bridge near Beaver Slide. I did not find any marmots in these areas.

The Kigluaik Mountains north of Nome, AK, on the Seward Peninsula, were surveyed on foot from the road system and by helicopter from July 21-24, 2006. I searched the area where Juday (1984) claimed to have observed marmots. The habitat in that area, on the north side of the mountains and southeast of Windy Cove, seemed ideal for marmots, though I did not find any marmots or signs of marmot activity.

I surveyed approximately 36 miles of the Kongakut River drainage from Drain Creek to Caribou Pass between July 31 and August 10, 2006. The habitat in this area was marginal for supporting marmots. Though some areas appeared suitable, no marmots were found.

The mountainous areas surrounding Lake Peters were surveyed from July 21 - August 1, 2006. Two marmots were observed in the Chamberlin Creek drainage at the south end of Lake Peters at 3,400 ft elevation. Two marmots were observed in the Kelly Creek drainage at 3,900 ft

elevation. One voucher specimen was collected from each drainage. No other marmots, or marmot signs, were found though I surveyed the area from the Whistler Creek drainage to the peak of Mt. Chamberlin. The habitat in many areas without marmots appeared identical to that in areas supporting marmots.

The Kokrines Hills were surveyed from June 10-14, 2007 at the same locality from where the marmot skin (UAM 15044) tentatively identified as *Marmota broweri* was collected in 1983. I found the habitat to be well suited for marmots with rock outcrops and large boulder fields but no marmots or evidence of recent marmot activity were found. The habitat I surveyed was fairly small and relatively isolated from other, more expansive alpine areas to the northeast. Marmots may still be present in the Kokrines Hills though further north and east of where UAM 15044 was collected.

On July 3-4, 2007, I surveyed three localities in the northwestern Brooks Range, including the type locality, "near the head of the Kukpowruk River (p.117)," (Rausch 1953). No other specimens have been collected from this area since the type specimen was delivered to Charles D. Brower by a native hunter in Point Lay, AK in 1931 (Hall and Gilmore 1934). I collected one specimen from the bluffs above the Kukpowruk River north of Tupikchak Creek. Six specimens were collected thirty miles to the east, at Tupikchak Mountain. A single *Marmota broweri* specimen (UAM 35015) was collected in June 1981 from south of Archimedes Ridge near the Utukok River. I surveyed the same area, though not the exact locality, and observed four marmots at two locations near the Utukok River. I was unable to collect any specimens from those localities.

Gardner (1974) reported marmots from the Mulik Hills, north of Kotzebue near the Noatak River. I surveyed that area on July 2, 2007 but found no evidence of marmot activity. It is possible marmots will be found in the Igichuk Hills, a larger alpine range just north of the Mulik

Hills. In 1963, Dean and Chesemore (1974) stated that an active marmot den was present in the highlands south of the Noatak River near Nakolik Mountain, northeast of the Igichuk Hills. Further to the west and south, the pilot Eric D. Sieh of Kotzebue claimed to have seen marmots at the headwaters of the Eli River.

In 1979, Farquhar and Schubert (1980) conducted a biological survey of the Ray Mountains. They collected a single, unidentifiable marmot cranium from Spooky Valley (UAM 15043). I revisited the Ray Mountains from September 7-11, 2007. A population of *Marmota broweri* was found on the south-facing slope of the ridge south of the source of Gishna Creek. I observed ten individuals, including adults, yearlings, and juveniles, documented 12 unique borrows, and collected six specimens. All the marmots were observed between 3,200 and 4,400 ft elevation.

A previously unknown population of hoary marmots (*Marmota caligata*) was discovered at Elephant Mountain, south of the Yukon River. I surveyed this area from June 16-19, 2006. I observed eight individual hoary marmots during a twelve-mile transect of the mountain's ridge at elevations between 3,000 and 3,700 feet and collected two voucher specimens. This extends the known range of *M. caligata* 150 miles west of the nearest known hoary marmot population in the White Mountains, north of Fairbanks, AK.

I surveyed the Nulatto Hills from July 5-12, 2005. Habitat in this area was unsuitable for marmots, and none was found.

1.4.2 Specimen Identification

Maximum parsimony and maximum likelihood analyses produced the same tree topology, grouping both the Ray Mountains and Kokrines Hills museum specimens with *Marmota broweri* and not *M. caligata* (Figure 3). The average pairwise distances of the mtDNA sequence data from the Ray Mountains and Kokrines Hills specimens to the *M. broweri*

sequences were 0.4% and 1.1%, respectively, whereas the average distances from the *M. caligata* sequences were 10.1% and 11.3%, respectively. These results indicate that both museum specimens are *M. broweri*, not *M. caligata*.

1.5 Discussion

With the new records and museum specimen identifications reported here, a revised distribution of the Alaska marmot is shown in Figure 4. Based on museum specimens and all published observations of *Marmota broweri*, Alaska marmots are patchily distributed across the Brooks Range, from Cape Lisburne in the west to Lake Peters in the east, and in the Ray Mountains of interior Alaska. This species likely occurs east of Lake Peters, perhaps into the Yukon Territory, but I was unable to find them within the Kongakut River drainage. Further field surveys are necessary to establish the eastern distributional limits of *M. broweri*.

Alaska marmots were previously assumed to be restricted to the Brooks Range (Anderson 1934, Rausch 1953, Barash 1989). The positive identification of the museum specimens from the Kokrines Hills and the Ray Mountains as *Marmota broweri*, and the discovery of a population of Alaska marmots currently inhabiting the Ray Mountains, extends the known range of this species 250 miles to the south. These are the first specimens of this species to be collected outside the Brooks Range. Additionally, with the discovery of hoary marmots (*M. caligata*) inhabiting Elephant Mountain, directly south of the Ray Mountains across the Yukon River (see Figure 4), the Kokrines Hills and Ray Mountains constitute the southern limit of the Alaska marmot's distribution. The ecological similarity of the two species makes it unlikely that they will be found in sympatry. It appears that the Yukon River forms the boundary between the peripatric distributions of *M. broweri* and *M. caligata* in Alaska, although its historical influence on their distributions is unknown.

From July 29 through August 15, 1952, Bee and Hall (1956) surveyed the Lake Peters area for marmots. They reported observing marmots in eleven locations surrounding the lake and that "the marmot was common and lived in loose communities (p. 37)." Lake Peters lies at an elevation of 2,900 feet with the peak of Mt. Chamberlin to the southeast at 9,000 feet. Despite this elevation range, Bee and Hall found marmots only inhabiting the mountainsides between 3,250 and 4,000 feet with an average elevation of 3,700 feet. During a ten-day survey effort in July 2006, I searched the area from Whistler Creek to the peak of Mt. Chamberlin. I found marmots at just two locations and observed a total of four individuals. The marmots I observed occurred within the elevation range reported by Bee and Hall, though they were not common and no community structure was apparent at either of the two localities. Fifty-four years after Bee and Hall's original survey, Alaska marmots appear to have declined in both distribution and abundance in the Lake Peters area.

Further field surveys are needed to establish the eastern boundary of the Alaska marmot's distribution. Observations and reports of marmots east of Lake Peters and in northwestern Canada (Anderson 1934, Hoffman et al. 1979, B. Smith pers. comm.) as well as the presence of seemingly suitable habitat suggests that marmots occur further east of the Kongakut River drainage, where I did not find marmots. Additionally, the Seward Peninsula remains an area potentially supporting *Marmota broweri*. Though I failed to find marmots in the area cited by Juday (1984), I did not have sufficient time to exhaustively search the Kigluaik Mountains or other alpine areas of the Seward Peninsula and remain unconvinced that marmots are completely absent from those areas.

Knowledge of where a species naturally occurs is essential to understanding that species' ecology, evolution, and historical biogeography. Museum voucher specimens establish species' distributions and provide a historical baseline for evaluating change in distributions over time. As

specimens represent populations, the value of large series of specimens increases through time, particularly as the habitat quality of many localities is degraded. Baseline data are critical to the interpretation of ecological and environmental impacts. Without the preservation of specimens, field surveys such as this would have extremely limited value. Funding used for biodiversity assessments is most efficiently spent if agencies recognize the critical need for vouchers and provide support in both field and museum budgets for their preservation and maintenance.

1.6 Acknowledgements

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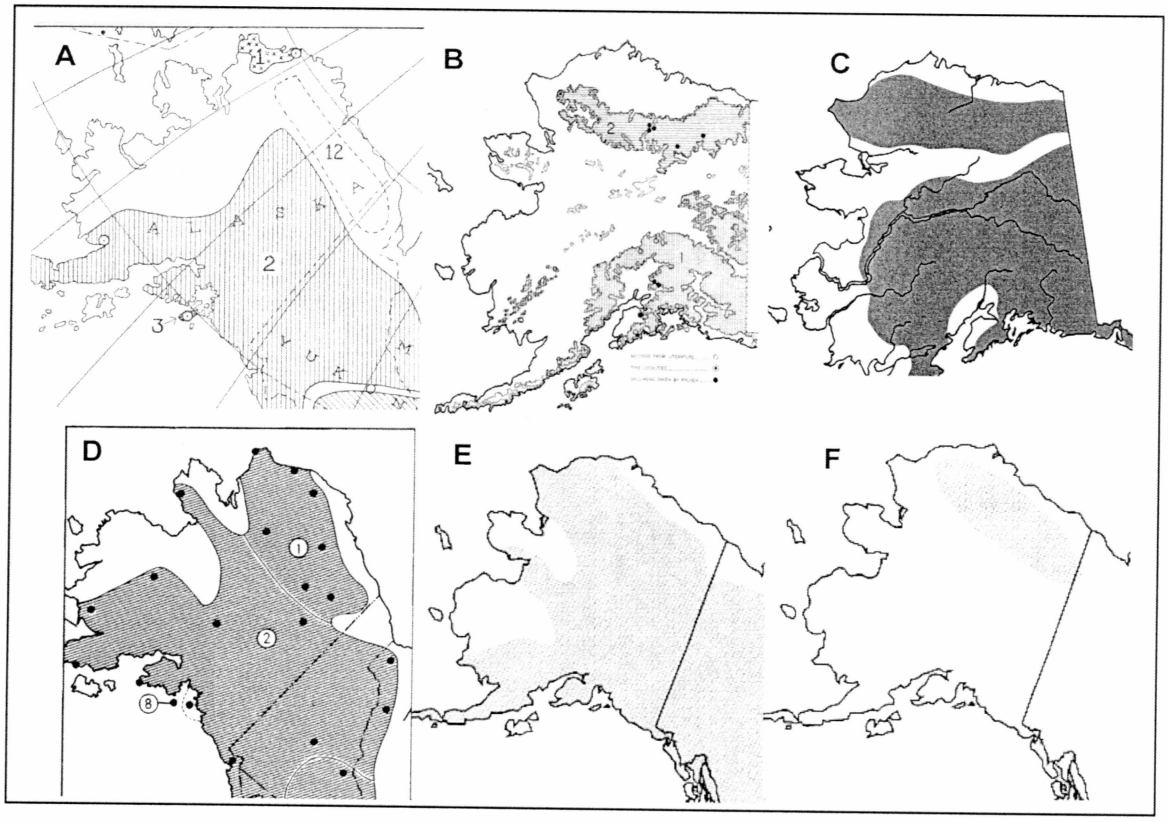

Figure 1 Past distribution maps for *Marmota broweri* and *M. caligata*. A = distribution of *M. caligata* including *M. c. broweri* from northwestern Alaska (Anderson 1934). B = distribution of *M. marmota caligata* (south) and *M. m. broweri* (north) (Rausch 1953). C = distribution of *M. caligata* (ADFG 1978). D = distribution of *M. caligata* (Hoffmann 1981). E = distribution of *M. caligata* (Hoffmann 1999). F = distribution of *M. broweri* (Hoffmann 1999).

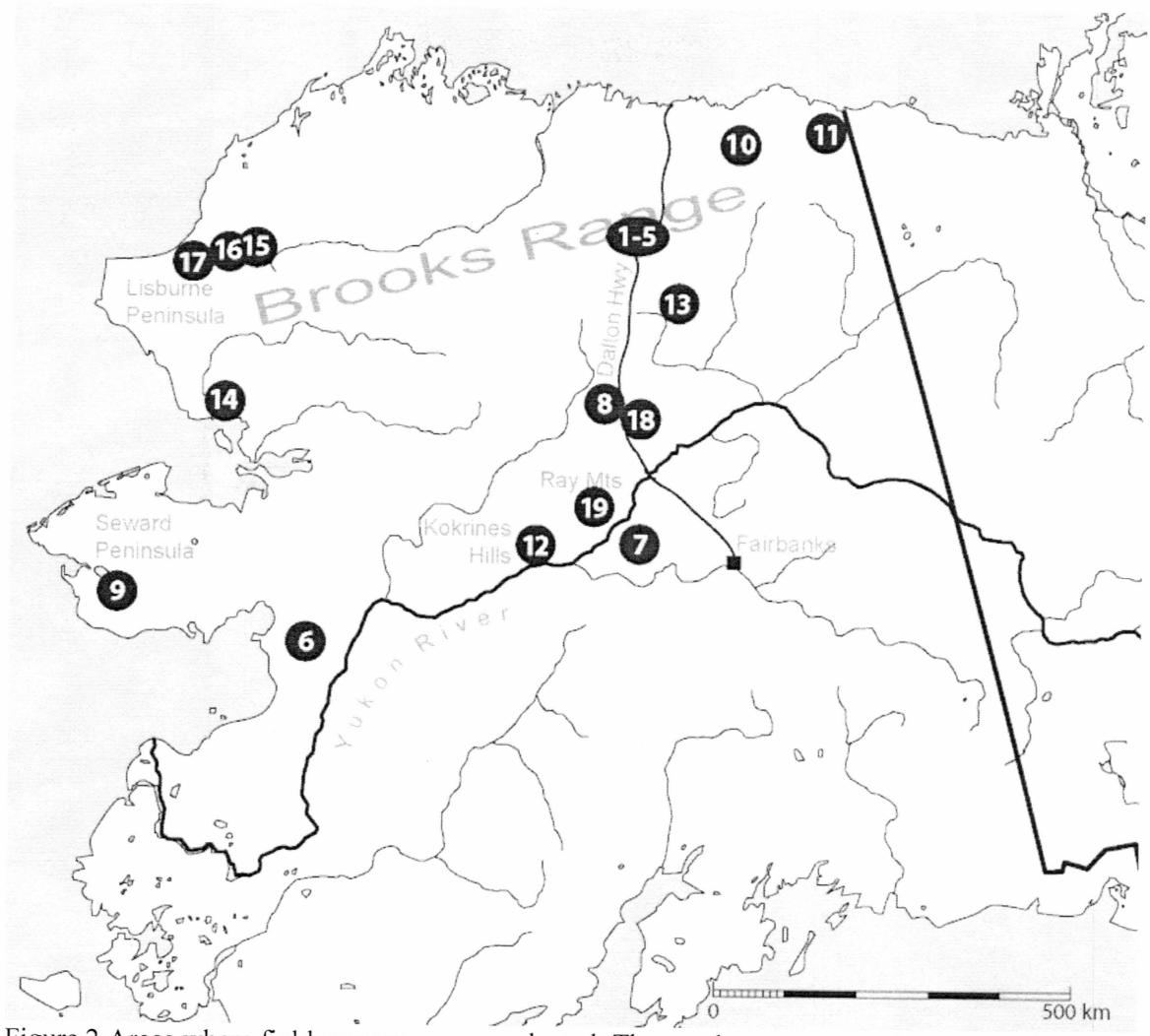

Figure 2 Areas where field surveys were conducted. The numbers correspond to survey sites in Table 1.

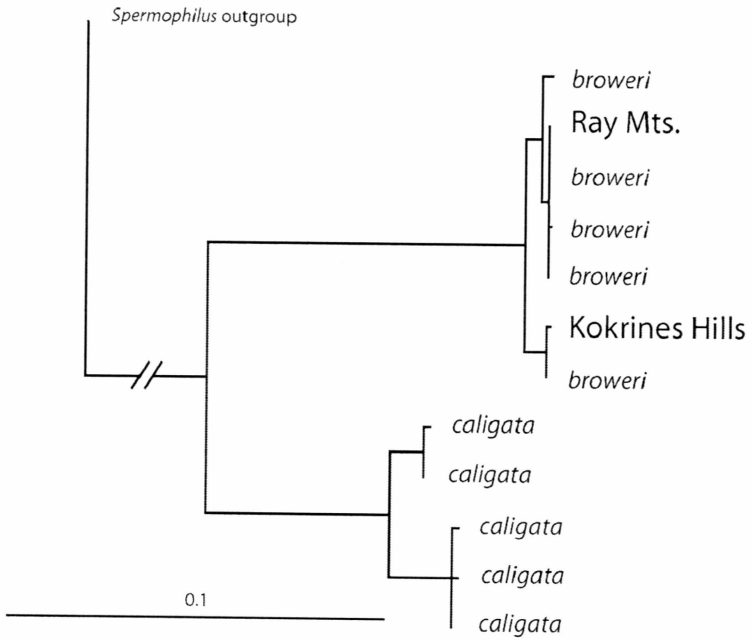

Figure 3 The maximum likelihood tree for five *Marmota broweri*, five *M. caligata*, and the museum specimens from central Alaska. Both specimens (Ray Mts. and Kokrines Hills) are confirmed to be *M. broweri*.

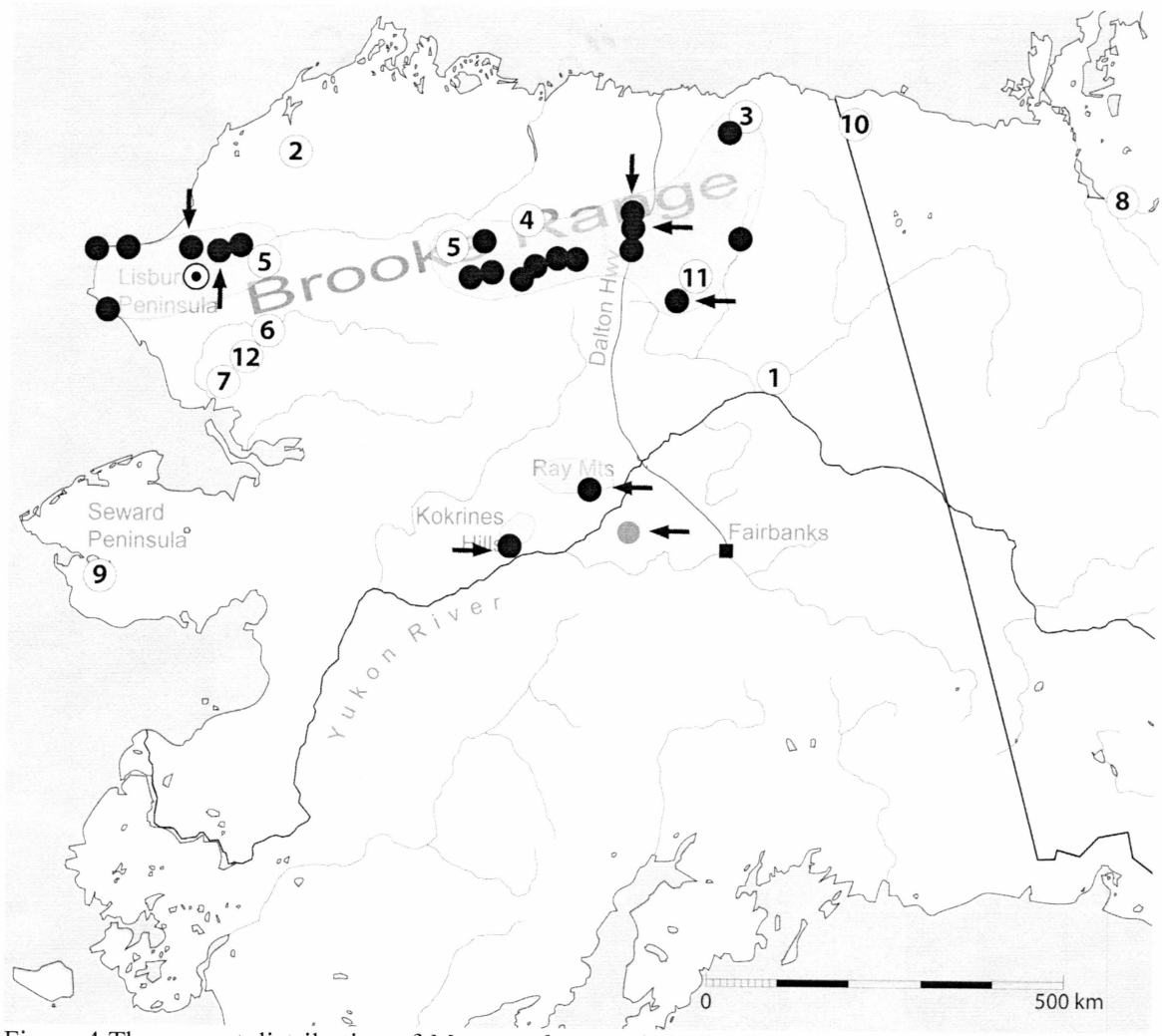

Figure 4 The current distribution of *Marmota broweri* is indicated by the shaded gray areas. The black circles represent localities with museum voucher specimens. The double black circle is the type locality. The numbered circles represent authoritative but unconfirmed observations of *M. broweri* and the numbers correspond to the following references: 1. Howell (1915). 2. Bailey and Hendee (1926). 3. Anderson (1934). 4. Rausch (1951). 5. Bee and Hall (1956). 6. Dean and Chesemore (1974). 7. Gardner (1974). 8. Hoffman et al. (1979). 9. Juday (1984). 10. Barney Smith (pers. comm.), Canadian Wildlife Service. 11. Dusty MacDonald (pers. comm.), University of Alaska Museum 12. Eric D. Sieh (pers. comm.), Kotzebue, AK. Arrows indicate previously undocumented localities. The gray circle represents a newly documented population of *M. caligata*.

Table 1 Summary of field survey effort.

	Survey Area	Dates Surveyed	Latitude	Longitude	Results
1	Dalton Hwy, Slope Mt.	18 Jun 2005	N 68° 43' 46"	W 149° 1' 57"	3 *broweri* collected
1	Dalton Hwy, Slope Mt.	27 Jun 2006	N 68° 44' 13"	W 149° 1' 38"	1 *broweri* collected
2	Dalton Hwy, Jade Mt.	28 Jun 2006	N 68° 37' 4"	W 149° 40' 33"	no marmots observed
3	Dalton Hwy, Imnavait Mt.	25 Aug 2006	N 68° 44' 40"	W 149° 24' 55"	no marmots observed
4	Dalton Hwy, Galbraith	24 Aug 2006	N 68° 31' 4"	W 149° 27' 9"	3 *broweri* collected
5	Dalton Hwy, Toolik Field Station	6 Aug 2007	N 68° 36' 51"	W 149° 29' 53"	1 *broweri* collected
6	Nulatto Hills	5-12 Jul 2005	N 64° 22' 22"	W 159° 32' 43"	no marmots observed
7	Elephant Mt.	16-19 Jun 2006	N 65° 15' 30"	W 150° 3' 28"	2 *caligata* collected
8	Dalton Hwy, Beaver Slide	29 Jun 2006	N 66° 28' 45"	W 150° 43' 34"	no marmots observed
9	Kigluaik Mountains	21-24 Jul 2006	N 65° 2' 27"	W 165° 25' 58"	no marmots observed
10	Lake Peters	21 Jul-1 Aug 2006	N 69° 17' 31"	W 145° 0' 38"	2 *broweri* collected
11	Kongukut River	31 Jul-10 Aug 2006	N 69° 14' 54"	W 141° 44' 24"	no marmots observed
12	Kokrines Hills	10-14 Jun 2007	N 64° 57' 0"	W 154° 51' 0"	no marmots observed
13	Little Squaw Lake	7 Jun, 31 Jul 2007	N 67° 33' 57"	W 148° 11' 00"	2 *broweri* collected
14	Mulik Hills	1 Jul 2007	N 67° 9' 53"	W 162° 19' 13"	no marmots observed
15	Utukok River	3 Jul 2007	N 68° 57' 38"	W 161° 19' 18"	4 *broweri* observed, none collected
16	Tupikchak Mt.	3-4 Jul 2007	N 68° 51' 42"	W 161° 49' 22"	6 *broweri* collected
17	Kukpowruk River	4 Jul 2007	N 68° 56' 55"	W 162° 53' 27"	1 *broweri* collected
18	Dalton Hwy, Finger Mt.	4 Aug 2007	N 66° 21' 27"	W 150° 27' 38"	no marmots observed
19	Ray Mountains	7-12 Sep 2007	N 65° 42' 41"	W 151° 7' 14"	6 *broweri* collected

Table 2 Summary of specimen data from collection notes and museum records. Measurements were made in the field prior to preservation (TL=total length, HF=hind foot, EFN=ear from notch).

Catalog Number	Species	Locality	Sex	TL-Tail-HF-EFN ≡ Weight (kg)
UAM Mamm 15043	*Marmota broweri*	Ray Mountains	?	X
UAM Mamm 15044	*Marmota broweri*	Kokrines Hills	M	591-152-83-35 ≡ 2.83
UAM Mamm 85224	*Marmota broweri*	Dalton Hwy, Slope Mountain	F	635-145-88-35 ≡ 3.85
UAM Mamm 85225	*Marmota broweri*	Dalton Hwy, Slope Mountain	F	640-160-87-22 ≡ 3.75
UAM Mamm 85226	*Marmota broweri*	Dalton Hwy, Slope Mountain	M	640-166-90-33 ≡ 3.70
UAM Mamm 85514	*Marmota broweri*	Dalton Hwy, Galbraith	F	404-95-67-23 ≡ X
UAM Mamm 85760	*Marmota broweri*	Dalton Hwy, Slope Mountain	M	517-140-74-27 ≡ 1.60
UAM Mamm 85847	*Marmota broweri*	Lake Peters	F	552-147-80-18 ≡ 2.12
UAM Mamm 85848	*Marmota broweri*	Lake Peters	F	x-121-71-26 ≡ X
UAM Mamm 85858	*Marmota caligata*	Elephant Mountain	M	715-190-96-34 ≡ 4.50
UAM Mamm 85859	*Marmota caligata*	Elephant Mountain	M	527-50-85-27 ≡ X
UAM Mamm 86397	*Marmota broweri*	Dalton Hwy, Galbraith	F	628-130-83-28 ≡ 3.30
UAM Mamm 86399	*Marmota broweri*	Dalton Hwy, Galbraith	F	615-136-88-28 ≡ 4.25
UAM Mamm 87300	*Marmota broweri*	Tupikchak Mountain	F	607-143-83-27 ≡ 4.8
UAM Mamm 87301	*Marmota broweri*	Tupikchak Mountain	M	654-158-87-28 ≡ 4.7
UAM Mamm 87302	*Marmota broweri*	Ray Mountains	F	567-120-78-27 ≡ 3.15
UAM Mamm 87303	*Marmota broweri*	Ray Mountains	M	519-123-82-24 ≡ 2.6
UAM Mamm 87304	*Marmota broweri*	Tupikchak Mountain	M	700-172-90-32 ≡ 5.9
UAM Mamm 87305	*Marmota broweri*	Ray Mountains	F	504-127-77-23 ≡ 2.0
UAM Mamm 87306	*Marmota broweri*	Tupikchak Mountain	F	658-184-87-27 ≡ 5.1
UAM Mamm 87307	*Marmota broweri*	Ray Mountains	F	526-129-76-23 ≡ 2.2
UAM Mamm 87308	*Marmota broweri*	Ray Mountains	M	537-125-78-26 ≡ 2.4
UAM Mamm 87309	*Marmota broweri*	Ray Mountains	M	635-148-83-28 ≡ 3.65
UAM Mamm 87310	*Marmota broweri*	Tupikchak Mountain	M	622-193-93-32 ≡ 3.4
UAM Mamm 87311	*Marmota broweri*	Little Squaw Lake	M	488-129-76-15 ≡ X
UAM Mamm 87312	*Marmota broweri*	Tupikchak Mountain	F	583-155-87-30 ≡ 3.1
UAM Mamm 87313	*Marmota broweri*	Kukpowruk River	F	640-160-80-25 ≡ 4.6
UAM Mamm 87314	*Marmota broweri*	Little Squaw Lake	M	625-160-85-27 ≡ X
UAM Mamm 87946	*Marmota broweri*	Dalton Hwy, Toolik Field Station	F	X-X-X-X ≡ 3.09

Chapter 2 The phylogeography of the Alaska marmot (*Marmota broweri*) based on DNA sequence variation in the mitochondrial gene cytochrome *b*

2.1 Abstract

Beringia has been recognized as an important Pleistocene refugium and shaped the present diversity and distributions of many arctic species. Since *M. broweri* was a resident of Beringia during the Pleistocene, I expect the phylogeographic structure of Alaska marmots (*M. broweri*) to exhibit the signature of persistence in Beringia and subsequent expansion into glaciated areas. My objective was to investigate the phylogeographic structure of Alaska marmot populations through phylogenetic tree construction, measures of genetic diversity, a mismatch distribution, and nested clade analysis of DNA sequence data from the mitochondrial cytochrome *b* gene. I found significant geographic structure across the range of *M. broweri*. The highest levels of genetic diversity were recovered in the eastern Brooks Range populations and the southern populations from the Ray Mountains and Kokrines Hills. Populations in the western Brooks Range showed very little diversity. The results of my analyses suggest a recent population expansion from central Alaska (Beringia) into the formerly glaciated Brooks Range.

2.2 Introduction

Marmots are large sciurid rodents, the largest members of the ground squirrel subfamily Marmotinae (Barash 1989, Harrison et al. 2003). There are currently 14 recognized species of marmots that range across the holarctic. With one exception, the woodchuck (*Marmota monax*), marmots are restricted to alpine habitats, living on "sky islands" isolated by barriers in lower elevation ecosystems. This restricted distribution and dependence on high elevation habitats makes marmots particularly vulnerable to the warming climate and the subsequent changes to their preferred habitat (Krajick 2004). As shrublines and treelines move rapidly northward and upslope (Sturm et al. 2001, Overpeck et al. 1997), marmots must also move northward or upslope

if they are to survive. For this reason marmots have been called harbingers of changes occurring in alpine regions around the world (Krajick 2004). Due to their isolation and assumed limited dispersal ability I expect marmot species to exhibit high levels of population structure, but no phylogeographic studies have been conducted to establish a current measure of population structure or a baseline of genetic diversity for any species of marmot. In order to understand how climate change will affect marmots and other alpine restricted species we need to understand the current relationships among isolated populations and the genetic consequences of past climatic and geographic fluctuations.

The Alaska marmot, *Marmota broweri*, occurs only in alpine areas of northern Alaska, predominately in the Brooks Range -- the northernmost distribution of any marmot species. Steppan et al. (1999) determined *M. broweri* to be more closely related to Asian marmot species than to its nearest marmot neighbor the hoary marmot (*M. caligata*). Two hypotheses have been proposed for the origin of *M. broweri* in North America. Rausch and Rausch (1971) suggested the Alaska marmot was "a relict North American species (p. 96)," meaning it was left behind in the Alaska as an ancestral marmot crossed the Bering land bridge and radiated in Asia and Europe. Hoffmann and Nadler (1968) and Hoffman et al. (1979) proposed *M. broweri* originated in Asia and crossed back into North America during the Pleistocene Epoch. Steppan et al. (1999) were unable to reject either hypothesis but suggested the second was more likely. Both of these scenarios place *M. broweri* in Beringia during the Pleistocene.

Beringia was a large land area that remained ice-free during the repeated glacial advances and retreats that characterized the Pleistocene (Pielou 1991). It extended from eastern Siberia through central Alaska and into western Yukon Territory and served as both an isolating mechanism, separated from both North America and Asia by glaciers, and as a dispersal corridor allowing the exchange of flora and fauna between the two continents via the Bering Land Bridge.

Many studies have focused on Beringia and its role as a refugium, shaping the diversity of arctic species (Waltari et al. 2007). In many phylogeographic studies of arctic mammal species, Beringia served as a source for colonization of deglaciated areas (Eddingsaas et al. 2004, Federov and Goropashnaya 1999, Galbraith and Cook 2004, Hundertmark et al. 2002). I expect this common historical pattern of persistence in Beringia and subsequent expansion into previously glaciated areas to be found in *Marmota broweri*. My objective is to investigate the phylogeographic structure of Alaska marmot populations through phylogenetic tree construction, measures of genetic diversity, a mismatch distribution, and nested clade analysis of DNA sequence data from the mitochondrial gene cytochrome *b*.

2.3 Methods

2.3.1 Sampling

I collected 24 Alaska marmots from eight unique localities over three field seasons from June – September, 2005 – 2007. I obtained fresh tissue subsamples from the six individual specimens with such material from museum collections. An additional 27 "degraded" tissue samples were obtained from museum collections as skin subsamples taken from study skins or residual tissue left on skeletal material (crusties). Of the 27 degraded tissue sample extractions, four were unsuccessful or failed to amplify, leaving a total sample size of 53 individuals (Table 1) representing 18 localities (Figure 1).

2.3.2 Molecular methods

DNA was extracted from fresh tissue samples using the PureGene Genomic DNA Purification Kit (Gentra Systems, Minneapolis, MN) protocol. The resulting template was diluted into a 1:10 working solution for use in PCR. From fresh tissue extractions I amplified and sequenced the entire length of cytochrome-*b* (1140 base-pairs) in two overlapping segments using the primer pairs CB-F1 (5' CTCACCGTTGTTATTCAACTA 3') and CB-AGR1 (5'

GGGATTTTGTCTGAGTCAGA 3'), and CB-AGF1 (5' CAAAGCCACTCTAACACGAT 3') and CB-R3AG (5' GGTTTACAAGGCCAGGGTAATG 3'). Volumes and concentrations of reagents used in the fresh tissue amplifications were as follows: 0.6 μL DNA template (1:10), 0.6 μL each of primers (10 μM), 1.5 μL 10X Promega (Madison, WI) reaction buffer, 0.6 μL $MgCl_2$ (25 mM), 0.3 μL dNTPs (10 mM), 0.15 μL Promega GoTaq polymerase (5 U/μL), and 10.65 μL H_2O for a total reaction volume of 15 μL. The reactions were run on an MJ Research PTC-200 Peltier thermal cycler (Bio-Rad Laboratories, Inc. Hercules, CA) with the following cycling parameters: 94°C for one minute, then 30 cycles of 94°C for 20 seconds, 55°C for 15 seconds, 72°C for 20 seconds.

DNA extractions and PCR setups from dried study skin or crusty samples were performed in the Ancient DNA Laboratory at the University of Alaska Museum (a PCR-free building), a laboratory designed specifically for procedures with high risks of contamination. Each sample of approximately 20 mg tissue was digested in a 1.6 ml tube with 600 μL Cell Lysis Solution (PureGene Genomic DNA Purification Kit, Gentra Systems, Minneapolis, MN), 20 μL proteinase K (20 mg/ml), and 30 μL DTT (100 mM) for 24 - 48 hours, shaking at 55°C. For those samples that remained undigested after 24 hours, 20 μL more proteinase K was added and the samples were allowed to digest for another 24 hours. After digestion, the extractions proceeded according to the PureGene Genomic DNA Purification Kit protocol for DNA purification from 5-10 mg fresh or frozen solid tissue with the following modifications: RNAse treatment was omitted and all reagent/solution volumes were doubled (protein precipitation solution, isopropanol, ethanol, DNA hydration solution). Each extraction included a negative control to test for contamination from the extraction procedure. The resulting DNA template was not diluted for use in PCR. Due to the degraded nature of the DNA extracted from the skin and crusty samples, I amplified and sequenced the entire length of cytochrome *b* in seven overlapping sections using

the following primer pairs: CB-F1 and CB-R4AG (5' TGTGGGCAACTGATGAGAAA 3'), CB-F4AG (5' ATCCAAATCTTTACCGGACT 3') and CB-R5AG (5' TGACCTCAGGGGAGGACATA 3'), CB-F5AG (5' CTACGGCTCATATACCTACTC 3') and CB-R6AG (5' TAGGGCTGCGATGATAAAGG 3'), CB-AGF1 and CB-R7AG (5' ATCAGGGTCTCCCAGAAGGT 3'), CB-F6AG (5' AATCCCCTTTCACCCGTACT 3') and CB-R8AG (5' GAGAAGATTAGGGCTAGGACTC 3'), CB-F7AG (5' TACACCCGCAAACCCTCTAA 3') and CB-R9AG (5' AGATTGTCCTCCGATTCAGGT 3'), and CB-F8AG (5' TCGACCATTAAGCCAATGTG 3') and CB-R3AG. Volumes and concentrations of reagents used in these amplifications were as follows: 1 μL DNA template, 1 μL each of primers (10 μM), 2.5 μL 10X Promega reaction buffer, 1 μL $MgCl_2$ (25 mM), 0.5 μL dNTPs (10 mM), 0.25 Promega GoTaq polymerase (5 U/μL), and 17.75 μL H_2O for a total reaction volume of 25 μL. The reactions were run on the thermocycler with the following cycling parameters: 94°C for three minutes, then 40 cycles of 94°C for one minute, 55°C for one minute, 72°C for one minute. The extraction negatives were run along with DNA extracts; each PCR reaction also included a negative control to determine if any contaminating DNA was introduced from the PCR reagents, and a positive control to verify the PCR reaction was occurring as expected.

Prior to cycle sequencing, all PCR products were cleaned up with Exo-SAP-IT (USB, Cleveland, Ohio) according to the manufacturer's protocol. Purified PCR products (1-2 μL) were cycle sequenced using BigDye Terminator (Perkin-Elmer, Boston, MA) (2 μL), 5X reaction buffer (1μL), water (6μL), and the same primers (1 μL) as were used in PCR. Sequencing reactions were purified using Sephadex beads before being electrophoresed on an ABI 3100 (Applied Biosystems, Foster City, CA) sequencer. All gene segments were sequenced in forward and reverse directions.

2.3.3 Data analysis

DNA sequences were aligned and assembled with reference to a *Marmota broweri* cytochrome *b* sequence obtained from GenBank (AF143918) and checked by eye with SEQUENCHER 4.7 (Gene Codes, Ann Arbor, MI). All the sequences have been deposited on GenBank (Accession numbers).

Phylogenetic analyses using maximum likelihood (ML) and maximum parsimony (MP) criteria were performed with PAUP* 4.0b10 (Swofford 2003). Heuristic MP and ML tree searches were conducted using stepwise addition of 100 random addition sequences with the tree bisection-reconnection branch-swapping algorithm. For the ML analysis a model of nucleotide substitution (GTR+G) and associated parameters were estimated using MODELTEST 3.7 from the Akaike Information Criterion (Posada and Buckley 2004, Posada and Crandall 1998). Bootstrap values of nodal support were generated for the ML tree from one hundred replicates. Bayesian inference was implemented with MRBAYES 3.1.2 (Huelsenbeck and Ronquist 2001) using two runs of four chains (one heated) for five million generations to produce posterior probabilities for the most likely tree topology. *Marmota caudata*, *M. menzbieri*, and *M. monax* sequences obtained from GenBank (AF143923-143925, AF143931, AF143932-143934) were used as an outgroup for rooting trees in all analyses.

Based on the proximity of the sites and the continuity of suitable habitat, samples from sites M and N (Table 1) were considered a single population, as were samples from F and G, and A, B and C. Also, because Rausch (1953) claimed the likely source of the specimens from Point Lay was near the head of the Kukpowruk River, the samples from sites D and E were considered a single population. All other localities were considered unique populations. Nucleotide diversity (π) was estimated using ARLEQUIN 2.000 (Schneider et al. 2000) for each population with more than one individual and also for combined regional samples from the western Brooks Range,

eastern Brooks Range, and southern mountain ranges (Ray Mountains and Kokrines Hills). Smaller values of π for one area indicate the population has recently expanded into that area whereas larger values indicate a population has persisted for longer periods of time.

I used ARLEQUIN to construct a mismatch distribution plot of pairwise differences among individuals. A mismatch distribution is used to infer whether a population has undergone recent expansion. A unimodal distribution with concordance between the observed distribution and the expected distribution under a sudden expansion model indicates recent expansion, whereas a ragged distribution indicates population stability (Rogers and Harpending 1992, Schneider and Excoffier 1999). Parametric bootstrapping implemented in ARLEQUIN was used to test the goodness-of-fit of the observed distribution to the expected model. The null hypothesis for this test is recent population expansion. The raggedness index was also calculated to further test for a signal of recent expansion (Harpending 1994).

The relationships between *Marmota broweri* haplotypes were further explored with a haplotype network constructed using the program TCS 1.21 (Clement et al. 2000) and through nested clade phylogeographic analysis performed using the program GEODIS 2.0 (Posada et al. 2000). In a nested clade analysis the haplotype network is nested according to the published nesting rules of Templeton et al. (1987) and Templeton and Sing (1993) into a clade hierarchy of one-step clades, two-step clades, etc. until the entire network is contained in a single clade. Then the geographic association of clades is tested though the calculation of clade distances (D_c) and nested clade distances (D_n). Clade distance (D_c) is the mean geographic distance of all individuals in a clade (in km) from that clade's geographic center (Templeton et al. 1995). When considering a single haplotype as a clade, D_c is the mean distance of each individual with that haplotype from the geographic center of that haplotype. A statistically significant value of D_c indicates that the geographic spread of individuals within a clade, or with a given haplotype, is smaller

(significantly small D_c) or larger (significantly large D_c) than expected by chance. Nested clade distance (D_n), is the mean geographic distance (in km) of all individuals within a clade from the center of the next higher level nested clade (Templeton et al. 1995). For my nested clade analysis, the haplotype network was not nested according to the published nesting rules. My nested design allowed each clade of interest to be tested for geographic association in relation to the entire cladogram instead of the next higher level nesting clade. I calculated clade distances (D_c) as described by Templeton et al. (1995), but nested clade distances (D_n) were calculated using the geographic center of the total cladogram. In this way the total cladogram was considered as the next higher level nesting clade for all D_n calculations. Statistically significant values for D_n indicate individuals within a clade, or with a given haplotype, are nearer to (significantly small D_n) or farther from (significantly large D_n) the geographic center of the total cladogram than is expected by chance. With this method I can show statistically significant geographic associations of haplotypes or clades with reference to the entire range of *M. broweri*. Because I modified the nested design, no inferences were made based on the key published by Templeton (1995). The null hypothesis of no geographic structure among haplotypes was tested by comparing observed clade distances to expected distances obtained from 10,000 random chi-squared permutations. In order to eliminate any bias resulting from the sampling family groups, I removed all individuals that I knew were collected from the same burrow. Of the samples from museum specimens I did not collect myself, I removed redundant individuals that were collected by the same collector on the same date from a single locality. This left a sample size of 43 for the nested clade analyses.

2.4 Results

Among the 53 individual specimens from 18 localities I found 12 unique haplotypes. There were 24 polymorphic sites within the total 1140 base pairs of the cytochrome *b* gene, consisting of 22 transitions and two transversions. The mean number of pairwise differences for the entire sample was 4.85 and the average uncorrected pairwise distance (*p*-distance) between individuals was 0.42% with a range of 0.0-1.4%. Nucleotide diversity estimates (π) and *p*-distances for each population and region are shown in Table 2.

The maximum likelihood tree with branch lengths and nodal support values is shown in Figure 2. Both maximum parsimony and bayesian inference produced the same tree topology as the maximum likelihood analysis. Four main clades were resolved, although only clade IV was well supported by both ML bootstrap values and posterior probabilities. Clade IV contained individuals from three localities in the eastern and southern extremes of the sampled distribution. Individuals from the southern populations were also found in two other clades. The two most common haplotypes were geographically segregated into western and eastern/southern regions. A single individual from the eastern Brooks Range (USNM 290275) had a unique haplotype that grouped among the western samples. Nucleotide diversity estimates (π) for populations and for each region (east, west, south) (Table 2) also indicate more diversity in populations from the eastern Brooks Range and from the southern mountain ranges than in populations from the western Brooks Range. A mismatch distribution of all individuals was not significantly different from the simulated distribution under a model of population expansion as tested by the goodness-of-fit (SSD=0.041, P= 0.59) and the raggedness index (0.095, P=0.20) (Figure 3). The null hypothesis of recent population expansion could not be rejected.

The haplotype network estimation yielded a single most parsimonious network (Figure 4) with a maximum of 16 mutational steps between haplotypes. The network shows more clearly the

short branch lengths found between clades I, II, and III. The network also illustrates the higher levels of diversity found in samples collected from the eastern Brooks Range (eight haplotypes from 11 localities) and in the southern region (three haplotypes from two localities) than was found in samples from the western Brooks Range (two haplotypes from seven localities). The nested clade analysis revealed significant geographic association of haplotypes and higher level clades. The null hypothesis of no geographic association was rejected for clade III and the total cladogram (Table 3). The geographic distance statistics, clade distance (D_c) and nested clade distance (D_n) showed significant differences for haplotypes 1-4, 8, 9, and 11 and for clades I-IV (Table 4).

2.5 Discussion

While my sample included only seven individuals from the southernmost populations of *Marmota broweri* (Kokrines Hills and Ray Mountains), three different haplotypes were found which were recovered in three of the four major clades produced by the phylogenetic analyses (Figure 2). The high levels of diversity and more ancestral haplotypes recovered from individuals from the southern populations (Kokrines Hills and Ray Mountains) and eastern populations (Arctic Village and Lake Peters) suggest that those populations have persisted longer than other populations. Both the Kokrines Hills and the Ray Mountains occurred in the ice-free refugium, Beringia, during the glacial cycles of the Pleistocene Epoch and would have been available to Alaska marmots (Brigham-Grette 2001, Clark and Mix 2002). During that period the Brooks Range was covered with glaciers and would therefore presumably not have supported marmots. Samples from the two easternmost populations in the Brooks Range, at Lake Peters and Arctic Village, were also found in clade IV with ancestral haplotypes, but among the eight individuals from those populations only two haplotypes were found in two of the four major clades, indicating less diversity in those populations than was found in the southern region. All other

populations show lower levels of diversity over the broad expanse of the Brooks Range. The pattern of geographic structure among *M. broweri* populations, evident from the measures of genetic diversity, mismatch distribution, phylogenetic analyses, and nested clade analysis, is consistent with a recent population expansion into the Brooks Range from central Alaska at the end of the Pleistocene.

No other mammal species (or any species I am aware of) shares the unique restricted distribution of the Alaska marmot in northern Alaska. Arctic ground squirrels (*Spermophilus parryii*) have a much more expansive distribution than Alaska marmots, including southern Alaska, Canada, and Siberia, but their ranges overlap in the Brooks Range and the Ray Mountains. Eddingsaas et al. (2004) found significant geographic structure among populations of *S. parryii* across its distribution. However, most of the divergence in *S. parryii* was among southern populations. They found a single well-supported clade of arctic ground squirrels from the Brooks Range, isolated from southern populations by the invasion of boreal forests as glaciers retreated. They state,

> "the polytomy formed by the populations in the north [Brooks Range] clade could reflect a recent population expansion, possibly due to an increase in suitable habitat (p. 605)."

This is the same pattern I observed in *Marmota broweri*. Alternatively, Eddingsaas et al. (2004) hypothesized that "populations of the north clade [of *S. parryii*] might have persisted in a refugium in arctic Canada and then expanded westward into northern Alaska following glacial retreat...(p. 605)." This Canadian arctic refugium has been hypothesized for the collared lemming and rock ptarmigan as well (Federov and Stenseth 2002, Holder 1999). The pattern of expansion I observed in *M. broweri*, including higher levels of diversity in eastern populations than in western

populations, could also be the result of expansion into the Brooks Range from a northwestern Canadian refugium, although *M. broweri* is not known to occur in Canada at present.

More fieldwork is needed to fill in the gaps of the Alaska marmot's distribution in the Brooks Range. Future specimen collecting efforts should focus on populations in the western Brooks Range, the Ray Mountains, and the Kokrines Hills. It is possible marmots will be found on the Seward Peninsula in western Alaska (Bailey and Hendee 1926, Juday 1984) and in the British or Richardson Mountains of northern Yukon Territory, Canada (Hoffmann and Nadler 1979). Samples from those areas would help resolve the source and direction of post-glacial expansion by *M. broweri.*

This is the first intraspecies phylogeographic study of any species of the genus *Marmota.* In 1999, Steppan et al. published a phylogeny including all 14 recognized species in the genus *Marmota* based on cytochrome *b* sequence data and tested various biogeographical hypotheses about the divergence of marmot species. Among their conclusions, *Marmota broweri* was not most closely related to its nearest North American neighbor, the hoary marmot (*M. caligata*), or its Siberian cogener, the black-capped marmot (*M. camtschatica*). *Marmota broweri* was shown to be more closely related to Asian marmots (subgenus *Marmota*) than to North American species (subgenus *Petromarmota*), but its position within subgenus *Marmota* was unresolved. Consequently, Steppan et al. (1999) were unable to reject either of the two competing hypotheses about the origin of *M. broweri* -- whether it invaded North America from Asia (Hoffmann and Nadler 1968, Hoffmann et al. 1979) or was left behind in Alaska when marmots first crossed Beringia from North America to Asia and is a North American descendant of the most recent common ancestor of all Asian species (Rausch and Rausch 1971). Both of those scenarios place *M. broweri* in Alaska during the Pleistocene when the Bering land bridge permitted the exchange of flora and fauna between North America and Asia. This would have been the same time period

when the only available habitat suitable for marmots occurred in the ice-free region of central Alaska and eastern Siberia. As such, both of these origin hypotheses would place the oldest and most diverse populations of *M. broweri* in central Alaska. That is what I found; therefore, this study cannot lend support to, or reject either of the two hypotheses concerning the origin of *M. broweri* in North America.

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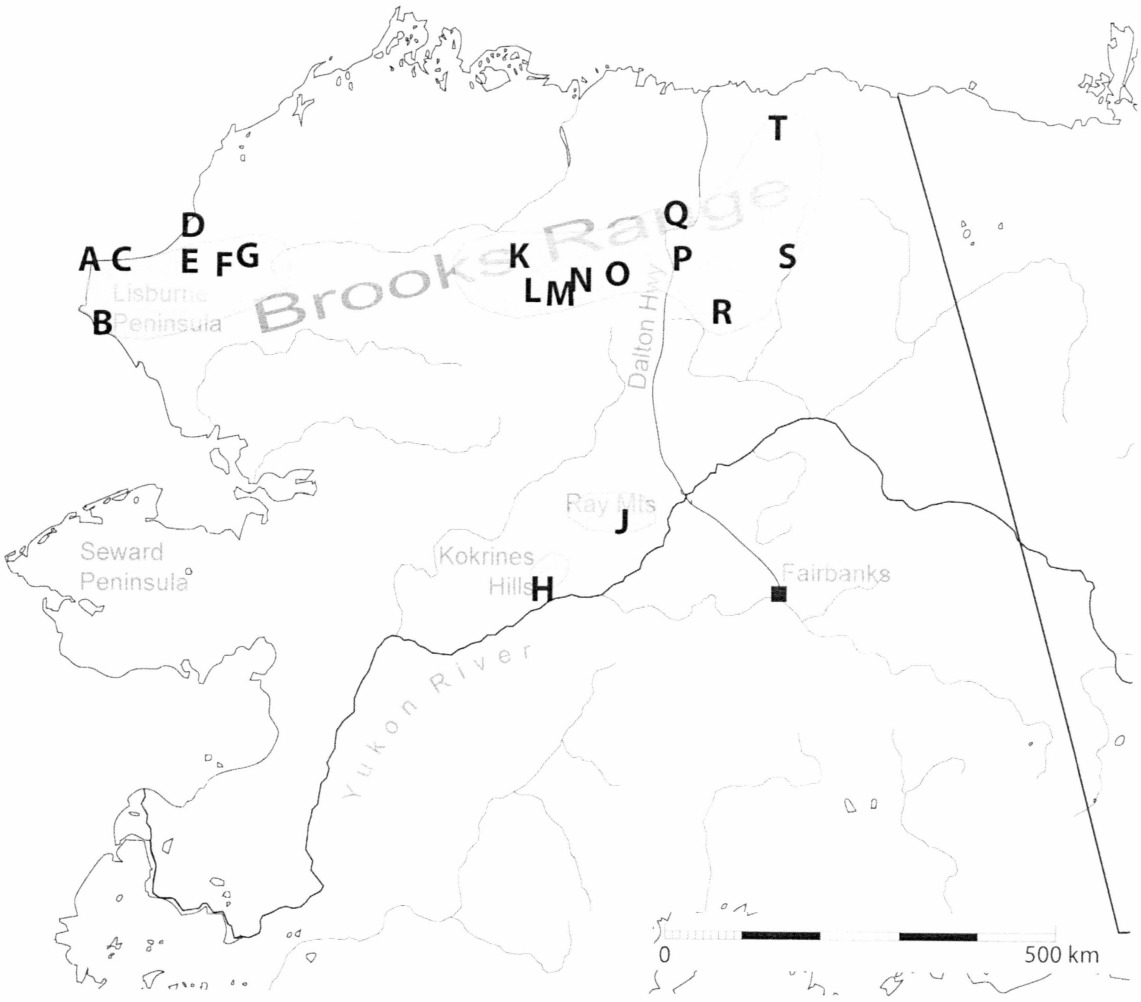

Figure 1 The distribution of *Marmota broweri* (shaded gray) and the localities sampled for this study (letters). The letters correspond specimens listed in Table 1.

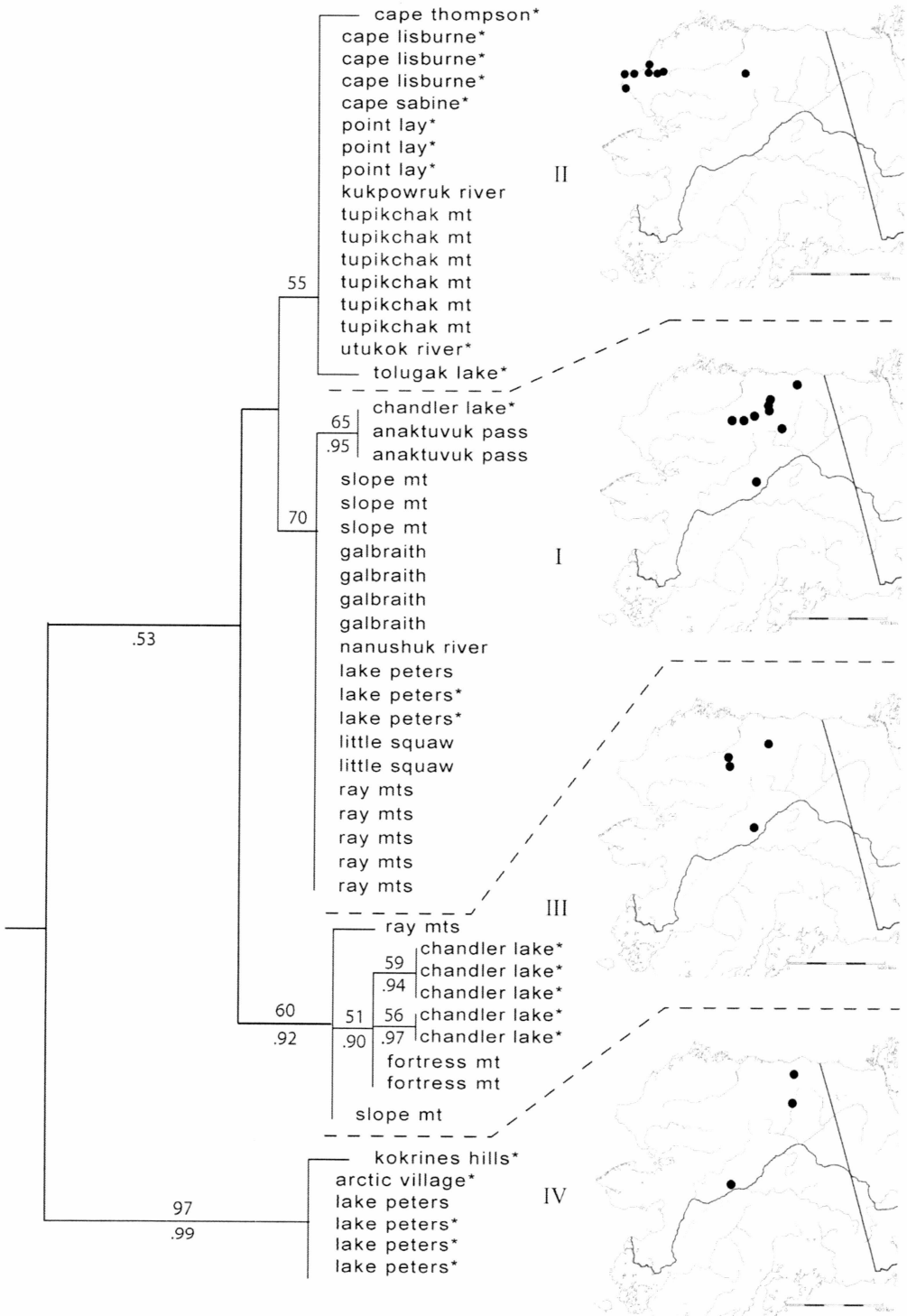

Figure 2 Maximum likelihood phylogram and clade distribution. Terminal labels correspond to the collecting locality of individuals. * indicates samples from degraded tissue. Bootstrap support values greater than 50 are shown above clade branches. Posterior probabilities greater than .50 are shown below clade branches. Clade numbers correspond to Tables 3 and 4 and Figure 4.

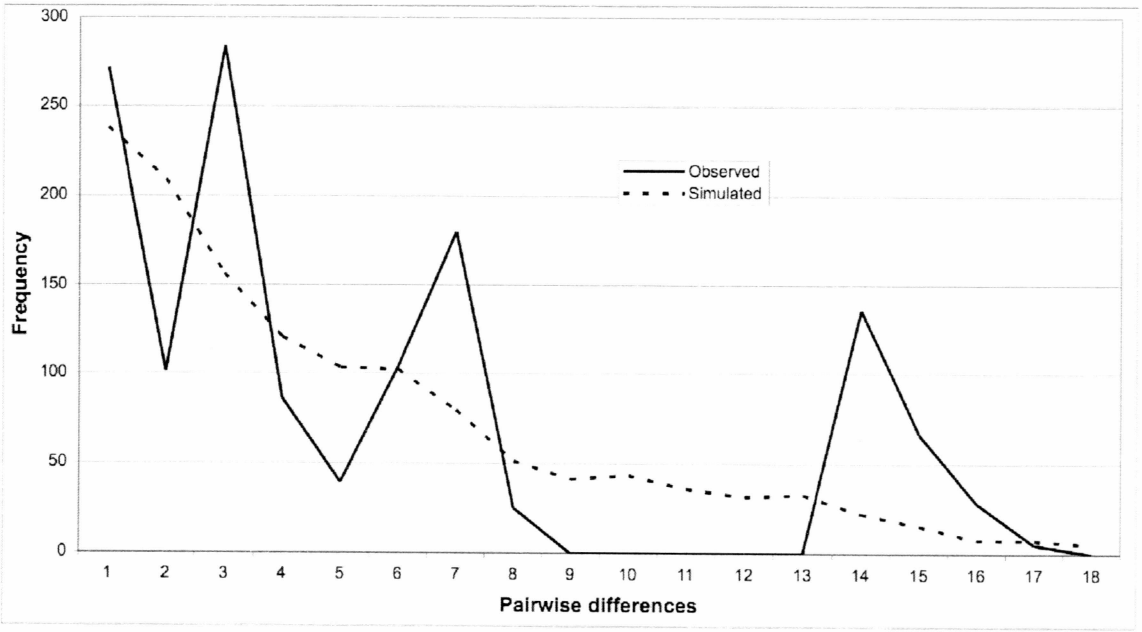

Figure 3 Mismatch distribution of *Marmota broweri* haplotypes. The solid line is the observed distribution and the dashed line is the expected distribution under a model of population expansion. The null hypothesis of recent population expansion could not be rejected (SSD=0.041, P=0.59, raggedness index=0.095, P=0.20).

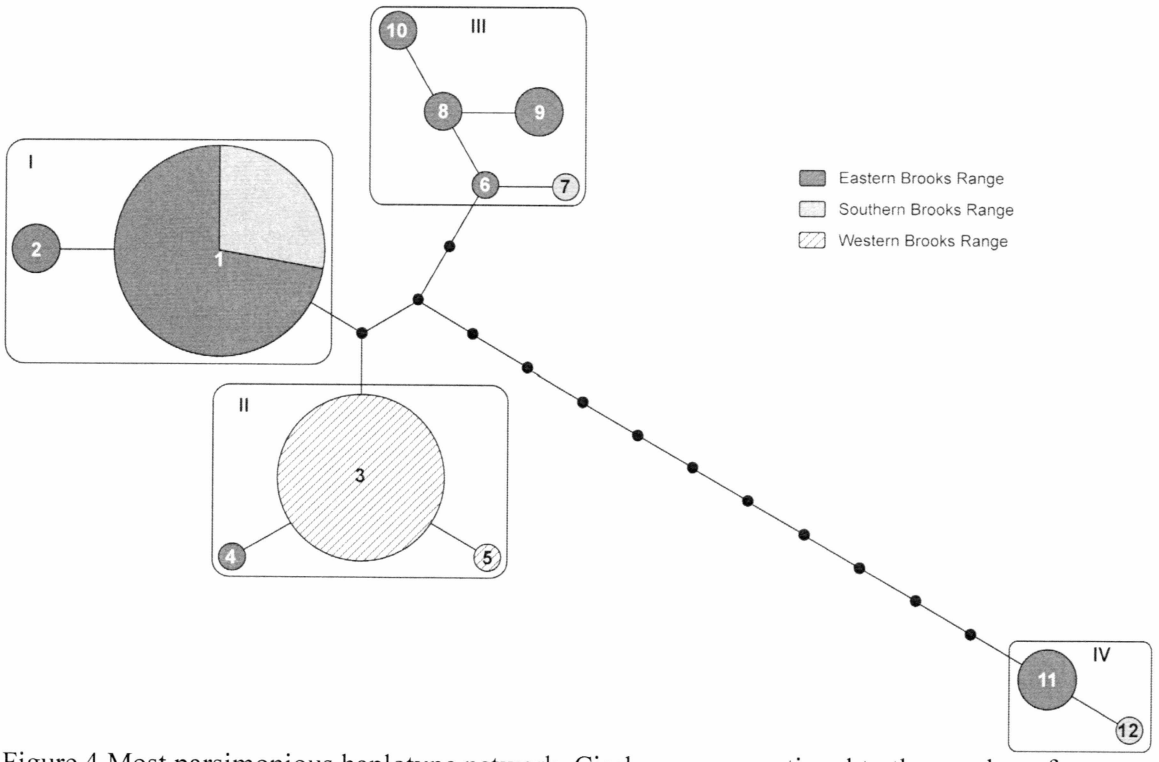

Figure 4 Most parsimonious haplotype network. Circles are proportional to the number of individuals with that haplotype. Haplotype and clade numbers correspond to Tables 3 and 4 and the nested clade analyses described in the text.

Table 1 Museum specimens sampled for this study. Site letters correspond to localities in Figure 1. UAM = University of Alaska Museum, MVZ = Museum of Vertebrate Zoology, KU = University of Kansas Museum of Natural History, MSB = Museum of Southwestern Biology, USNM = Smithsonian Institution Museum of Natural History. Tissue = fresh frozen tissue, skin = dried study skin, crusty = dried residual tissue left on the skeleton.

Site	Catologue number	Locality	Latitude (°N)	Longitude (°W)	Sample type
A	UAM 12613	Cape Lisburne	68.8827	166.22015	skin
	UAM 12614	Cape Lisburne	68.8827	166.22015	skin
	UAM 12615	Cape Lisburne	68.8827	166.22015	skin
B	UAM 7014	Cape Thompson	68.14929	165.46997	skin
C	MVZ 123895	Cape Sabine	68.9141667	164.6325	skin
D	MVZ 51654	Point Lay	69.7575	163.0511111	skin
	MVZ 51655	Point Lay	69.7575	163.0511111	skin
	MVZ 51675	Point Lay	69.7575	163.0511111	crusty
E	UAM 87313	Kukpowruk River	68.94864	162.89095	tissue
F	UAM 87312	Tupikchak Mt.	68.87946	161.82711	tissue
	UAM 87300	Tupikchak Mt.	68.87946	161.82711	tissue
	UAM 87301	Tupikchak Mt.	68.87946	161.82711	tissue
	UAM 87304	Tupikchak Mt.	68.87946	161.82711	tissue
	UAM 87306	Tupikchak Mt.	68.87946	161.82711	tissue
	UAM 87310	Tupikchak Mt.	68.87946	161.82711	tissue
G	UAM 13425	Utukok River	69.06619	161.13697	skin
H	UAM 15044	Kokrines Hills	64.94945	154.85266	skin
J	UAM 87302	Ray Mountains	65.70605	151.10979	tissue
	UAM 87303	Ray Mountains	65.70605	151.10979	tissue
	UAM 87305	Ray Mountains	65.70605	151.10979	tissue
	UAM 87307	Ray Mountains	65.70605	151.10979	tissue
	UAM 87308	Ray Mountains	65.70605	151.10979	tissue
	UAM 87309	Ray Mountains	65.70605	151.10979	tissue
K	UAM 78513	Fortress Mt.	68.56894	152.9395	tissue
	UAM 79182	Fortress Mt.	68.56894	152.9395	tissue
L	KU 43227	Chandler Lake	68.20000	152.75293	crusty
	MSB 137646	Chandler Lake	68.20000	152.75293	crusty
	MSB 137647	Chandler Lake	68.20000	152.75293	crusty
	MSB 137649	Chandler Lake	68.20000	152.75293	crusty
	MSB 141158	Chandler Lake	68.20000	152.75293	crusty
	USNM 305036	Chandler Lake	68.20000	152.75293	crusty
M	USNM 583154	Anaktuvuk Pass	68.14308	151.73907	tissue
	USNM 583155	Anaktuvuk Pass	68.14308	151.73907	tissue
N	USNM 290275	Tolugak Lake	68.2818	151.47419	skin
O	UAM 79245	Nanushuk River	68.27777	150.67435	tissue
P	UAM 85514	Galbraith	68.51709	149.45519	tissue
	UAM 86397	Galbraith	68.51709	149.45519	tissue
	UAM 86399	Galbraith	68.51709	149.45519	tissue
	UAM 35015	Galbraith	68.48465	149.42533	tissue
Q	UAM 85224	Slope Mt.	68.73544	149.03968	tissue

Table 1 continued.

Site	Catologue number	Locality	Latitude (°N)	Longitude (°W)	Sample type
Q	UAM 85225	Slope Mt.	68.73544	149.03968	tissue
	UAM 85226	Slope Mt.	68.73544	149.03968	tissue
	UAM 85760	Slope Mt.	68.73544	149.03968	tissue
R	UAM 87311	Little Squaw Lake	67.55756	148.11736	tissue
	UAM 87314	Little Squaw Lake	67.55756	148.11736	tissue
S	MSB 136465	Arctic Village	68.12694	145.54106	crusty
T	KU 50417	Lake Peters	69.3189	145.00804	skin
	KU 50418	Lake Peters	69.3189	145.00804	skin
	MSB 141153	Lake Peters	69.3189	145.00804	crusty
	MSB 85688	Lake Peters	69.3189	145.00804	crusty
	MSB 85707	Lake Peters	69.3189	145.00804	crusty
	UAM 85847	Lake Peters	69.3189	145.00804	tissue
	UAM 85848	Lake Peters	69.3189	145.00804	tissue

Table 2 Summary of molecular diversity statistics by population and region.

Population	*n*	# haplotypes	Mean # pairwise differences	Nucleotide diversity, π
A,B,C	5	2	0.400000	0.000351
E,D	4	1	0	0
F,G	7	1	0	0
J	6	2	1.666667	0.001462
K	2	1	0	0
L	6	3	3.133333	0.002749
M,N	3	2	2.666667	0.002339
P	4	1	0	0
Q	4	2	2.000000	0.001754
R	2	1	0	0
T	7	2	7.428571	0.006516
West (A-G)	16	2	0.125000	0.000110
South (H,J)	7	3	5.238095	0.004595
East (K-T)	30	8	5.997701	0.005261
Total sample	53	12	4.847605	0.004252

Table 3 Chi-square statistics and probability values (significant at $P<0.05$) for higher level clades.

Clade	Permutational X^2 statistic	Probability
I	17	0.0535
II	26	0.1266
III	27	0.0035
IV	6	0.3371
Total cladogram	96.89	0.0000

Table 4 Results of the nested geographic analysis. D_c and D_n for all haplotypes and clades are shown. Significantly small and significantly large values are indicated by *S and *L respectively (P<0.05).

Haplotypes			Higher level clades		
Clade	**D_c**	**D_n**	**Clade**	**D_c**	**D_n**
1	**116.03*S**	260.05			
2	11.77	**119.22*S**	I	**112.99*S**	231.66
3	**66.93*S**	**358.13*L**			
4	0	**440.76*L**			
5	0	137.30	II	**139.91*S**	338.91
6	0	242.91			
7	0	316.15			
8	0	**87.95*S**			
9	**0*S**	**84.26*S**			
10	0	84.26	III	**60.45*S**	**117.39*S**
11	**56.35*S**	**391.66*L**			
12	0	357.61	IV	275.51	**379.19*L**

General Conclusion

Alaska marmots were previously assumed to be restricted to the Brooks Range. The positive identification of the museum specimens from the Kokrines Hills and the Ray Mountains as *Marmota broweri*, and the discovery of a population of Alaska marmots currently inhabiting the Ray Mountains, extends the known range of this species 250 miles to the south. Based on museum specimens and all published observations of *M. broweri*, Alaska marmots are patchily distributed across the Brooks Range, from Cape Lisburne in the west to Lake Peters in the east, and in the Ray Mountains of interior Alaska. This species likely occurs east of Lake Peters, perhaps into the Yukon Territory, but we were unable to find them within the Kongakut River drainage. Further field surveys are necessary to establish the eastern distributional limits of *M. broweri*. The Seward Peninsula remains an area potentially supporting *Marmota broweri*. It appears that the Yukon River forms the boundary between the peripatric distributions of *M. broweri* and *M. caligata* in Alaska as *M. broweri* was found in the Ray Mountains (north of the Yukon River) and *M. caligata* was found at Elephant Mountain (south of the Yukon River).

The phylogeographic analyses of *Marmota broweri* show significant geographic structure across this species distribution. The pattern of geographic structure among *M. broweri* populations, evident from the measures of genetic diversity, mismatch distribution, phylogenetic analyses, and nested clade analysis, is consistent with a recent population expansion into the Brooks Range from central Alaska at the end of the Pleistocene.

Appendix

Table 1 A list of all known museum specimens of *Marmota broweri*.

Institution	Catalog number	Locality	Collection date
British Museum of Natural History		Anaktuvuk Pass	
University of Kansas Natural History Museum	KU 43227	Chandler Lake	1951
University of Kansas Natural History Museum	KU 50417	Lake Peters	1952
University of Kansas Natural History Museum	KU 50418	Lake Peters	1952
University of Kansas Natural History Museum	KU 50419	Lake Peters	1952
University of Kansas Natural History Museum	KU 50420	Lake Peters	1952
University of Kansas Natural History Museum	KU 50421	Lake Peters	1952
Museum of Comparative Zoology	MCZ 47133	Anaktuvuk Pass	
Museum of Southwestern Biology	MSB 137454	Chandler Lake	5 Jun 1964
Museum of Southwestern Biology	MSB 136435	Anaktuvuk Pass	5 Sep 1950
Museum of Southwestern Biology	MSB 136465	Arctic Village	20 Sep 1951
Museum of Southwestern Biology	MSB 137385	No specific locality recorded	
Museum of Southwestern Biology	MSB 137443	Captive, from Anaktuvuk Pass stock	16 Jun 1964
Museum of Southwestern Biology	MSB 137455	Captive, from Anaktuvuk Pass stock	
Museum of Southwestern Biology	MSB 137456	Captive, from Anaktuvuk Pass stock	
Museum of Southwestern Biology	MSB 137457	Captive, from Anaktuvuk Pass stock	
Museum of Southwestern Biology	MSB 137460	Captive, from Anaktuvuk Pass stock	
Museum of Southwestern Biology	MSB 137461	Captive, from Anaktuvuk Pass stock	
Museum of Southwestern Biology	MSB 137463	Captive, from Anaktuvuk Pass stock	
Museum of Southwestern Biology	MSB 137464	Captive, from Anaktuvuk Pass stock	
Museum of Southwestern Biology	MSB 137470	Captive, from Anaktuvuk Pass stock	
Museum of Southwestern Biology	MSB 137472	Captive, from Anaktuvuk Pass stock	
Museum of Southwestern Biology	MSB 137473	Captive, from Anaktuvuk Pass stock	
Museum of Southwestern Biology	MSB 137645	Chandler Lake	31 May 1966
Museum of Southwestern Biology	MSB 137646	Chandler Lake	31 May 1966
Museum of Southwestern Biology	MSB 137647	Chandler Lake	
Museum of Southwestern Biology	MSB 137649	Chandler Lake	
Museum of Southwestern Biology	MSB 137651	Chandler Lake	7 Jun 1966
Museum of Southwestern Biology	MSB 137732	No specific locality recorded	
Museum of Southwestern Biology	MSB 141142	Captive, from Anaktuvuk Pass stock	10 Mar 1969
Museum of Southwestern Biology	MSB 141144	Captive, from Anaktuvuk Pass stock	28 Mar 1971
Museum of Southwestern Biology	MSB 141145	Captive, from Anaktuvuk Pass stock	10 Oct 1969
Museum of Southwestern Biology	MSB 141146	Captive, from Anaktuvuk Pass stock	10 Oct 1969
Museum of Southwestern Biology	MSB 141147	Captive, from Anaktuvuk Pass stock	16 Mar 1972
Museum of Southwestern Biology	MSB 141148	Captive, from Anaktuvuk Pass stock	10 Oct 1969
Museum of Southwestern Biology	MSB 141150	Captive, from Anaktuvuk Pass stock	16 Mar 1972
Museum of Southwestern Biology	MSB 141151	Captive, from Anaktuvuk Pass stock	16 Mar 1972
Museum of Southwestern Biology	MSB 141152	Captive, from Anaktuvuk Pass stock	10 Oct 1969
Museum of Southwestern Biology	MSB 141153	Lake Peters	12 Jun 1963
Museum of Southwestern Biology	MSB 141155	Captive, from Anaktuvuk Pass stock	10 Oct 1969
Museum of Southwestern Biology	MSB 141156	Captive, from Anaktuvuk Pass stock	16 Mar 1972
Museum of Southwestern Biology	MSB 141158	Chandler Lake	31 May 1966
Museum of Southwestern Biology	MSB 141159	Ukuminilagat Creek	11 Jun 1964
Museum of Southwestern Biology	MSB 141160	Captive, from Anaktuvuk Pass stock	16 Mar 1972
Museum of Southwestern Biology	MSB 25899	Anaktuvuk Pass	22 Aug 1967
Museum of Southwestern Biology	MSB 85688	Lake Peters	14 Jun 1963
Museum of Southwestern Biology	MSB 85689	Chandler Lake	5 Jun 1964
Museum of Southwestern Biology	MSB 85707	Lake Peters	12 Jun 1963
Museum of Vertebrate Zoology	MVZ 39719	Cape Thompson	Aug 1927
Museum of Vertebrate Zoology	MVZ 51654	Point Lay	Sep 1931
Museum of Vertebrate Zoology	MVZ 51655	Point Lay	Sep 1931
Museum of Vertebrate Zoology	MVZ 51675	Point Lay	10 Dec 1931
Museum of Vertebrate Zoology	MVZ 123895	Cape Sabine	10 Jun 1958
Puget Sound Museum	PSM 27500	Arctic Village	1951
Puget Sound Museum	PSM 3201	Anaktuvuk Pass	1950
Puget Sound Museum	PSM 4161	Anaktuvuk Pass	1950

Table 1 continued.

Institution	Catalog number	Locality	Collection date
Puget Sound Museum	PSM 4162	Anaktuvuk Pass	1950
Puget Sound Museum	PSM 4163	Anaktuvuk Pass	1950
University of Alaska Museum	UAM 12612	Cape Lisburne	24 Jul 1957
University of Alaska Museum	UAM 12613	Cape Lisburne	25 Aug 1957
University of Alaska Museum	UAM 12614	Cape Lisburne	25 Aug 1957
University of Alaska Museum	UAM 12615	Cape Lisburne	25 Aug 1957
University of Alaska Museum	UAM 13425	Utukok River	11 Jun 1981
University of Alaska Museum	UAM 13725	No specific locality recorded	
University of Alaska Museum	UAM 15043	Ray Mountains	8 Aug 1979
University of Alaska Museum	UAM 15044	Kokrines Hills	18 Jun 1983
University of Alaska Museum	UAM 35015	Galbraith	15 Jun 1994
University of Alaska Museum	UAM 7014	Cape Thompson	29 Jul 1961
University of Alaska Museum	UAM 78513	Fortress Mountain	30 Jul 2002
University of Alaska Museum	UAM 79182	Fortress Mountain	31 Jul 2002
University of Alaska Museum	UAM 79245	Nanushuk River	4 Aug 2002
University of Alaska Museum	UAM 85224	Slope Mountain	18 Jun 2005
University of Alaska Museum	UAM 85225	Slope Mountain	18 Jun 2005
University of Alaska Museum	UAM 85226	Slope Mountain	18 Jun 2005
University of Alaska Museum	UAM 85227	Slope Mountain	2004
University of Alaska Museum	UAM 85514	Galbraith	24 Aug 2006
University of Alaska Museum	UAM 85760	Slope Mountain	27 Jun 2006
University of Alaska Museum	UAM 85847	Lake Peters	24 Jul 2006
University of Alaska Museum	UAM 85848	Lake Peters	28 Jul 2006
University of Alaska Museum	UAM 86397	Galbraith	24 Aug 2006
University of Alaska Museum	UAM 86399	Galbraith	24 Aug 2006
University of Alaska Museum	UAM 87300	Tupikchak Mountain	4 Jul 2007
University of Alaska Museum	UAM 87301	Tupikchak Mountain	4 Jul 2007
University of Alaska Museum	UAM 87302	Ray Mountains	10 Sep 2007
University of Alaska Museum	UAM 87303	Ray Mountains	11 Sep 2007
University of Alaska Museum	UAM 87304	Tupikchak Mountain	4 Jul 2007
University of Alaska Museum	UAM 87305	Ray Mountains	11 Sep 2007
University of Alaska Museum	UAM 87306	Tupikchak Mountain	3 Jul 2007
University of Alaska Museum	UAM 87307	Ray Mountains	11 Sep 2007
University of Alaska Museum	UAM 87308	Ray Mountains	10 Sep 2007
University of Alaska Museum	UAM 87309	Ray Mountains	11 Sep 2007
University of Alaska Museum	UAM 87310	Tupikchak Mountain	4 Jul 2007
University of Alaska Museum	UAM 87311	Little Squaw Lake	17 Jun 2007
University of Alaska Museum	UAM 87312	Tupikchak Mountain	4 Jul 2007
University of Alaska Museum	UAM 87313	Kukpowruk River	4 Jul 2007
University of Alaska Museum	UAM 87314	Little Squaw Lake	30 Jul 2007
University of Alaska Museum	UAM 87946	Toolik Field Station	5 Aug 2007
Smithsonian National Museum of Natural History	USNM 290273	Alaska	
Smithsonian National Museum of Natural History	USNM 290274	Alaska	
Smithsonian National Museum of Natural History	USNM 290275	Tolugak Lake	
Smithsonian National Museum of Natural History	USNM 290276	Tolugak Lake	
Smithsonian National Museum of Natural History	USNM 305036	Chandler Lake	25 Aug 1951
Smithsonian National Museum of Natural History	USNM 583154	Anaktuvuk Pass	
Smithsonian National Museum of Natural History	USNM 583155	Anaktuvuk Pass	
University of Washington Burke Museum	UWBM 32251	Lake Peters	13 Jun 1963
University of Washington Burke Museum	UWBM 39676	Anaktuvuk Pass	1 Sep 1951
University of Washington Burke Museum	UWBM 39793	Brooks Range	10 Oct 1969
University of Washington Burke Museum	UWBM 39810	Mount Wachsmuth	3 Jun 1966
Yale Peabody Museum	YPM 523	Brooks Range, AK	1955
Yale Peabody Museum	YPM 524	Brooks Range, AK	1955