Limited phylogeographic structure and genetic variation in Alaska’s arctic and alpine endemic, the Alaska marmot

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Alpine and arctic environments are thought to be more vulnerable to climate change than other lower-elevation and lower-latitude regions. Being both arctic and alpine distributed, the Alaska marmot (Marmota broweri) is uniquely suited to serve as a harbinger of the effects of climate change, yet it is the least-studied marmot species in North America. We investigated the phylogeography and genetic diversity of M. broweri throughout its known distribution in northern Alaska using the mitochondrial cytochrome b gene to better understand how post-Pleistocene changes and population fragmentation have structured genetic diversity. Our results show significant, although shallow, geographic structure among Alaska marmot populations. The diversity within and among populations is consistent with 2 phylogeographic hypotheses: Alaska marmots persisted in the eastern Brooks Range, Ray Mountains, and Kokrines Hills during the Pleistocene and have only recently expanded into the western Brooks Range; and the western Brooks Range served as a refugium as well and those populations have undergone a bottleneck resulting in reduced genetic variation in extant populations. Levels of mitochondrial deoxyribonucleic acid diversity are lower in M. broweri than in any other codistributed small mammal species and alpine mammal species with comparable data available. This is the 1st phylogeographic study of any marmot species and provides a baseline measure of the current structure and diversity within M. broweri.

Key words: Alaska marmot, alpine, arctic, Beringia, climate change, GEODIS, Marmota broweri, phylogeography

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There are 14 currently-recognized species of marmots (Rodentia: Sciuridae; Marmota) ranging across the Holarctic. With 1 exception (woodchuck, Marmota monax), marmots are largely restricted to alpine habitats, living on sky islands isolated by ecological barriers in lower-elevation ecosystems. Their restricted distributions and dependence on high-elevation habitats make alpine marmots particularly vulnerable to climate change and the subsequent contraction or expansion of their preferred habitat (Griffin et al. 2008; Inouye et al. 2000). For these reasons, marmots have been called harbingers of changes occurring in alpine regions around the world (Krajick 2004). In a review of ecological and evolutionary effects of recent climate change, Parmesan (2006:637) concluded that, ‘‘[r]ange-restricted species, particularly polar and mountaintop species, show severe range contractions and have been the first groups in which entire species have gone extinct due to recent climate change.’’ As shrublines and treelines in the Northern Hemisphere move rapidly northward and upslope (Overpeck et al. 1997; Sturm et al. 2001), marmots and other alpine-obligate species must shift their distributions accordingly or adapt to their new environments if they are to survive the changes in their habitat. A recent study of the effects of 100 years of climate change on small mammal species in Yosemite National Park demonstrated an average 500-m upward shift in the distributions of half of the species surveyed (Moritz et al. 2008). These authors also found that while low-elevation species have expanded their ranges upslope, the ranges of high-elevation species contracted. Like most other marmot species, Alaska marmots (M. broweri) occur at or near mountain peaks where talus and rock outcrops provide shelter, and nearby alpine meadows provide forage. However, the Alaska marmot occurs primarily in the Brooks Range of northern Alaska, the northernmost mountain range in North America (Gunderson et
Along with its congener, the black-capped marmot (M. camtschatica) of eastern Russia, the Alaska marmot is the most northerly distributed alpine mammal; its distribution cannot shift northward and it already occupies the highest elevations available (Gunderson et al. 2009). Furthermore, M. broweri may face competition from the northward expansion of hoary marmots (M. caligata), which have recently been found to occur in near parapatry with and directly south of the southernmost Alaska marmot populations (Gunderson et al. 2009). To understand how Alaska marmots, and other alpine-restricted species, will be affected by rapidly accelerating climate change, and to assess the conservation status of this vulnerable species, we need to understand the current genetic diversity and phylogeographic structure among extant populations. This study is the first of its kind for any species of marmot and is focused on the most remotely distributed and least-studied marmot in the world. It provides an initial characterization of population structure, geographic history, and genetic diversity of M. broweri—a mammal uniquely amenable to studying, and presumably uniquely vulnerable to the effects of climate change.

The Alaska marmot currently occurs in alpine areas of northern Alaska, primarily in the Brooks Range but also in central Alaska in the Ray Mountains and Kokrines Hills (Gunderson et al. 2009; Fig. 1). Both molecular and morphological analyses suggest that M. broweri is more closely related to Asian marmot species (subgenus Marmota) than to its nearest North American congener, the hoary marmot (M. caligata; Cardini et al. 2005; Steppan et al. 1999). Two hypotheses have been proposed for the origin of M. broweri in North America. Rausch and Rausch (1971) suggested that the Alaska marmot was left behind in Alaska as an ancestral marmot crossed the Bering Land Bridge and radiated across Asia and Europe. Hoffmann and Nadler (1968) and Hoffman et al. (1979) proposed that M. broweri originated in Asia and crossed back into North America during the Pleistocene. Steppan et al. (1999) were unable to reject either hypothesis using statistical methods available at the time but suggested that the 2nd was more likely. Both of these scenarios place M. broweri in the ice-free region of Beringia at the end of the Pleistocene.

Beringia was a huge land area that remained ice-free during the repeated glacial advances and retreats that characterized the Pleistocene (Hopkins 1967). It extended from eastern Siberia through central Alaska and into western Yukon Territory and served as a refugium, separated from North America and Asia by glaciers and ice sheets, and as a dispersal corridor allowing the dispersal of flora and fauna between the 2 continents. Many studies have focused on Beringia’s role as a refugium, shaping the present diversity and distribution of arctic species. Phylogeographic structure observed in many mammal species indicates that Beringia has served as a source for colonization of
recently deglaciated areas (Eddingsaas et al. 2004; Fedorov and Goropashnaya 1999; Galbreath and Cook 2004; Hundertmark et al. 2002; Waltari et al. 2007). We predict this common historical pattern of persistence in Beringia with subsequent expansion into previously glaciated areas to be found in *M. broweri* and for the genetic diversity within and among marmot populations to exhibit a pattern of divergence in isolation resulting from their fragmented and insular-like distribution.

**Materials and Methods**

*Sampling.*—We collected 24 Alaska marmot specimens from 8 localities from June through September 2005–2007. All fieldwork was carried out in accordance with guidelines approved by the American Society of Mammalogists (Sikes et al. 2011) and with the approval of the Institutional Animal Care and Use Committee of the University of Alaska Fairbanks. We obtained fresh tissue subsamples from the 6 existing museum specimens with such material available. An additional 27 dry tissue samples were obtained from museum skins or dried residual tissue left on cranial or skeletal material. These degraded samples included the 1st *M. broweri* specimens ever collected as well as the type specimen collected in 1931 (Hall and Gilmore 1934). Of the 27 degraded tissue sample extractions, 4 did not yield amplification products, leaving a total sample size of 53 individuals (Appendix I). This represents 47% of all *M. broweri* museum specimens, collected from across the distribution of Alaska marmots with 19 of 22 known localities represented, including 7 localities newly documented with voucher specimens in our previous work (Gunderson et al. 2009; Fig. 1). The 3 localities not included were considered redundant due to their proximity to other localities within the data set. We understand this sample may be of limited statistical power, but it is the best representation of *M. broweri* currently available. Given the significant financial and logistical challenges involved in collecting specimens or noninvasive material of Alaska marmots, this is likely to remain the case well into the future.

**Molecular methods.**—Deoxyribonucleic acid (DNA) was extracted from fresh or frozen tissue samples using the PureGene Genomic DNA Purification Kit (Gentra Systems, Minneapolis, Minnesota). The resulting template was diluted into a 1:10 working solution for use in polymerase chain reaction (PCR). From fresh tissue extractions we amplified and sequenced the entire length of the mitochondrial cytochrome *b* gene (1,140 base pairs) in 2 overlapping segments using the primer pairs F1/AGR1 and AGF1/R3AG (all primers were designed by the authors; Table 1).

Deoxyribonucleic acid extractions from samples of study skins and dried tissue were performed in the Ancient DNA Laboratory at the University of Alaska Museum (a PCR-free building), a facility designed specifically for procedures with high risks of contamination. Each sample of approximately 20 mg of tissue was digested in 600 μl of cell lysis solution (PureGene Genomic DNA Purification Kit, Gentra Systems, Minneapolis, Minnesota), 20 μl of proteinase K (20 mg/ml), and 30 μl dithiothreitol (100 mM) for 24–48 h, with agitation in a dry heat block at 55°C. For those samples that remained undigested after 24 h, 20 μl of additional proteinase K was added and the samples were allowed to digest for another 24 h. After digestion, the extractions proceeded according to the PureGene Genomic DNA Purification Kit protocol for DNA purification from fresh tissue. Each extraction included a negative control to test for contamination from the extraction procedure. All PCR and other downstream reactions were conducted in a lab in a separate building. Due to the degraded nature of the DNA extracted from the skin and dried tissue samples, we amplified and sequenced the entire length of cytochrome *b* in 7 overlapping segments using the following primer pairs: F1/R4AG, F4AG/R5AG, F5AG/R6AG, AGF1/R7AG, F6AG/R8AG, F7AG/R9AG, and F8AG/R3AG (Table 1). Volumes and concentrations of reagents used in these amplifications were as follows: 1 μl of undiluted DNA template, 1 μl each of primers (10 μM), 2.5 μl of 10× Promega reaction buffer, 1 μl of MgCl₂ (25 mM), 0.5 μl of deoxyribonucleotide triphosphates (10 mM), 0.25 μl of Promega GoTaq polymerase (5 U/μl), and 17.75 μl of H₂O for a total reaction volume of 25 μl. The reactions were conducted with the following cycling parameters: 94°C for 3 min, then 40 cycles of 94°C for 1 min, 55°C for 1 min, and 72°C for 1 min. 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 during the PCR protocol as well as a positive control to verify that the PCR reaction occurred as expected.

Before cycle sequencing, all PCR products were purified with Exo-SAP-IT (USB, Cleveland, Ohio) according to the manufacturer’s instructions. Purified PCR products were cycle sequenced using BigDye Terminator (Perkin-Elmer, Boston, Massachusetts) and the same primers used in PCR. Sequencing was performed on an ABI 3100 (Applied Biosystems, Foster City, California) sequencer. All gene segments were bidirectionally sequenced.

Data analysis.—DNA sequences were aligned and assembled with reference to a *M. broweri* cytochrome *b* sequence

**TABLE 1.**—Primer sequences used in PCR and sequencing reactions.

<table>
<thead>
<tr>
<th>Name</th>
<th>Sequence (5′–3′)</th>
</tr>
</thead>
<tbody>
<tr>
<td>F1</td>
<td>CTCACGGTTGTATTCACAATA</td>
</tr>
<tr>
<td>AGR1</td>
<td>GGGATTTTGTCGATGTCAGA</td>
</tr>
<tr>
<td>AGF1</td>
<td>CAAGGGCTACTTTACCAGAATC</td>
</tr>
<tr>
<td>R3AG</td>
<td>GGTTCAGAAGCAGGATATG</td>
</tr>
<tr>
<td>R4AG</td>
<td>TGGGGCAACTTGATGAA</td>
</tr>
<tr>
<td>F4AG</td>
<td>ATCCAAATCCTTTACCAGAATC</td>
</tr>
<tr>
<td>R5AG</td>
<td>TGACCTACGAGGAGAGCATA</td>
</tr>
<tr>
<td>F5AG</td>
<td>CTCAGGCTCATATATCCACTC</td>
</tr>
<tr>
<td>R6AG</td>
<td>TACCCTGGGATGATAA</td>
</tr>
<tr>
<td>R7AG</td>
<td>ATCCAGGATCCTCCAGAAGT</td>
</tr>
<tr>
<td>F6AG</td>
<td>AATCCCTTTCACCCGACT</td>
</tr>
<tr>
<td>R8AG</td>
<td>GAGAAGATTAGGCTAGGACT</td>
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<td>F7AG</td>
<td>TACCACCGCAAAACCTTAA</td>
</tr>
<tr>
<td>R9AG</td>
<td>AGATTGTCTTCCAGATCAGT</td>
</tr>
<tr>
<td>F8AG</td>
<td>TCCCACTTAAGCCAATAGT</td>
</tr>
</tbody>
</table>
obtained from GenBank (AF143918) and checked by eye with SEQUENCHER 4.7 (Gene Codes, Ann Arbor, Michigan). All new sequences have been deposited in GenBank (FJ438931-FJ438934, FJ438936, JN024574-JN024621).

Phylogenetic analyses under the 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 and selected on the basis of the Akaike information criterion (Posada and Buckley 2004; Posada and Crandall 1998). Bootstrap values of nodal support were generated for the ML tree from 1,000 replicates. Bayesian inference was implemented with MRBAYES 3.1.2 (Huelsenbeck and Ronquist 2001) using 2 runs of 4 chains (3 heated) for 10 million generations (sampling every 1,000 with a burn-in of 2,000) to produce posterior probabilities for the most probable tree topology. *Marmota caudata*, *M. menzibieri*, and *M. monax* sequences obtained from GenBank (AF143923-143925, AF143931, AF143932-143934) were used to root trees in all analyses.

Standard molecular diversity statistics were calculated using Arlequin 2.0 (Schneider et al. 2000) for combined regional samples from the western Brooks Range (sample sites A–G, referred to hereafter as West), eastern Brooks Range (sample sites K–T, referred to hereafter as East), and southern mountain ranges (Kokrines Hills and Ray Mountains, sample sites H and J, referred to hereafter as South). Smaller values of π (nucleotide diversity) can indicate that a population has recently expanded into that area, whereas larger values can indicate that a population has persisted for longer periods of time. We used Arlequin to conduct an analysis of molecular variance (AMOVA), run the Ewens–Watterson test for selective neutrality (Watterson 1978), calculate Tajima’s *D* (Tajima 1989) and Fu’s *F*<sub>S</sub> (Fu 1997), and plot mismatch distributions to test for population expansion in each of the 3 regions (East, West, and South) of the Alaska marmot’s known distribution as well as in the entire sample (Rogers and Harpending 1992). Arlequin uses coalescent simulations under the infinite-sites model to test the significance of Tajima’s *D* and Fu’s *F*<sub>S</sub>. DnaSP (Librado and Rozas 2009) was used to estimate the *R*<sub>2</sub> neutrality test (Ramos-Onsins and Rozas 2002) and to test the significance of *R*<sub>2</sub> using coalescent simulations under the infinite-sites model. In the absence of selection, negative values of Tajima’s *D* and unimodal mismatch distributions are indicative of population expansion, whereas positive values of Tajima’s *D* are suggestive of population contraction. Significantly low values of Fu’s *F*<sub>S</sub> and *R*<sub>2</sub> would reject the null hypothesis of population stability in support of population expansion. We used Harpending’s raggedness index (rg; Harpending 1994) to test for a departure from the sudden expansion model for the mismatch distributions. Lower values of rg are expected under a population growth model. We defined regions as populations and compared within-population molecular variance among the 3 regions and in a grouping of South and East populations separate from the West.

The phylogeographic structure of *M. broweri* was further explored with a haplotype network constructed using TCS 1.21 (Clement et al. 2000) and through a modified nested-clade phylogeographic analysis using the program GEODIS 2.0 (Posada et al. 2000). In a standard nested clad analysis the haplotype network is nested according to the published nesting rules of Templeton et al. (1987) and Templeton and Sing (1993) into a clad hierarchy of 1-step clades, 2-step clades, etc., until the entire network is contained in a single clad. Then the geographic association of clades is tested through the calculation of clad distances (*D*<sub>c</sub>) and nested clad distances (*D*<sub>n</sub>) and inferences about the biological meaning of those statistics are made using an inference key provided with the program. Our use of GEODIS is limited to the calculation of those statistics and tests of their statistical significance; we do not make use of the inference key to draw biological conclusions from these statistics.

Clade distance, *D*<sub>c</sub>, is the mean geographic distance of all individuals in a clad, in kilometers, from that clad’s geographic center (Templeton et al. 1995). When considering a single haplotype as a clad, *D*<sub>c</sub> is the mean distance of each individual with that haplotype from the geographic center of that haplotype. A statistically significant value of *D*<sub>c</sub> indicates that the geographic spread of individuals within a clad, or with a given haplotype, is smaller (significantly small *D*<sub>c</sub>) or larger (significantly large *D*<sub>c</sub>) than would be expected by chance. Nested clad distance, *D*<sub>n</sub>, is the mean geographic distance of all individuals within a clad from the center of the next higher-level nested clad (Templeton et al. 1995). This is where our analysis differs from a traditional nested clad analysis. For our modified nested clad analysis, the haplotype network was not nested according to the published nesting rules. We calculated clad distances (*D*<sub>c</sub>) as described by Templeton et al. (1995), but all nested clad distances (*D*<sub>n</sub>) were calculated using the geographic center of the total cladogram as the next higher-level nesting clad. This design allowed each clad of interest to be tested for geographic association in relation to the entire cladogram, not just in relation to the next higher-level nesting clad. In this manner the geographic distribution of each clad is tested for statistically significant geographic structure in reference to the entire geographic distribution of *M. broweri*. Statistically significant values of *D*<sub>n</sub> indicate that individuals within a clad are nearer to (significantly small *D*<sub>n</sub>) or farther from (significantly large *D*<sub>n</sub>) the geographic center of *M. broweri* than would be expected by chance. We used this method to provide statistical significance to the phylogeographic associations observed in the phylogenetic tree and haplotype network. Because we modified the nested design, we made no use of the inference key provided with GEODIS (Posada et al. 2000; Templeton et al. 1995). The null hypothesis of no geographic structure was tested by comparing observed clad distances with expected distances obtained from 10,000
random chi-squared permutations. To eliminate any bias resulting from the sampling of family groups, we removed all but 1 of the individuals that were collected from the same burrow. Of the samples from museum specimens we did not collect ourselves, we 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 this analysis.

**RESULTS**

Among the 53 individual specimens from 19 localities we recovered 12 unique haplotypes. There were 24 polymorphic sites within the total 1,140 base pairs of the cytochrome \( b \) gene, consisting of 22 inferred transitions and 2 transversions. The mean number of pairwise differences for the entire sample was 4.64 and the average uncorrected pairwise distance (\( p \)-distance) between individuals was 0.42%, with a range of 0.0–1.4%. The Ewens–Watterson test for selective neutrality was nonsignificant (\( P = 0.785 \)). Molecular diversity statistics for each region and the total sample are summarized in Table 2.

The optimal ML tree with branch lengths and nodal support values is shown in Fig. 2. Both MP and Bayesian inference produced the same optimal tree topology as the ML analysis. Four main haplotype clades were recovered, although only clade IV was well supported by both ML bootstrap values and Bayesian posterior probabilities. Clade IV contained individuals from 3 localities in the eastern and southern extremes of the Alaska marmot’s distribution. Individuals from the South were also found in clades II and III, suggesting higher levels of diversity in the South. The 2 most common haplotypes were geographically segregated into West and East/South regions. A single individual from the East (Toługak Lake) had a unique haplotype that grouped among the samples from the West.

Nucleotide diversity estimates (\( \pi \)) for each region (Table 2) also indicate more diversity in populations from the East and from the South than in populations from the West. A mismatch distribution plot could not reject the null hypothesis of recent population expansion in any of the 3 regional samples or the total sample. Tajima’s \( D \) values are negative for the regional samples from the West and South and for the whole data set, but slightly positive for the East samples (Table 2). These results suggest a recent population expansion in the western Brooks Range and in the southern mountain ranges and perhaps a population contraction in the eastern Brooks Range, although none of the values is statistically significant. Fu’s \( F_S \) and \( R_2 \) tests failed to reject the null hypothesis of population stability, suggesting that a refugium for Alaska marmots may have existed in the western Brooks Range as well.

Results of our AMOVA show that 71% of variation is found within regions (East, West, and South) and that the East + South versus West division explained 31% of variation. The South versus East split accounts for −1.85% of variation (negative due to sharedhaplotypes between the 2 regions). The haplotype network estimation yielded a single most parsimonious network (Fig. 3) with a maximum of 16 mutational steps inferred 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 East (8 haplotypes from 10 localities) and in the South (3 haplotypes from 2 localities) than was found in samples from the West (2 haplotypes from 7 localities). Our modified nested clad analysis revealed significant geographic association of haplotypes and higher-level clades. The null hypothesis of no geographic association was rejected for clade III (Table 3) and the total cladogram (\( P < 0.001 \)). The geographic distance statistics further support a pattern of population structure within *M. broweri*—clade distance (\( D_n \) and nested clade distance (\( D_D \)) values were significant for haplotypes 1–4, 8, 9, and 11 and for clades I–IV (Table 3).

**DISCUSSION**

The results from our modified nested clad analysis provide a statistically significant rejection of the null hypothesis of no phylogeographic structure within *M. broweri*. Alaska marmot populations have diverged in isolation, presumably due to their restriction to sky island habitats, limited dispersal abilities, and the glacial history of central and northern Alaska. Overall levels of genetic diversity within *M. broweri* are low compared with other small mammals distributed within Alaska (Brunhoff et al. 2003; Lanier 2010; Weksler et al. 2010) and marmot populations of the western Brooks Range show less diversity than those of the eastern Brooks Range and southern ranges of the Ray Mountains and Kokrines Hills.

The phylogenetic tree we recovered further supports population structure across the range of *M. broweri*. Although our sample included only 7 individuals from the southernmost populations (Kokrines Hills and Ray Mountains), within those samples we found 3 different haplotypes recovered in 3 of the 4 major clades (Fig. 2). Measures of molecular diversity and
the AMOVA results also indicate higher levels of genetic variation in these southern and eastern Brooks Range populations than in populations from the western Brooks Range. The higher levels of diversity found in the southern and eastern regions of the Alaska marmot’s distribution could be the result of marmots having persisted there longer than in the genetically less diverse western Brooks Range. Both the Kokrines Hills and the Ray Mountains were nearly ice-free during the glacial cycles of the Pleistocene and would have been available to Alaska marmots (Brigham-Grette 2001; Clark and Mix 2002; Kaufman and Manley 2004). During that time large portions of the Brooks Range were periodically covered by glaciers (Kaufman and Manley 2004), which would have limited the distribution and dispersal of marmots. Areas of the eastern Brooks Range may have remained unglaciated or contained nunataks (ice-free areas within a glacier) of sufficient size to allow marmots to persist there (Kaufman and Manley 2004). These results are consistent with a recent range expansion into the western Brooks Range from the east and south as habitat and dispersal corridors became available after the Last Glacial Maximum.

The lack of genetic diversity in marmots of the western Brooks Range could also be the result of a population bottleneck within a refugium in that region. The statistical tests for a signature of a recent population expansion produced conflicting results. Although the Harpending’s raggedness index failed to reject the null hypothesis of population expansion for the mismatch distributions of the western Brooks Range, Fu’s $F_S$ and $R_2$ did not reject a hypothesis of population stability. A negative value of Tajima’s $D$ in the western populations is suggestive of recent expansion; however, that value was not statistically significant. The western Brooks Range is described as having been nearly

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**Fig. 2.**—Maximum likelihood phylogram and clade distribution. Terminal labels correspond to the collecting locality of individuals. Numbers in parentheses indicate the number of samples with a haplotype. Bootstrap support values greater than 50 are shown above clade branches. Posterior probabilities greater than 0.50 are shown below clade branches. Clade numbers correspond to Table 4 and Fig. 3.
ice-free, except for high mountain valleys, during the Late Wisconsinan glaciation (Kaufman and Manley 2004). With suitable habitat available, the persistence of Alaska marmots in the western Brooks Range through the late Pleistocene is plausible. Under this scenario, the lack of diversity in the western populations could be the result of a recent population bottleneck.

Neither hypothesis—a population expansion into the western Brooks Range or a refugium in the west followed by a bottleneck—can be rejected by our results from the current data set. Further sampling of the western Brooks Range and the addition of nuclear loci could clarify the geographic history of M. broweri.

No other mammal species shares the unique restricted distribution of the Alaska marmot in northern Alaska. Arctic ground squirrels (Spermophilus parryii) are ecologically similar but have a much more expansive distribution than Alaska marmots. The ranges of the 2 species 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, presumably isolated from southern populations by the invasion of boreal forests as glaciers retreated, and concluded that the Brooks Range populations could be the result of a recent population expansion due to an increase in suitable habitat. A more exhaustive study of S. parryii supports a distinct arctic lineage, and suggests it is a result of isolation north of Brooks Range during glacial maxima (Galbreath et al. 2011). As Alaska marmots and Arctic ground squirrels exhibit similar ecological requirements, a shared pattern of persistence north of the Brooks Range or expansion into the Brooks Range after deglaciation may be likely. Alternatively, Eddingsaas et al. (2004) hypothesized that arctic ground squirrels may have persisted in a northern Canadian refugium and expanded westward into the Brooks Range following the expansion of suitable habitat. This Canadian arctic refugium has been proposed for the collared lemming and rock ptarmigan as well (Fedorov and Stenseth 2002; Holder 1999). The possible expansion of Alaska marmots across the Brooks Range could be the result of dispersal from northwestern Canada. However, Alaska marmots are not known to occur in Canada at present and arctic ground squirrels are absent from the northern Canadian archipelago. A refugium in that area is unlikely for either species. Eddingsaas et al. (2004) included only 7 S. parryii specimens from 3 localities within the distribution of M. broweri. An increase in sampling effort for each of these species would better elucidate their respective, and possibly shared, geographic histories.

The measures of nucleotide diversity found in M. broweri are lower than those in other Beringian small mammals for which data are available, including singing voles (Microtus miurus), tundra voles (M. oeconomus), and collared pikas (Ochotona collaris; Brunhoff et al. 2003; Lanier 2010; Weksla et al. 2010). A recent phylogeographic study of the collared pika, another alpine specialist and Beringian denizen, found that O. collaris populations exhibit low levels of genetic variation and a shallow branching pattern similar to that in M. broweri, and that among pika species, those occurring at higher latitudes show less genetic variation (Lanier 2010). Without any comparable published studies on other marmot species, we cannot test whether a pattern of lower diversity at higher latitudes might exist among marmots. However, a microsatellite study of the lower-latitude alpine marmot (M. marmota) describes that species as exhibiting levels of genetic variation comparable with numerous other mammal species (H_0 = 0.63, Goossens et al. 2001) and a similar study showed that yellow-bellied marmots (M. flaviventris) of the Great Basin region exhibit even higher microsatellite variation (H_0 = 0.73, Floyd et al. 2005).

American pikas (O. princeps) are known to exhibit lower levels of diversity at the northern margins of their distribution in the Rocky Mountains, due to recent colonization of...
previously glaciated areas, while maintaining higher levels of
diversity at lower latitudes in the Great Basin region, where
suitable habitat persisted below (in both latitude and elevation)
the advancing ice (Galbreath et al. 2009). Within Beringia,
Alaska marmots had no vast southern refugium to retreat to
during glacial maxima (Kaufman and Manley 2004). They
would have been limited to the available habitat at lower
elevations and within the ice-free alpine areas of central
Alaska and perhaps parts of the Brooks Range. A pattern of
repeated extirpation, retreat to relatively few suitable alpine
refugia, and subsequent recolonization during interglacials
would serve to reduce overall genetic diversity and limit
detectable population structure in M. broweri to only the most
recent subdivisions (Hewitt 2004).

Current climate warming is affecting the distributions of
species, with a general trend of northward (in the Northern
Hemisphere) and upslope range shifts occurring within the last
100 years (Moritz et al. 2008; Parmesan and Yohe 2003). Alplane and arctic regions are more dramatically affected by
celimate change than other regions and the species adapted to
those ecosystems are considered more vulnerable to popula-
dtion declines or extinction (Hansen et al. 2006; Krajick 2001,
2004; Parmesan 2006; Walther et al. 2002). Recent declines or
extirpations of populations have been documented in pika
and marmot species (Beever et al. 2003; Griffin et al. 2008;
Morrison and Hik 2007; Wei-Dong and Smith 2005),
including a decline in Alaska marmot abundance and eleva-
tional range at Lake Peters in the eastern Brooks Range,
50 years after an initial survey (Gunderson et al. 2009). The
habitat of the Alaska marmot, specifically in the Brooks
Range, is shrinking due to an increased abundance and upslope migration of shrubs and trees (Hinzman et al. 2005;
Sereze et al. 2000; Sturm et al. 2001; Tape 2010), which will
likely further restrict gene flow among isolated marmot
populations and increase their vulnerability to extirpation. As
inhabitants of the highest elevations in the northernmost
mountains in North America, Alaska marmots will have to
adapt to their changing environment if they are to survive.
A recent increase in the population size of yellow-bellied
marmots (M. flaviventris) from one locality in Colorado, linked
to earlier emergence from hibernation and a longer growing
season, illustrates the complexity of variables affected by recent
climate change and some possible phenotypic and phenological
consequences marmots may experience (Ozgul et al. 2010). The
data to make any determination about status of Alaska marmot
populations or how they will respond to their changing
environment do not yet exist. Studies such as this one, and
our previous work on M. broweri (Gunderson et al. 2009),
provide a baseline measure of current distribution and genetic
diversity from which species can be monitored, specifically for
changes resulting from the rapidly changing climate.

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APPENDIX I

Museum specimens included in this study. Site letters correspond to localities in Fig. 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 = National Museum of Natural History, Smithsonian. Frozen tissue = fresh frozen tissue, skin = dried study skin, dried tissue = dried residual tissue left on the skeleton.

<table>
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<tr>
<th>Site</th>
<th>Catalogue number</th>
<th>Locality</th>
<th>Latitude (°N)</th>
<th>Longitude (°W)</th>
<th>Sample type</th>
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<td>C</td>
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<td>Cape Sabine</td>
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<tr>
<td>D</td>
<td>MVZ 51654-5, 51675 (holotype)</td>
<td>Point Lay</td>
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<td>163.0511</td>
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<tr>
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<td>J</td>
<td>UAM 87303, -5, -7-9, 100000</td>
<td>Ray Mountains</td>
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