Fire and ice: genetic structure of the Uinta ground squirrel (Spermophilus armatus) across the Yellowstone hotspot

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Abstract

The range of the Uinta ground squirrel, Spermophilus armatus, is centred over one of the most tectonically active regions today, the Yellowstone hotspot. We document the role of Quaternary tectonic and climatic history on the genetic structure of this species by screening museum and extant individuals throughout its range. Phylogeographic, divergence time, and demographic analyses of partial mitochondrial cytochrome b and control region DNA sequences yield insight into the cadence of evolution across three spatiotemporal scales: (i) a relatively deep intraspecific divergence of S. armatus into three lineages coincident with the last major volcanic eruption in the region and maintained by the Snake River Plain; (ii) demographic expansion in two lineages corresponding to the time of last deglaciation of the region; and (iii) a recent (< 50 years) local extinction of the third lineage coincident with climatic change and conversion of habitat for agricultural purposes in eastern Idaho. Beyond these inferences, our study highlights the unique value of museum material to phylogeography, and shows that small mammal recolonization of previously glaciated montane ‘islands’ differs from northward postglacial expansion observed in areas previously covered by continental ice sheets. Montane ‘islands’ may harbour high genetic diversity because of admixture and recurrent expansion/extinction.

Keywords: glaciation, ground squirrels, Lava Creek Caldera, phylogeography, postglacial recolonization, Snake River Plain, Yellowstone hotspot

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Introduction

A frequent observation in phylogeographic studies is that the modern distribution of genetic diversity remains associated with the geographic landscape in which species evolved, thus giving credence to vicariance as an important mechanism of species and population subdivision (Avise et al. 1987; Riddle 1996). Palaeoclimatic, orogenic or tectonic change is often correlated with species or subspecies divergence through the inference of fossil-calibrated molecular clocks (van Tuinen et al. 2004). A prime example of palaeoclimatic change stimulating isolation and divergence of populations involves the waxing and waning of continental ice sheets throughout the Pleistocene (Avise et al. 1987; Brunsfield et al. 2001; Lessa et al. 2003; Hewitt 2004).

Small boreal mammals in particular have provided a good test of the importance of glacial/interglacial cycling to shallow genetic history with recent investigations indicating a central role of dispersal in montane mammal phylogeography (Brant & Orti 2003; Dembski & Sullivan 2003; Eddingsaas et al. 2004; Hewitt 2004; Runck & Cook 2005; Waltari & Cook 2005). In high-latitude species, postglacial recovery generally has been rapid after population expansion from individuals surviving in southern refugia (Hewitt 2004). Because mutational buildup is too slow to fix novel genetic diversity subsequent to the Pleistocene, standing genetic diversity in previously glaciated areas is often low.

In contrast, genetic diversity may be much higher in areas previously covered with isolated ice sheets not connected to the continental ice sheets, such as montane

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glaciers or ‘islands’, but this concept has little empirical support (Knowles 2000). Understanding the process of recolonization of these isolated glaciated areas is of interest to us for several reasons. First, these areas may be repositories of genetic diversity because of the shorter times between glacial cycles and more frequent, multidirectional recolonization events (Hadly et al. 2004). Second, in the face of global warming, they are thought to be vulnerable to population extinctions as cool climate species are forced off these montane islands and are replaced by lower-altitude species (Knowles 2000; Masta 2000; DeChaîne & Martin 2005). Montane glaciers are not uncommon, particularly in western North America, where many are found throughout the Rocky Mountains as far south as Mexico (Halfter 1987).

Members of the squirrel family Sciuridae are an informative mammalian system for ascertaining the role that climate plays in diversification among species (Lamb et al. 1997; Mercer & Roth 2003). For several reasons, ground squirrels of the genus Spermophilus provide for valuable phylogeographic study of mammals. Several species occur today in intermontane regions that have been profoundly influenced by extreme, nonseasonal environmental perturbations such as repeated montane glaciation cycles and volcanism during the Quaternary. In addition, previous work on the phylogenetic relations among North American Spermophilus found that closely related species are geographically proximate, suggesting that most species evolved in or near their current ranges (Harrison et al. 2003). Thus, geographic barriers that have contributed to allopatric speciation in the genus are likely to be found within the present distribution of the group. In addition, although they have restricted ranges relative to other small herbivores, spermophilines are among the most locally abundant mammals in the north-central Rocky Mountains (Yensen & Sherman 2003). To date, phylogeographic investigation among ground squirrels has been limited to two North American species, the arctic (Spermophilus parryi) and antelope ground squirrels (Ammospermophilus leucurus). These studies describe two opposing genetic scenarios: (i) a northwest postglacial expansion of antelope ground squirrels from southern relict but more genetically diverse populations (Whorley et al. 2004), and (ii) maintenance of high genetic diversity through glacial vicariance combined with a Beringian refugium in the arctic ground squirrels (Eddingsaas et al. 2004). However, neither study involved species recolonization of isolated glaciers.

Among the North American Spermophilus species, the Uinta ground squirrel (Spermophilus armatus) is a montane species with a relatively small species range (Fig. 1B) centered over one of the most tectonically active regions in the world today, the Yellowstone hotspot (Pierce & Morgan 1992). The species thus provides an important test for the relative influence of dispersal among montane basins vs. the vicariance caused by separation between basins during glaciation and/or volcanism. The Yellowstone hotspot is so named because it currently resides in Yellowstone National Park and is causing the topographic uplift of the Beartooth Plateau. The uplift increased the altitude of this region enough that it is thought to have contributed to the formation of montane ice caps, as much as a mile thick (Smith & Siegel 2000), that formed during the last glaciation and covered the region as recently as 12 000 yr B.P. (Pierce 1979). Thus, the animals present in Yellowstone National Park today have only recently recolonized the region since the last glaciation (Pinedale glaciation 40 000–12 000 yr B.P.).

The Yellowstone hotspot has had a long history of influence on the region in which S. armatus evolved. Over the last 17 million years, the continent has migrated over the hotspot in a southwestern course resulting in a swath of extreme tectonic instability from the southeast of Oregon, through Idaho and into the Greater Yellowstone ecosystem (GYE). As the hotspot ‘migrated’, it caused topographic uplift. Repeated caldera eruptions, layers of heavy basalt lava flows, and the gradual cooling and shrinking of the earth’s crust that took place after the hotspot moved on resulted in the subsequent topographic collapse that formed the massive snake river plain (SRP) (Smith & Siegel 2000). The SRP, a 500-mile long, 50-mile wide swath of basalt plain (Pierce & Morgan 1992) (see Fig. 1B), has been shown to be a geographic barrier for some fish species (Johnson 2002) and has been hypothesized to restrict movement of S. armatus (Davis 1939) and other squirrels in the area (Zegers 1984; Demboski & Sullivan 2003; Yensen & Sherman 2003).

Here, we investigate the recolonization of the previously glaciated parts of the GYE and the influence of tectonic activity in shaping contemporary patterns of genetic diversity of S. armatus. We hypothesize that genetic diversity in the montane island situated on the Yellowstone Plateau will be high relative to what would be expected from a unidirectional post-Pleistocene expansion from other portions of the species range and that the SRP has served as a barrier to gene flow. To study these questions, we required a comprehensive sampling of the entire species range. Comprehensive sampling of modern populations across the entire range is challenging because most populations are found in montane regions and have extremely short active seasons (3–4 months). Thus, we have utilized a combination of mostly historic and limited modern specimens from numerous mammal collections. Here, we present results from a phylogeographic study of S. armatus through genetic analysis of cytochrome b (cyt b) and control region (D-loop) sequences obtained from museum, tissue and raptor pellet samples that represent the entire species’ distribution. We report the presence of three intraspecific genetic lineages structured by the dynamic tectonic and climatic history of this region, and the historic loss of one
of these lineages. Divergence times estimated for the faster marker (D-loop) yield dates consistent with the timing of tectonic and climatic events across the Yellowstone region. These results reveal the value of museum specimens for phylogeographic study over historic time and provide unique insight into the direct influence of Quaternary environmental change linked to the evolution of mammals of the intermontane American west.

Materials and Methods

Taxon sampling

Individuals were sampled from throughout the current species range from a variety of sources: tissues from field-trapped individuals (n = 7); dental material found in raptor pellets from Yellowstone National Park (n = 5), and museum skins from several North American museums (n = 78). Sequences obtained from the sister species, *Spermophilus beldingi* (Harrison et al. 2003), serve as an outgroup (n = 2). Specimen number and sampling localities are found in Table S1, Supplementary material. Our total sampling equals 92 individuals from 81 localities, including nine localities originally used in determination of the species’ marginal records and three museum specimens collected in 1936, 1940, and 1987 from outside those established margins (Hall & Kelson 1959). Two of the 92 specimens were identified as *S. armatus* and therefore not used in our analyses. Our total geographic coverage spans 39 counties, and is distributed across the major mountain ranges (Uinta, Wasatch, Wyoming, Wind River, Teton, Absaroka, Lost River), plateaus (Beartooth, Yellowstone, Wasatch), and other suitable habitat within the current distribution of *Spermophilus armatus*. It also
DNA extraction and amplification in separate buildings by different personnel, (iii) sequencing of both forward and reverse directions for multiple overlapping fragments, (iv) repeated extraction and amplification for historic individuals showing unique haplotypes, (v) use of two linked markers for a representative taxon subset to confirm topological consistency, and (vi) cloning (TOPO TA) from PCR products of two representatives from each of the two most divergent lineages.

Table 1 Primer pairs for cytochrome b and D-loop fragments. Fragments for each gene are overlapping

<table>
<thead>
<tr>
<th>Primer name</th>
<th>Primer sequence (5′−3′)</th>
<th>Gene</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sarm1</td>
<td>AACCCCGCTTAAGGACCCCACTC</td>
<td>Cytochrome b</td>
</tr>
<tr>
<td>Sarm2</td>
<td>TAAAGATCTATATATGCTTAC</td>
<td>Cytochrome b</td>
</tr>
<tr>
<td>Sarm3</td>
<td>CCTCTACATCAAAGAAGAAAAA</td>
<td>Cytochrome b</td>
</tr>
<tr>
<td>Sarm4</td>
<td>TTTTGGATTAGGCTGAGGCTG</td>
<td>Cytochrome b</td>
</tr>
<tr>
<td>Sarm10</td>
<td>ACTATCAAAGATATCTCTTTG</td>
<td>D-loop</td>
</tr>
<tr>
<td>Sarm11</td>
<td>CACCCTCCCGATTTATGAGG</td>
<td>D-loop</td>
</tr>
<tr>
<td>SarmD10</td>
<td>ACTCCTATGTTAAATCTGATTT</td>
<td>D-loop</td>
</tr>
<tr>
<td>SarmD11</td>
<td>TCCAAGATCTATGTTACGCTG</td>
<td>D-loop</td>
</tr>
<tr>
<td>SarmD12</td>
<td>CTTGCTATATTACTACCTGTAC</td>
<td>D-loop</td>
</tr>
<tr>
<td>SarmD13</td>
<td>GAGACCAAATTGCTAGGGATGTC</td>
<td>D-loop</td>
</tr>
</tbody>
</table>

Phylogenetic analyses

Phylogenetic analyses were run in PAUP 4.0 beta (Swofford 2003) using the NJ and ML algorithm and with model parameters established from the Akaike information criterion in MODESTTEST version 3 (Posada & Crandall 1998). We performed an analysis using unweighted MP with indels specified as a fifth state. To establish the phylo-geographic information content and consistency of the observed indels, we compared the resulting MP tree to the unweighted MP, ML/NJ trees in which indels were excluded from analyses. Nodal support was determined by NJ bootstrapping (BS) and ML quartet puzzling with 1000 iterations. Because multiple MP trees were found for every data set, we determined nodal consistency in the MP analysis by estimating the majority rule consensus values with a 50% cutoff and setting the Maxtrees option to 500. Consistency between different methods (NJ, ML and MP) was determined through comparison of nodal support values in the presented mtDNA gene trees (Figs 2–5).

Genetic structure

We used tcs (Clement 2000), which does not assume a bifurcating pattern of genetic divergence, to identify unique haplotypes and to generate an unrooted minimum-spanning network with a 95% plausibility of each linkage between haplotypes. We performed a series of analyses of molecular variance (AMOVA) in ARLEQUIN 3.1 (Excoffier &
Fig. 2 mtDNA gene tree of modern and historic individuals of *Spermophilus armatus* based on cytochrome *b* (*n* = 34, bp = 381). Depicted is the maximum-likelihood tree using the HKY model (*T* ratio = 22.6) as specified by *modeltest*. Numbers shown above nodes are bootstrap values using neighbour-joining and 1000 iterations (left), and bootstrap values using maximum likelihood in combination with quartet-puzzling and 500 iterations (right). Numbers below nodes identify the frequency of branching support from equally likely maximum-parsimony trees.
Schneider 2005) to determine how much of the observed genetic structure could be explained by distinct geographic divisions. Standard estimates of genetic distance were calculated in *arlequin* 3.1 using the best model of evolution for our data set as specified by *modeltest*.

**Demographic history**

We tested for past changes in population size using several methods. We used Fu’s neutrality test (Fu 1997) in *arlequin* 3.1, which is a particularly powerful test for detecting sudden and recent expansions in populations with an excess of rare alleles. We also examined the distribution of pairwise differences (mismatch distributions) for each group to look for evidence of past expansion (Rogers & Harpending 1992). In general, populations undergoing recent and sudden expansion exhibit a Poisson-shaped mismatch distribution while populations in equilibrium tend to have ragged distributions (Slatkin & Hudson 1991).
Divergence times

Approximate sublineage ages were estimated from the faster marker (D-loop) because of its increased resolution for the shallow history of S. armatus and our interest in dating population expansions and recent admixture. The fossil record of S. armatus in the Pleistocene is too discontinuous to be of use for internal calibration (Eshelman & Sonnemann 2000), which prevented direct calibration of the D-loop molecular rate. We therefore estimated the observed rate of the D-loop data set relative to the cyt b rate of molecular evolution and converted this to an absolute rate based on a published cyt b rate for Spermophilus (1.52% per million years, Eddingsaas et al. 2004). This rate was originally calibrated from fossil and geologic evidence suggesting a divergence time of 5.16 million years ago (Ma) between S. beecheyi and S. parryi. Likelihood models were run with and without a molecular clock constraint using the likelihood ratio test under a chi-square probability distribution to assess whether the data were significantly clock-like. We used MEGA 3.0 to estimate sublineage divergence times from ‘net’ distances after correction for within-lineage polymorphism. We approximated the modeltest-preferred model of TrN + G + I using a TrN + G model with application of a stringent correction for rate heterogeneity across sites (G = 0.19) estimated from the Akaike information criterion-averaged alpha (G), [not alpha (IG)] output.

Results

Overall amplification success and resulting phylogeographic structure

DNA was readily amplified from skins when hair is removed and amplification is limited to small length (100–150 bp) fragments. Our protocols resulted in a 92% amplification rate based on 85 skins attempted, five primer pairs (Table 1), and two mitochondrial markers spanning ~650 bp. Genetic analyses reveal that the genetic diversity throughout the entire modern range of Spermophilus armatus is relatively low and can be traced to three lineages. The most widespread and abundant lineage is present throughout the south and southwest of the modern distribution (southern lineage, ‘SL’) and is found exclusively south or east of the SRP (Fig. 1B, yellow and gold: the SRP on this map runs in a north–northeast direction along the Yellowstone hotspot). A second lineage is predominantly found north of the SRP in the northeast of the current distribution (northeast lineage, ‘NEL’) (Fig. 1B, blue). A third lineage is very rare (represented by only three individuals out of the 88 S. armatus that we sampled) and only found historically north of the SRP in the northwest of the species range (northwest lineage ‘NWL’) (Fig. 1B, purple).

Phylogenetic analyses

Cyt b. Our observed substitution pattern for cytochrome b (cyt b) is consistent with the average mitochondrial pattern among mammals (Irwin et al. 1989), with abundance of substitutions at third codon positions, low
Fig. 5 mtDNA gene tree of D-loop sequences from modern and historic individuals of *Spermophilus armatus* sampled throughout the species range (n = 88, bp = 263). Depicted is the maximum-likelihood tree using a TN + G (alpha = 0.19) model specified by modeltest. Numbers shown above nodes are: bootstrap values using neighbour-joining and 1000 iterations (left), and bootstrap values using maximum likelihood in combination with quartet-puzzling and 500 iterations (right). Numbers below nodes identify the frequency of branching support from equally likely maximum-parsimony trees. Support < 50% is not shown. Dotted line depicts a genetically distinct lineage only found in historic individuals.
GC content across all sites and especially at third codon positions. All observed substitutions in cyt b were transitional, suggestive of a recent species history. Phylogenetic results show tentative geographic clustering among S. armatus, low genetic diversity (HKY model, T ratio = 22:23% overall pairwise divergence = 2.3%; mean pairwise divergence = 0.95%; see Johns & Avise 1998 for comparison to other species) and limited bootstrap support (Fig. 2). Intermediate support is found for a north and south of the SRP division (75% BS). Three historic individuals north of the SRP and at the western edge of the species range in the Lost River Range form their own grouping (91% BS). A second lineage found primarily north of the Snake River has strong support (89% BS), and includes individuals from northeast Idaho, Montana, northern Wyoming, and the Wind River Mountains. Cytochrome b variation was too low (< 1%) to detect structure in the southern lineage (Fig. 2).

D-loop. Use of the faster-evolving D-loop mitochondrial marker for these individuals added considerable resolution (Fig. 3). The HKY model again best described this data set, but with an additional correction for rate heterogeneity among sites (T ratio = 63.21, G = 0.08). The unrooted D-loop phylogeny and that of the cytochrome b for the same individuals lack conflict, although the two genes differ in the placement of the root. In species with shallow lineage coalescence, this difference is not unexpected because of a long branch leading from the in-group to the sister-group (Demboski & Sullivan 2003). The D-loop data support the grouping of a distinct northeast lineage (85% BS), and a southern lineage subgrouping in Idaho (90% BS), both of which have support from several unique substitutions and a 1-bp deletion or insertion (Fig. 3).

Cyt b and D-loop. As expected from the observed congruence, analysis of the combined fragments (under model TiM + G + I and parameters Rmat = 1, 20.2, 0, 0, 36.3, G = 0.5151, I = 0.5824) increases support for both lineages to 96–100% and again supports a distinct lineage in the northwest of the species range near the Lost River Range (100% BS), as well as a clustering of these Lost River individuals within an expanded northeast lineage grouping (73% BS) (Fig. 4). The combined data still provides little information on S. armatus from Utah, which is likely due to the limited sampling from the southern range relative to the diversity found there. Thus, we expanded our sampling to include individuals from the entire range, focusing our sequencing efforts on the faster evolving D-loop which is better suited for shallow phylogeographic analysis of the Uinta ground squirrel.

Expanded D-loop. The expanded D-loop phylogeny is consistent with that based on cytochrome b, but with added resolution from both variable sites and informative indels. The expanded D-loop data set again shows a 100% consistency index for the two indels. Furthermore, it confirms the Snake River Plain as a phylogeographic break, and indicates two areas of admixture (east of the Snake River Plain and Teton Mountains in the Wind River Range, and at the confluence of the Bear River Range and Wasatch Mountains) (Fig. 5).

Genetic structure and diversity
Significant $F_{ST}$ values were found between samples taken from north of the SRP and those existing south of the SRP (D-loop: $F_{ST} = 0.454$, $P < 0.001$). Variation between these two groups (ΦSC) explained more than 45% of the variation across the entire species range. Grouping individuals by the four clades represented in Fig. 5 (northeast lineage, northwest lineage, southern lineage south of the SRP and southern lineage east of the SRP) also resulted in a significant $F_{ST}$ value (D-loop: $F_{ST} = 0.482$, $P < 0.001$), increasing the ΦSC from 45% to 48%. The unrooted haplotype cladogram generated by TCS with a 0.95 probability however, depicts only three haplogroups (Fig. 1A) that correspond with the three best-supported lineages depicted in the mtDNA gene tree in Fig. 5 (northeast, northwest, southern).

The southern lineage (SL) is the most widespread and abundant lineage across the range of the species and is present throughout the south and southwest of the modern distribution. It is the only lineage represented immediately south of the Snake River Plain and west of the Teton and Salt River Mountains (Fig. 1B, yellow and gold). The southern lineage also contains the greatest amount of genetic diversity both in terms of the number of unique haplotypes (31) as well as the mean pairwise distance (6.83 ± 3.26). The northeast lineage (NEL) is found predominantly to the north and northeast part of the current range with only two of 27 individuals from that lineage found in the southern region (Morgan County and Rich County, Utah) of the current range (Fig. 1B, blue). This NEL contains 21 unique haplotypes from 27 individuals and a mean pairwise distance of 5.62 ± 2.78. The northwest lineage (NWL) was found historically north of the SRP in the Lost Rivers Mountains (Fig. 1B, purple) and is represented by only three individuals with two unique haplotypes and a mean pairwise distance of 0.76 ± 0.67.

Demographic analyses
The demographic analyses showed evidence for recent expansion in the SL and the NEL. For example, the haplotype network exhibited a star phylogeny indicating recent population expansion in the SL (Fig. 1A, yellow). Fu’s test of neutrality also produced significant $F_{S}$ values
(F_{S} = -1.92, P < 0.001) further supporting the finding of recent expansion within the SL. While recent expansion is much less apparent from visual inspection of the NEL haplotype network (there is no obvious star phylogeny), Fu’s $F_{S}$ were also significant for the NEL ($F_{S} = -1.53$, $P < 0.001$). The mismatch distributions for the NEL and SL were both unimodal and fall well within the 95% confidence limits showing recent population expansion in each lineage (Fig. 6A). As expected, the mismatch distribution of all haplotypes divided into groups either north or south/southeast of the SRP based entirely on geography (vs. by lineage) show a bimodal distribution because of the presence of gene flow to the east of the Salt River and Teton Mountains along the Idaho–Wyoming border (Fig. 6B). This also explains why Fu’s $F_{S}$ is significant for the haplotypes found east of the SRP, suggesting expansion, but the mismatch distribution is very ‘ragged’, suggesting stasis. The individuals sampled southeast of the SRP are not reciprocally monophyletic but made up of several rare haplotypes derived from both the SL and NEL, indicative of admixture.

**Divergence times**

A likelihood ratio test on the D-loop data set did not reject clock-like behaviour ($2\Delta \text{LnL} = 88.02; P > 0.10$). Comparison of distances based on the D-loop and cytochrome b for the same pairwise groupings indicates that the intraspecific D-loop distances increase linearly with time, at a 7.5 times faster rate. Thus, we estimated an 11.5% per million-year divergence rate from a previously proposed *Spermophilus* cytochrome b rate (see Methods). Application of this rate puts the deepest divergence within all extant *S. armatus* lineages at 0.58 million years.

The separation of the two northern lineages (NWL and NEL) from the southern (SL) lineage occurred relatively early in the history of *S. armatus* (0.43 Ma), as did the initial divergence within the northern Snake River between the NWL and NEL (0.33 Ma). We estimated a relatively recent age for the common ancestor of the majority of haplotypes found in the Yellowstone Plateau (0.11 Ma), which was completely covered with ice at the end of the Pleistocene. Expansion of an Idaho population south of the Snake River Plain (12 000 years ago) and northward expansion of southern haplotypes (13 500 years ago) both are estimated to have occurred near the end of the Pleistocene. The faster marker lacks resolution for evidence of Holocene expansion but the presence of identical haplotypes across the Bear River Range and Wasatch Range, parts of which were glaciated in the Pleistocene (Laabs et al. 2006), does not conflict with this notion.

**Discussion**

Our analyses of two linked mitochondrial markers provided us with a multifaceted look into the evolution of *Spermophilus armatus*. The deepest genetic divergence within *S. armatus* is approximately 580 000 years ago. This follows the cataclysmic explosion of the Lava Creek caldera at ~640 000 years ago (Laahere et al. 2002) which formed a massive caldera in what is now the middle of the species range and may explain the low maximum diversity within this species. The Lava Creek volcanic eruption and ash-fall dumped between 1 m and 10 m of ash over most of the western USA (Izett & Wilcox 1982; Perkins & Nash 2002). Smaller ash-fall than the Lava Creek eruption is known to have caused extreme population fragmentation and loss of genetic diversity in some modern rodent populations (Gallardo et al. 1995).
A second, relatively deep divergence (0.43 Ma) between the NWL, NEL, and SL falls within local glacial cycles beginning with the Sacajawea Ridge (0.6 Ma) (Pierce 2004) and ending with the initiation of Bull Lake glaciation (Fullerton et al. 2004). These glacial cycles caused repeated separation of intermontane basins within the present range of *S. armatus*. Late Pleistocene glaciation (18 000 years ago) of the Yellowstone plateau (Pierce 2004) and other high montane regions within the species range did not cause appreciable divergence within the lineages. However, movement since deglaciation, about 14 000 years ago, has caused admixture along the eastern front of the continental divide near the Idaho–Wyoming border. Recolonization of the previously glaciated montane terrains came from two genetically distinct lineages (NEL and SL) and admixture between these lineages occurred exclusively east or south of the SRP at the southern edge of the Yellowstone Plateau leading into the Wind River and Salt River Range and at the confluence of the Bear River Range and Wasatch Mountains. The NEL shows evidence of recent (13 000 years ago) population expansion, consistent with population size increase since the terminal Pleistocene. Wholesale postglacial recolonization of the northern range of the GYE in the Yellowstone Plateau is demonstrated here to be from both the northeast and southern lineages, with coalescence times for both lineages significantly preceding the terminal Pleistocene. Admixture of distinct genetic lineages in the Yellowstone Plateau and Wind River Range has been found (Hadly et al. 2004; Hadly et al. unpublished findings) also in montane and long-tailed voles (*Microtus montanus* and *M. longicaudus*). Gene flow of *S. armatus* into Idaho immediately south of the SRP has been restricted to populations solely derived from the SL lineage, which shows evidence of the most recent population expansion. The SRP thus is an obvious barrier to north–south migration in the Uinta ground squirrel and is presently unoccupied by the species.

Finally, very recently (<50 yr), the populations representing the NWL, found only in eastern Idaho north of the SRP in the Lost River drainage, have become locally extirpated (Madison et al. 2004). The NWL is not represented in any extant populations that we have sampled from throughout the species range today; thus, it is likely extinct. Local extirpation north of the SRP near Craters of the Moon National Park has also been observed in other species. *Spermophilus mollis artemisiae* and *S. elegans aureus*, both of which occupied the same region, are hypothesized to have been extirpated due to habitat degradation and agricultural conversion (Zegers 1984; Yensen & Sherman 2003). It is possible that the NWL of *S. armatus* was once more widespread north of the Snake River Plain. We aim to further test this hypothesis by using a phylochronologic approach from subfossils described from two caves at the northern edge of the species range (Waterfall Locality, Lamar Cave), as well as by increased modern field sampling from other localities within the current species range.

**Cautionary notes**

The consistency of tracing shallow genealogical events to Quaternary environmental events in the Central Rocky Mountains is convincing, especially when considering extensive evidence for genetic subdivisions linked to Pleistocene climate changes elsewhere (the Pacific Northwest, Northern Rocky Mountains) (e.g. Demboski & Sullivan 2003; Eddingsaas et al. 2004). Nonetheless, we point out that the scenario depicted above is the maternal side of the total story that is likely more complex given strong male-biased dispersal in *S. armatus*. A nuclear gene phylogeographic investigation will prove more difficult, but not impossible (Zhang & Hewitt 2005), if based mostly on museum specimens. Also, the divergence times presented here are current best estimates, yet still approximate because of the paucity of ground squirrel fossils that can be linked to extant species. Additionally, the estimates of the tectonic and climatic events we describe are not necessarily precise because few are within the time period spanned by radiocarbon dating. Caution also must be advised because we pooled samples from different years (1920–2003) to represent a single phylogeographic story. If gene flow is extremely rapid in species with a small range, phylogeographic structure could theoretically vary over short time periods. Over periods spanning thousands of years, recent ancient DNA research indicated that current phylogeography does not always paint an entire picture of species history, and that ancient gene flow could have left different traces in the past not reflected today (Barnes et al. 2002; Hadly et al. 2004; Hofreiter et al. 2004). Although over a period of less than a century we have observed extirpation of an entire lineage, phylogeographic turnover is not readily apparent in our sampling of the other lineages from 1920 to 2003. Our data instead support a long-term geographic separation of haplotypes across the SRP, with recent admixture of the two largest lineages (NEL, SL) occurring to the east of the SRP where the mountains run in north–south direction.

**Conclusions**

We report low levels of maximum intraspecific genetic diversity in the cytochrome *b* sequences of Uinta ground squirrels, suggesting significant loss of diversity consistent with the last cataclysmic eruption of the Yellowstone hotspot. Using a faster-evolving marker, we recovered shallow-time phylogeographic resolution and found that the deepest split within the species is consistent with advance of the Sacajawea Ridge glaciation. Screening of this faster marker across a reasonably large set of
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References

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**Supplementary material**

The following supplementary material is available for this article:

**Table S1** Museum and specimen numbers, sampling localities, and GenBank Accession numbers for the control region (D-loop) and cytochrome b (cyt b)

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-294X.2008.03671.x

(This link will take you to the article abstract).

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