

Hares on ice: phylogeography and historical demographics of *Lepus arcticus*, *L. othus*, and *L. timidus* (Mammalia: Lagomorpha)

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Abstract

Phylogeographical investigations of arctic organisms provide spatial and temporal frameworks for interpreting the role of climate change on biotic diversity in high-latitude ecosystems. Phylogenetic analyses were conducted on 473 base pairs of the mitochondrial control region in 192 arctic hares (*Lepus arcticus*, *Lepus othus*, *Lepus timidus*) and two individual *Lepus townsendii*. The three arctic hare species are closely related. All *L. othus* individuals form one well-supported clade, *L. arcticus* individuals form two well-supported clades, and *L. timidus* individuals are scattered throughout the phylogeny. Arctic hare distribution was altered dramatically following post-Pleistocene recession of continental ice sheets. We tested for genetic signatures of population expansion for hare populations now found in deglaciated areas. Historical demographic estimates for 12 arctic hare populations from throughout their range indicate that *L. arcticus* and *L. othus* persisted in two separate North American arctic refugia (Beringia and High Canadian Arctic) during glacial advances of the Pleistocene, while the high genetic diversity in *L. timidus* likely reflects multiple Eurasian refugia.

Keywords: Arctic, Beringia, *Lepus*, phylogenetics, phylogeography, refugia

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Introduction

During the Pleistocene, climate fluctuations led to striking changes in Arctic geography, with continental and montane ice sheets episodically covering portions of Eurasia and North America. The effects of these changes on the diversification of high-latitude organisms have been increasingly studied (Weider & Hobæk 2000; Hewitt 2004; Weir & Schluter 2004). Arctic organisms contracted to refugia during glacial maxima, then during interglacial periods, these organisms colonized or expanded into newly available habitats as glaciers receded (Hewitt 1996, 2001). A growing number of studies are examining the phylogeography of terrestrial arctic organisms to test the existence, location and duration of hypothesized refugia (e.g. Wenink *et al.* 1996; Holder *et al.* 2000; Fedorov *et al.* 2003). These studies are representative of a fundamental maturation of phylogeography, with increasing use of statistical tests, especially estimates of historical demographic parameters, to infer

processes affecting species' history (Edwards & Beerli 2000; Knowles 2004).

Extensive evidence exists for one refugium, Beringia, in Arctic North America during glacial maxima, but additional high-latitude Arctic refugia also have been hypothesized. Beringia extended from northwestern Canada and Far East Russia and remained largely unglaciated (Hultén 1937; Pielou 1991; Abbott & Brochmann 2003). Researchers have long hypothesized that Beringia played a role in the diversification and evolution of high-latitude biota (e.g. Rand 1954; MacPherson 1965; Hoffmann 1981). Although there is little fossil evidence (see Harington 1990 for one possible exception), researchers have also proposed a High Canadian Arctic refugium (MacPherson 1965; Pielou 1991). Recently identified divergent lineages and high genetic diversity in populations of dryads, lemmings, and saxifrage in the High Canadian Arctic and Greenland (Tremblay & Schoen 1999; Abbott *et al.* 2000; Fedorov & Stenseth 2002) are consistent with this hypothesis. Furthermore, palaeoclimatic studies suggest that some coastlines in the High Canadian Arctic were ice free during the last glacial maximum (Clark & Mix 2002; Dyke *et al.* 2002; Miller *et al.* 2002). Eurasia was

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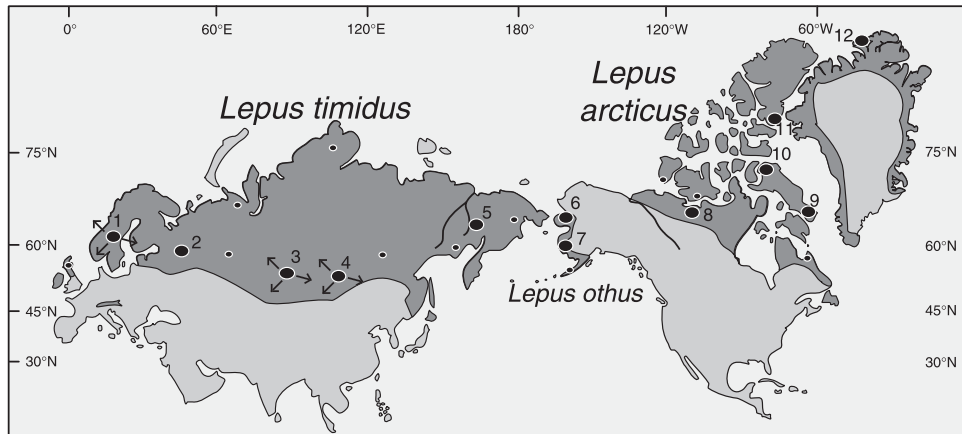


Fig. 1 Distribution of arctic hares. Small dots indicate sampling localities, and large dots indicate sampled populations used in historical demographic analyses. The three dots with surrounding arrows indicate populations showing significant population growth. Population numbers refer to Table 1.

less heavily glaciated than North America during glacial maxima (Andersen & Borns 1994). However, a large ice sheet in northern Europe and extensive montane glaciers across Asia may have led to multiple refugia across these continents (Andersen & Borns 1994; PALE Beringian Working Group 1999).

To explore the potential impact of high-latitude refugia on arctic organisms, we studied the arctic hare complex, with three nominal species allopatrically distributed across the Holarctic (Fig. 1): *Lepus timidus* (Eurasia), *Lepus othus* (western Alaska), and *Lepus arcticus* (northern Canada and Greenland). A preliminary molecular study examined evolutionary relationships among arctic hares, identified them as a monophyletic clade, and found relatively shallow genetic structure, with genetic discontinuities that generally corroborate other phylogeographical studies of arctic taxa (Waltari *et al.* 2004). We expanded that earlier work by doubling the number of samples, increasing the spatial extent of sampling, particularly in Siberia and northern Canada, and testing for genetic signatures of population expansion. We used coalescent-based analyses to estimate historical demographics for populations located in purported refugia and those now found in deglaciated territory.

The current range of arctic hares extends across the Beringian refugium, the proposed High Canadian Arctic refugium, recently deglaciated regions of Canada, as well as less disturbed ice-free habitats of Eurasia. We compare molecular diversity and corresponding coalescence times, and estimates of population growth rates across these regions. If postglacial colonization took the form of sequential dispersal by few individuals into newly available habitat, then populations in recently deglaciated regions should have relatively low genetic diversity compared to presumably stable populations persisting in refugia. Colonizing popu-

lations also should have signatures of subsequent growth in population size following dispersal (Hewitt 1996, 1999; Lessa *et al.* 2003; Galbreath & Cook 2004).

Materials and methods

We examined 473 base pairs of the mitochondrial control region gene from 192 arctic hares (61 *Lepus othus*, 62 *Lepus timidus*, 69 *Lepus arcticus*) and two *Lepus townsendii* (see Appendix). *Lepus townsendii* (Halanych *et al.* 1999; Pierpaoli *et al.* 1999) was designated as the outgroup due to its close evolutionary association with arctic hares.

Genomic DNA was isolated from museum skins, blood, or frozen tissues. Methods for DNA extraction, polymerase chain reaction (PCR) amplification, and cycle sequencing followed those summarized in Lessa & Cook (1998) and Halanych *et al.* (1999). Two primer pairs were used for amplification and sequencing of the control region: LEPUS3' and DLOOP1R (Waltari *et al.* 2004), and DLOOP2F (Waltari *et al.* 2004) and TDKD (Slade *et al.* 1994). PCR products were sequenced in both directions using Applied Biosystems 373 and 3100 DNA sequencers. The resulting sequences were assembled and aligned using SEQUENCE NAVIGATOR, version 1.01 (ABI). New sequences (97) have been catalogued in GenBank with Accession numbers DQ067324–DQ067420 and combined with 95 sequences from Waltari *et al.* (2004).

Phylogenies and nodal support, in the form of posterior probabilities, were estimated using MRBAYES, version 3.0b4 (Huelsenbeck & Ronquist 2001), under a Bayesian framework (Shoemaker *et al.* 1999; Lewis 2001). MODELTEST, version 3.06 (Posada & Crandall 1998) used hierarchical likelihood-ratio tests to determine the optimal model of DNA substitution. Nodal support was also estimated using 1000 nonparametric bootstrap replicates (Felsenstein 1985) using the neighbour-joining method.

Bayesian analyses were initiated with random starting trees, run for 5×10^6 generations, and the Markov chain was sampled every 1000 generations. Model parameters were estimated directly from the data and three independent replicates were conducted to avoid entrapment in local optima (Huelsenbeck & Imennov 2002). Stationarity of the Markov chain was determined by plotting log-likelihood values against number of generations. Trees sampled from generations preceding stationarity were discarded as 'burn-in' (Huelsenbeck & Ronquist 2001). Data collected following burn-in were used to estimate nodal support as posterior probabilities.

We further examined historical demographic estimates of 12 arctic hare populations (5 *L. arcticus*, 2 *L. othus*, 5 *L. timidus*; Fig. 1) to explore whether these populations are located in potential refugia. In addition, we estimated these parameters for each of the three arctic hare species.

For each population, we estimated the population growth parameter g using FLUCTUATE (Kuhner *et al.* 1998), a program incorporating coalescent theory. Each search used five short chains of 100 000 steps and two long chains with 1 000 000 steps. The parameter g expresses the change between present-day size and size at mutational time t in the past by the equation $\theta(\text{present}) = \theta(t)^{-g}$. Thus, positive values of g indicate population growth over time and negative values indicate population decline. While this method is most sensitive to demographic change because it incorporates aspects of the genealogy not used in other tests, its estimates of the growth rate may be biased upwards (Kuhner *et al.* 1998). Consequently, we have conservatively used 99.9% confidence intervals for g to test significance of difference from zero. This estimation assumes no selection or migration between populations. To examine the effects of migration, we conducted a second estimation of g for the three arctic hare species using the program LAMARC, version 1.2.2 (Kuhner *et al.* 2004), which incorporates both migration and growth. To examine whether the control region was in mutation-drift equilibrium, we estimated Tajima's D (Tajima 1993) using ARLEQUIN, version 2.000 (Schneider *et al.* 2000). We also examined Fu's F_s (Fu 1997) for a second independent test of demographic expansion, because it does not suffer from upward bias (Lessa *et al.* 2003). Significance of Fu's F_s was examined using 4000 permutations using ARLEQUIN (Schneider *et al.* 2000).

In addition, we estimated nucleotide diversity for each arctic hare population using ARLEQUIN (Schneider *et al.* 2000). Positive estimates of g significantly different from zero and lower nucleotide diversity estimates would suggest recent population size increase, indicative of a recent colonization. Insignificant growth estimates (change in effective population size) and higher nucleotide diversity estimates are indicative of historically stable populations, suggesting the region was a potential refugium.

Results

Alignment of DNA sequences was unambiguous, with no insertions or deletions observed among the arctic hares. One insertion and two deletions were observed when these sequences were compared to *Lepus townsendii* sequences. Of the 194 hares examined, 102 haplotypes were observed (see Appendix). The Hasegawa–Kishino–Yano (HKY; Hasegawa *et al.* 1985) model of DNA substitution incorporating rate heterogeneity and a proportion of invariable sites was determined to be the most appropriate for our data (HKY + I + Γ ; I = 0.59; α = 0.74).

The arctic hare phylogeny (Fig. 2) reflects differing levels of nodal support for some clades based on neighbour-joining bootstrap and Bayesian values. Given that a Bayesian posterior probability of 0.80 or greater has been suggested to indicate strong support (Whittingham *et al.* 2002), we only discuss clades with support values above this threshold (Fig. 2). Some of these described clades have low bootstrap support, likely due to the complicated relationship between bootstrap values and Bayesian branch support (Huelsenbeck *et al.* 2002). Within the arctic hares, *Lepus arcticus* haplotypes form two clades, one with only three haplotypes (four individuals), and a second with all other *L. arcticus* (Fig. 2). All *Lepus othus* haplotypes form a single well-supported clade (1.00 posterior probability), while haplotypes of *Lepus timidus* appear throughout the phylogeny (Fig. 2).

In our examination of historical demographics of arctic hares by species, *L. arcticus* had a nonsignificant growth rate of 12.3 (99.9% CI: -6.3–30.9), a significant F_s of -8.5228 (P = 0.02) and nucleotide diversity of 0.0228 (95% CI: 0.0111–0.0345). Populations of *L. arcticus* had estimated growth rates ranging from -26.0 to 44.5, none significantly different from zero, and nucleotide diversities from 0.0083 to 0.0214 (Table 1). No *L. arcticus* populations had significant F_s values (Table 1). *Lepus othus* had a nonsignificant growth rate of -5.4 (99.9% CI: -62.2–51.5) and nucleotide diversity 0.0050 (95% CI: 0.0019–0.0081). Neither population of *L. othus* had significant growth rates or F_s values, and nucleotide diversity estimates were 0.0034 ± 0.0023 and 0.0109 ± 0.0080 (Table 1). *Lepus timidus* had a significant F_s value of -11.4203 (P = 0.01), significant positive growth rate of 33.3 (99.9% CI: 23.1–43.4) and nucleotide diversity of 0.0617 (95% CI: 0.0304–0.0920). Populations of *L. timidus* had growth rates ranging from 8.1 to 32.1, with three of five populations showing significant growth, while only one of five populations had a significant F_s value (Table 1). Nucleotide diversities of *L. timidus* populations ranged from 0.0309 to 0.0659 (Table 1).

Testing the assumptions used in FLUCTUATE, we found that estimates of growth rates of the three arctic hare species using LAMARC (Kuhner *et al.* 2004) were not significantly different than the results from FLUCTUATE, which assumes no migration (data not shown). Similarly, estimates

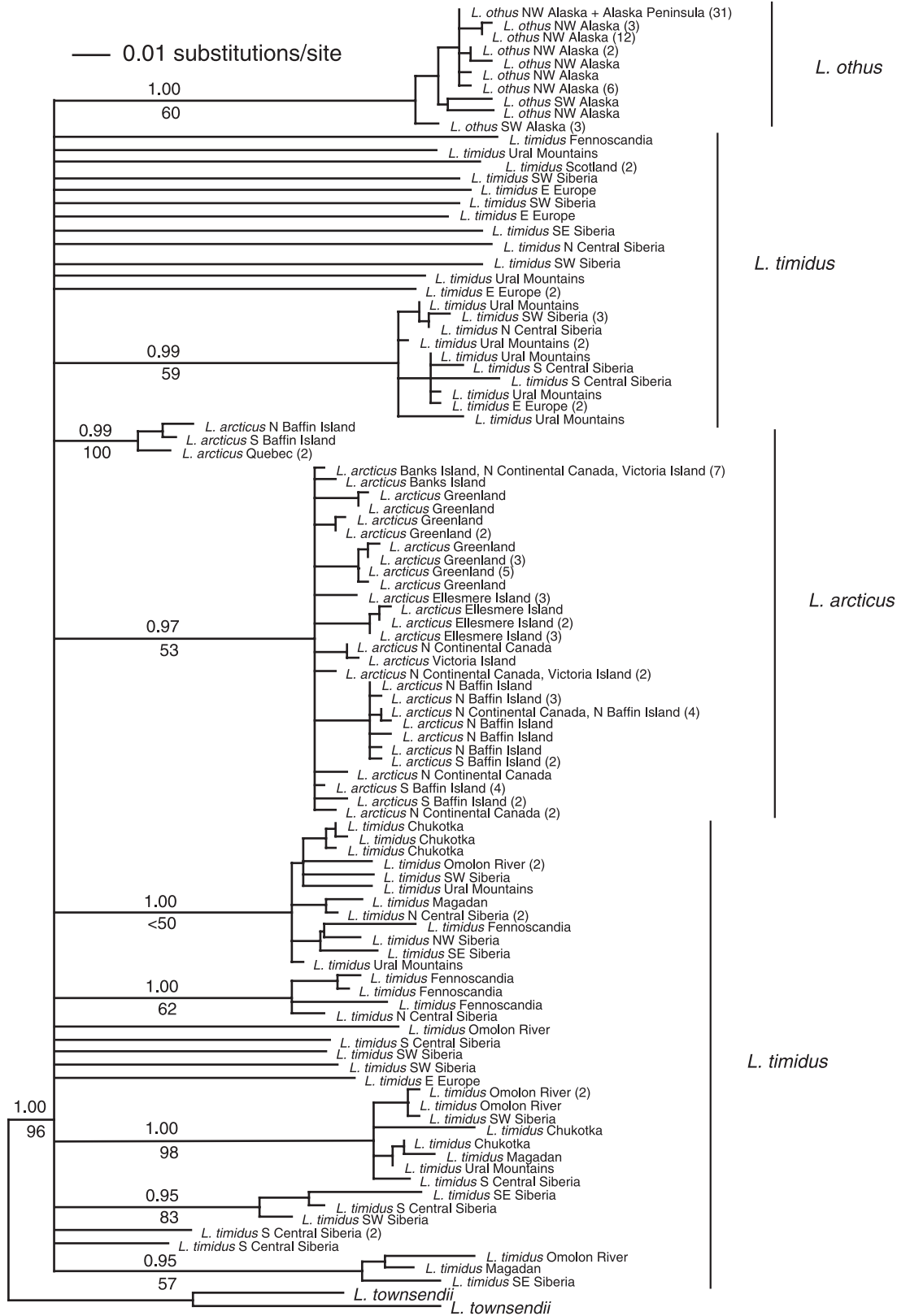


Fig. 2 Phylogeny of arctic hares and a closely related species, based on 473 base pairs of the mitochondrial control region estimated using a Bayesian approach. Numbers above branches are Bayesian posterior probabilities, and numbers below branches are nodal support values from neighbour-joining bootstrap analysis. Numbers in parentheses indicate number of individuals representing a particular haplotype.

Table 1 Genetic estimates with 95% confidence intervals of 12 arctic hare populations. Populations are numbered as in Fig. 1, and those with significantly positive growth rates and significantly negative F_s values ($P < 0.05$) are in bold

Species/population	Samples	Haplotypes	Nucleotide diversity	Growth rate	Fu's F_s
<i>Lepus timidus</i>	69	59	0.0617 ± 0.0303	33.3 ± 10.1	-11.4203
1 – Fennoscandia	5	5	0.0560 ± 0.0348	32.1 ± 23.4	0.4484
2 – E Europe	7	5	0.0301 ± 0.0177	16.9 ± 28.1	1.8923
3 – Central Russia	26	22	0.0494 ± 0.0250	25.1 ± 14.0	-4.9880
4 – S Central Siberia	7	6	0.0600 ± 0.0344	29.1 ± 17.6	1.2680
5 – Far East Russia	11	9	0.0659 ± 0.0352	8.1 ± 13.8	0.6943
<i>Lepus othus</i>	61	10	0.0050 ± 0.0031	-5.4 ± 56.8	-1.1960
6 – NW Alaska	54	7	0.0034 ± 0.0023	-14.5 ± 87.5	-0.4467
7 – SW Alaska	4	2	0.0109 ± 0.0080	-13.5 ± 76.0	3.7770
<i>Lepus arcticus</i>	62	31	0.0228 ± 0.0117	12.3 ± 18.6	-8.5228
8 – N Central Canada	17	8	0.0083 ± 0.0049	44.5 ± 78.3	-0.7862
9 – S Baffin Island	9	4	0.0212 ± 0.0122	-11.0 ± 26.1	3.8263
10 – N Baffin Island	10	7	0.0214 ± 0.0121	-10.8 ± 21.3	0.0210
11 – S Ellesmere Island	9	4	0.0126 ± 0.0075	-26.0 ± 67.1	2.7393
12 – Greenland	15	8	0.0109 ± 0.0063	17.6 ± 73.5	-0.4964

of Tajima's D for the three arctic hare species and 12 populations showed no deviations from mutation–drift equilibrium (data not shown).

Discussion

Phylogeographical studies of arctic organisms provide the opportunity to examine fundamental issues relating to biotic diversity such as the nature and extent of biotic interchange between continents, colonization in response to climate change, and the effects of large-scale habitat fragmentation on genetic diversity and ultimately speciation. We take a historical demographic approach, examining genetic signatures for evidence of post-Pleistocene expansion. We use the traditional genetic measure of nucleotide diversity and two growth estimates to examine potential refugia in the High Canadian Arctic, Beringia, and Eurasia. We also assess the impact of the Bering Strait on diversification in this species complex.

Arctic hare phylogenetics

In both Europe and North America, fossils of arctic hares have been found only from the Holocene, last glacial (Wisconsin or Würm), and interglacial (Eemian or Sangamonian) periods (Kurtén 1968; Kurtén & Anderson 1980). In Russia, no *Lepus timidus* fossils dated prior to the Holocene have been found (Hopkins *et al.* 1982; Averianov 1998). In North America, numerous arctic hare fossils from the last glacial period have been found in central Alaska and Yukon Territory. All of these fossils are outside the current range of either *Lepus arcticus* or *Lepus othus*, likely reflecting recent range shifts of arctic hares in western North America.

Previous morphological (Anderson 1974; Baker *et al.* 1983; Dixon *et al.* 1983) and molecular (Halanych *et al.* 1999; Waltari *et al.* 2004) studies suggest that the three recognized species of arctic hares are closely related. Specifically, Waltari *et al.* (2004) identified single lineages of *L. arcticus* and *L. othus*, multiple *L. timidus* lineages, and a genetic discontinuity in Far East Russia near the Kolyma/Omolon rivers.

Our more extensive sampling regime similarly suggests a close relationship among arctic hares. Monophyly of the Alaskan *L. othus* is well supported (Fig. 2). Most Canadian *L. arcticus* form a single, well-resolved (support value = 0.97) clade; however, four *L. arcticus* individuals from Baffin Island and Quebec form a separate clade (Fig. 2).

Overall, increased sampling across the range of *L. timidus* has painted a somewhat more complex picture compared to Waltari *et al.* (2004). The sister taxon to *L. othus* is not resolved, and we identified new lineage diversity in *L. timidus* and relatively deep divergence within *L. arcticus* (Fig. 2). Our study supports the morphological work of Anderson (1974), which determined that *L. othus* is distinct from *L. timidus*, with a break at the Bering Strait. Additional sampling in the Chukotka Peninsula, at the eastern extreme of Far East Russia is needed, however, to better define the relationship among populations of Alaskan *L. othus* and Far East Siberian *L. timidus*.

This expanded phylogeny does not resolve arctic hare taxonomy. Monophyly of *L. othus* supports species level status (Fig. 2). However, both *L. arcticus* and *L. timidus* are composed of multiple clades. Placement of *L. timidus* in several clades may reflect cryptic speciation, although comprehensive studies using morphology and nuclear DNA are needed before revising arctic hare taxonomy. For now, we accept the current taxonomy delineating three species, while recognizing the need to explore this issue further.

Historical demography/phylogeography

Examination of all *L. arcticus* for a genetic signature of expansion produced an equivocal result. We found a nonsignificant growth rate, but a significantly negative F_u 's F_S value (Table 1). In contrast, five *L. arcticus* populations did not show significant signatures of expansion (Table 1) and likely reflect stable populations. These findings are consistent with *L. arcticus* persisting in the hypothesized High Arctic refugium in northern Canada (MacPherson 1965; Pielou 1991), followed by limited postglacial expansion. Alternatively, postglacial colonization from a Holocene founder event could explain phylogenetic distinctiveness and population expansion in *L. arcticus*, but divergence between lineages of *L. arcticus* is 5%. This level suggests a deeper mid-Pleistocene divergence under both *Lepus* specific and conservative control region rates (respectively 12.4% and 33% per million years; Pierpaoli *et al.* 1999). Populations on Baffin Island have the highest nucleotide diversities, perhaps corroborating palaeontological evidence that the Atlantic coast of Baffin Island was ice free and thus a potential refugium (Clark & Mix 2002; Dyke *et al.* 2002; Miller *et al.* 2002). In addition, separate analyses of the two *L. arcticus* clades show significant growth in the more geographically widespread clade (99.9% CI: 5.3–105.2), while the clade restricted to Baffin Island and northern Quebec showed nonsignificant growth (99.9% CI: –51.4–171.6). Thus, Canadian arctic hares and other organisms may have persisted on Baffin Island during the last glacial maximum.

Although displaying significantly lower nucleotide diversities than Canadian *L. arcticus* or Eurasian *L. timidus*, Alaskan *L. othus* does not show a significant growth rate or F_S value (Table 1). The body of evidence for a Beringian refugium is considerable (e.g. Pielou 1991; Abbott & Brochmann 2003), and monophyly of hares located in eastern Beringia (Alaska, Fig. 2) is consistent with the existence of this refugium. Furthermore, placement of *L. othus* and *L. arcticus* in distinct clades is spatially congruent with findings of separate Canadian and Beringian clades in collared lemmings (*Dicrostonyx groenlandicus*; Fedorov & Stenseth 2002), ptarmigan (*Lagopus mutus*; Holder *et al.* 2000), and *Daphnia* (Weider & Hobæk 2003), and corroborates the persistence of at least two refugia in the Nearctic during full glacial maxima.

Overall, Eurasian *L. timidus* show a significant growth rate and F_S value. When analysed separately, three of five *L. timidus* populations show significant growth, and one of five has a significant F_S value (Table 1). These three expanding populations occur in central Asia and Fennoscandia (Fig. 1), and the large geographical distance between these regions suggests the possibility of colonization from multiple refugia. In addition, Eurasian hares harbour higher nucleotide diversity than *L. othus* and *L. arcticus*, indicating that these populations underwent less drastic population

decrease, perhaps due to persistence of suitable habitat during glacial cycles. Placement of *L. timidus* throughout the arctic hare phylogeny and with little geographical correlation may reflect higher levels of gene flow throughout Eurasia, although this pattern also may be a result of incomplete lineage sorting (Fig. 2).

The Bering Strait has long been identified as a significant physical barrier between Asian and American biotas (Wallace 1876). However, many terrestrial species span this barrier due to the periodic appearance of the Bering land bridge, most recently in existence 70 000–10 000 years before present (BP) (Hopkins *et al.* 1982; Elias *et al.* 1996). The Holarctic distribution of arctic hares provides another opportunity to explore the role of this crossroads of the northern continents in shaping the high-latitude fauna and flora. Lemmings (Fedorov *et al.* 1999, 2003), shrews (Demboski & Cook 2003), tundra voles (Brunhoff *et al.* 2003; Galbreath & Cook 2004), and northern red-backed voles (Cook *et al.* 2004) show no phylogeographical discontinuities at the Bering Strait, reflecting the strong historical connection at high latitudes between Asia and North America. In contrast, our phylogeny of arctic hares indicates monophyly of the Alaskan *L. othus* (Fig. 2) and these are distinctive from arctic hares in eastern Siberia (*L. timidus*), a finding consistent with historical gene flow across the Bering Strait, followed by vicariance (flooding of the Bering Strait) and divergence of *L. othus*.

What is the geographical origin of arctic hares and how many times have they colonized between the continents? Placement of *L. timidus* throughout the arctic hare phylogeny suggests a Eurasian origin, but the basal arctic hare lineage cannot be resolved (Fig. 2). The number of colonizations across the Bering Strait region is also equivocal. Placement of *L. othus* in the phylogeny suggests a separate colonization of North America from Asia. Placement of *L. arcticus* into two clades may be indicative of two separate crossings of the Bering Strait, or a single colonization of a genetically diverse population that subsequently lost variation due to lineage sorting (Fig. 2). In either case, at least two colonizations across the Bering Strait region are likely. This history is more complex than most previously studied arctic taxa, such as martens (Stone & Cook 2002), moose (Hundertmark *et al.* 2001) and pikas (Yu *et al.* 2000), but similar to proposed histories of ground squirrels (Harrison *et al.* 2003; Eddingsaas *et al.* 2004), voles (Conroy & Cook 2000; Cook *et al.* 2004), and marmots (Steppan *et al.* 1999).

For control region sequences, Eurasian *L. timidus* show high genetic diversity, Canadian and Greenland *L. arcticus* exhibit moderate genetic diversity, while Alaskan *L. othus* populations show the lowest nucleotide diversity. Low diversity in *L. othus* is consistent with reports of range retraction of this tundra-adapted species in the last century, perhaps due to climate warming and expansion of boreal forest (Klein 1995).

This molecular perspective on arctic hares sheds light on previous hypotheses of high-latitude refugia based on morphological, palaeontological, and geological evidence. arctic hares appear to have occupied multiple refugia across their distribution, a result that emphasizes the importance of a dynamic climate in the diversification and evolution of arctic organisms. In particular, our results corroborate the hypothesis that diversification of high-latitude organisms was heavily affected by Pleistocene climate fluctuations (Weir & Schluter 2004).

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This work forms a portion of Eric Waltari's PhD. dissertation. Eric is studying phylogeography and historical demography of arctic hares and shrews of the *Sorex cinereus* complex. The laboratory of Joe cook studies phylogenetics, biogeography, and conservation genetics of high-latitude mammals.

Appendix

Individuals used in this study, including species, location, population used for demographic analyses, museum collection numbers, haplotype, and GenBank Accession numbers

Species	Collection locality	Population	ID #	Catalogue #	Haplotype	GenBank#
<i>L. arcticus</i>	Nansen Land, Greenland	Greenland	arcticus1	UAM67719	arcticus c	AY422231
<i>L. arcticus</i>	Nansen Land, Greenland	Greenland	arcticus2	—	arcticus e	AY422232
<i>L. arcticus</i>	Nansen Land, Greenland	Greenland	arcticus3	—	arcticus g	AY422233
<i>L. arcticus</i>	Nansen Land, Greenland	Greenland	arcticus4	—	arcticus i	AY422234
<i>L. arcticus</i>	Nansen Land, Greenland	Greenland	arcticus5	—	arcticus f	AY422235
<i>L. arcticus</i>	Nansen Land, Greenland	Greenland	arcticus6	—	arcticus j	AY422236
<i>L. arcticus</i>	Nansen Land, Greenland	Greenland	arcticus7	—	arcticus d	AY422237
<i>L. arcticus</i>	Nansen Land, Greenland	Greenland	arcticus8	—	arcticus i	AY422238
<i>L. arcticus</i>	Nansen Land, Greenland	Greenland	arcticus9	—	arcticus i	AY422239
<i>L. arcticus</i>	Nansen Land, Greenland	Greenland	arcticus10	—	arcticus f	AY422240
<i>L. arcticus</i>	Nansen Land, Greenland	Greenland	arcticus11	—	arcticus i	AY422241
<i>L. arcticus</i>	Nansen Land, Greenland	Greenland	arcticus12	—	arcticus h	AY422242
<i>L. arcticus</i>	Nansen Land, Greenland	Greenland	arcticus13	—	arcticus h	AY422243
<i>L. arcticus</i>	Nansen Land, Greenland	Greenland	arcticus14	—	arcticus i	AY422244
<i>L. arcticus</i>	Nansen Land, Greenland	Greenland	arcticus15	—	arcticus h	AY422245
<i>L. arcticus</i>	Banks Island, Canada	North-central Canada	20118	UAM47252	arcticus a	AY422246
<i>L. arcticus</i>	Banks Island, Canada	North-central Canada	20119	UAM47253	arcticus a	AY422247
<i>L. arcticus</i>	Banks Island, Canada	North-central Canada	20120	UAM47254	arcticus a	AY422248
<i>L. arcticus</i>	Banks Island, Canada	North-central Canada	20121	UAM47255	arcticus a	AY422249
<i>L. arcticus</i>	Banks Island, Canada	North-central Canada	22343	UAM47257	arcticus b	AY422250
<i>L. arcticus</i>	Grise Fiord, Ellesmere Island, Canada	S Ellesmere Island	34101	UAM83630	arcticus k	DQ067324
<i>L. arcticus</i>	Grise Fiord, Ellesmere Island, Canada	S Ellesmere Island	34102	UAM83631	arcticus l	DQ067325
<i>L. arcticus</i>	Grise Fiord, Ellesmere Island, Canada	S Ellesmere Island	34103	UAM83632	arcticus m	DQ067326
<i>L. arcticus</i>	Grise Fiord, Ellesmere Island, Canada	S Ellesmere Island	34104	UAM83633	arcticus k	DQ067327
<i>L. arcticus</i>	Grise Fiord, Ellesmere Island, Canada	S Ellesmere Island	34105	UAM83634	arcticus k	DQ067328
<i>L. arcticus</i>	Grise Fiord, Ellesmere Island, Canada	S Ellesmere Island	34106	UAM83635	arcticus m	DQ067329
<i>L. arcticus</i>	Kugluktuk, Canada	North-central Canada	34107	UAM83791	arcticus o	DQ067330
<i>L. arcticus</i>	Kugluktuk, Canada	North-central Canada	34108	UAM83660	arcticus q	DQ067331
<i>L. arcticus</i>	Pond Inlet, Baffin Island, Canada	N Baffin Island	34109	UAM83663	arcticus r	DQ067332
<i>L. arcticus</i>	Pond Inlet, Baffin Island, Canada	N Baffin Island	34110	UAM83662	arcticus s	DQ067333
<i>L. arcticus</i>	Pond Inlet, Baffin Island, Canada	N Baffin Island	34111	UAM83638	arcticus t	DQ067334
<i>L. arcticus</i>	Pond Inlet, Baffin Island, Canada	N Baffin Island	34112	UAM83661	arcticus s	DQ067335
<i>L. arcticus</i>	Pond Inlet, Baffin Island, Canada	N Baffin Island	34113	UAM83640	arcticus t	DQ067336
<i>L. arcticus</i>	Pond Inlet, Baffin Island, Canada	N Baffin Island	34114	UAM83639	arcticus v	DQ067337
<i>L. arcticus</i>	Pond Inlet, Baffin Island, Canada	N Baffin Island	34115	UAM83641	arcticus w	DQ067338
<i>L. arcticus</i>	Pond Inlet, Baffin Island, Canada	N Baffin Island	34116	UAM83792	arcticus u	DQ067339
<i>L. arcticus</i>	Cambridge Bay, Victoria Island, Canada	North-central Canada	34117	UAM83642	arcticus a	DQ067340
<i>L. arcticus</i>	Pond Inlet, Baffin Island, Canada	N Baffin Island	34118	UAM83645	arcticus s	DQ067341
<i>L. arcticus</i>	Cambridge Bay, Victoria Island, Canada	North-central Canada	34119	UAM83646	arcticus a	DQ067342
<i>L. arcticus</i>	Pond Inlet, Baffin Island, Canada	N Baffin Island	34120	UAM83790	arcticus cc	DQ067343
<i>L. arcticus</i>	Kugluktuk, Canada	North-central Canada	34121	UAM83655	arcticus y	DQ067344
<i>L. arcticus</i>	Kugluktuk, Canada	North-central Canada	34122	UAM83654	arcticus t	DQ067345
<i>L. arcticus</i>	Cambridge Bay, Victoria Island, Canada	North-central Canada	34123	UAM83643	arcticus q	DQ067346
<i>L. arcticus</i>	Cambridge Bay, Victoria Island, Canada	North-central Canada	34124	UAM83644	arcticus p	DQ067347
<i>L. arcticus</i>	Grise Fiord, Ellesmere Island, Canada	S Ellesmere Island	34125	UAM83636	arcticus n	DQ067348
<i>L. arcticus</i>	Grise Fiord, Ellesmere Island, Canada	S Ellesmere Island	34126	UAM83637	arcticus n	DQ067349
<i>L. arcticus</i>	Grise Fiord, Ellesmere Island, Canada	S Ellesmere Island	34127	UAM83647	arcticus n	DQ067350
<i>L. arcticus</i>	Kimmirut, Baffin Island, Canada	S Baffin Island	34128	UAM66285	arcticus x	DQ067351
<i>L. arcticus</i>	Kimmirut, Baffin Island, Canada	S Baffin Island	34129	UAM66286	arcticus x	DQ067352
<i>L. arcticus</i>	Kimmirut, Baffin Island, Canada	S Baffin Island	34130	UAM66287	arcticus z	DQ067353
<i>L. arcticus</i>	Kimmirut, Baffin Island, Canada	S Baffin Island	34131	UAM66288	arcticus z	DQ067354
<i>L. arcticus</i>	Kimmirut, Baffin Island, Canada	S Baffin Island	34132	UAM66289	arcticus aa	DQ067355
<i>L. arcticus</i>	Kugluktuk, Canada	North-central Canada	34133	UAM83659	arcticus bb	DQ067356
<i>L. arcticus</i>	Kugluktuk, Canada	North-central Canada	34134	UAM83658	arcticus t	DQ067357
<i>L. arcticus</i>	Kugluktuk, Canada	North-central Canada	34135	UAM83657	arcticus bb	DQ067358

Appendix *Continued*

Species	Collection locality	Population	ID #	Catalogue #	Haplotype	GenBank#
<i>L. arcticus</i>	Kugluktuk, Canada	North-central Canada	34136	UAM83656	arcticus a	DQ067359
<i>L. arcticus</i>	Kimmirut, Baffin Island, Canada	S Baffin Island	34137	UAM66290	arcticus z	DQ067360
<i>L. arcticus</i>	Kimmirut, Baffin Island, Canada	S Baffin Island	34138	UAM66292	arcticus dd	DQ067361
<i>L. arcticus</i>	Kimmirut, Baffin Island, Canada	S Baffin Island	34139	UAM66293	arcticus aa	DQ067362
<i>L. arcticus</i>	Kimmirut, Baffin Island, Canada	S Baffin Island	34140	UAM66291	arcticus z	DQ067363
<i>L. arcticus</i>	Kuujuuaq, Quebec, Canada	not used	63955	UAM83621	arcticus ee	DQ067364
<i>L. arcticus</i>	Kuujuuaq, Quebec, Canada	not used	63956	UAM83622	arcticus ee	DQ067365
<i>L. othus</i>	Cold Bay, Alaska	not used	202	UAM42143	othus a	AY422251
<i>L. othus</i>	Chevak, Alaska	Southwest Alaska	UAM10521	UAM10521	othus h	AY422252
<i>L. othus</i>	Chevak, Alaska	Southwest Alaska	UAM10870	UAM10870	othus j	AY422253
<i>L. othus</i>	St. Mary's, Alaska	Southwest Alaska	33814	UAM62589	othus j	DQ067366
<i>L. othus</i>	St. Mary's, Alaska	Southwest Alaska	33820	UAM62590	othus j	DQ067367
<i>L. othus</i>	Kotzebue, Alaska	not used	4520	UAM4132	othus a	DQ067368
<i>L. othus</i>	Kotzebue, Alaska	not used	23771	UAM45545	othus f	AY422254
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	UAM5959	UAM5959	othus d	AY422255
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	UAM5960	UAM5960	othus e	AY422256
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	UAM5961	UAM5961	othus a	AY422257
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	UAM15851	UAM15851	othus b	AY422258
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	UAM15852	UAM15852	othus d	AY422259
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	UAM15853	UAM15853	othus i	AY422260
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	30192	UAM71986	othus a	AY422261
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	30401	UAM72014	othus a	AY422262
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	30402	UAM72015	othus a	AY422263
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	30403	UAM72016	othus a	AY422264
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	30405	UAM72018	othus g	AY422265
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	30406	UAM72019	othus a	AY422266
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	30407	UAM72020	othus c	AY422267
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	30408	UAM72021	othus a	AY422268
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	30734	UAM66665	othus a	AY422269
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	30735	UAM66666	othus a	AY422270
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	30736	UAM66667	othus a	AY422271
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	30737	UAM66668	othus c	AY422272
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	30738	UAM66669	othus a	AY422273
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	30739	UAM66670	othus c	AY422274
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	30740	UAM66671	othus b	AY422275
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	30741	UAM63104	othus c	AY422276
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	30743	UAM66672	othus g	AY422277
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	31697	UAM73076	othus a	AY422278
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	31698	UAM73077	othus a	AY422279
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	31699	UAM73078	othus a	AY422280
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	31700	UAM73079	othus c	AY422281
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	31701	UAM73080	othus a	AY422282
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	31702	UAM73081	othus a	AY422283
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	31703	UAM73082	othus c	AY422284
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	33516	UAM53322	othus g	AY422285
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	34201	UAM53520	othus a	AY422286
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	34277	UAM53737	othus c	AY422287
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	36160	UAM75260	othus b	AY422288
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	36593	UAM77105	othus a	AY422289
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	36594	UAM77099	othus a	AY422290
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	37981	UAM77098	othus a	AY422291
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	37973	UAM77107	othus c	AY422292
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	39266	UAM77102	othus a	AY422293
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	39267	UAM77103	othus a	AY422294
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	39268	UAM58607	othus g	AY422295
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	39347	UAM77097	othus c	AY422296
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	39603	UAM77100	othus a	AY422297
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	41355	UAM77104	othus a	AY422298

Appendix Continued

Species	Collection locality	Population	ID #	Catalogue #	Haplotype	GenBank#
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	41356	UAM66675	othus c	AY422299
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	41357	UAM66676	othus a	AY422300
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	41358	UAM66677	othus c	AY422301
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	41501	UAM66673	othus a	AY422302
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	41502	UAM66674	othus g	AY422303
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	41578	UAM77093	othus c	AY422304
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	41613	UAM77101	othus a	AY422305
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	41665	UAM77108	othus g	AY422306
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	41683	UAM77096	othus a	AY422307
<i>L. othus</i>	Seward Peninsula, Alaska	Northwest Alaska	42005	UAM77106	othus a	AY422308
<i>L. timidus</i>	Vaxvik, Sweden	Fennoscandia	tim30	UAM63915	timidus mm	AY422309
<i>L. timidus</i>	Ringebu, Norway	Fennoscandia	tim33	UAM61331	timidus a	AY422310
<i>L. timidus</i>	Kalix, Sweden	Fennoscandia	tim39	UAM61332	timidus ii	AY422311
<i>L. timidus</i>	Grimso, Sweden	Fennoscandia	tim40	UAM63887	timidus oo	AY422312
<i>L. timidus</i>	Salsta, Sweden	Fennoscandia	tim43	UAM63916	timidus nn	AY422313
<i>L. timidus</i>	Pechora Bay, Russia	not used	tim50	UAM61330	timidus jj	AY422314
<i>L. timidus</i>	Vicinity of Aberdeen, Scotland	not used	scot 9	—	timidus c	AY422315
<i>L. timidus</i>	Vicinity of Aberdeen, Scotland	not used	scot 11	—	timidus c	AY422316
<i>L. timidus</i>	Chukotka Peninsula, Russia	Far East Russia	UAM23260	UAM23260	timidus cc	AY422317
<i>L. timidus</i>	Omolon River Site 1, Russia	Far East Russia	38134	UAM80433	timidus vv	AY422318
<i>L. timidus</i>	Omolon River Site 1, Russia	Far East Russia	38135	UAM80434	timidus vv	AY422319
<i>L. timidus</i>	Omolon River Site 1, Russia	Far East Russia	38136	UAM80435	timidus w	AY422320
<i>L. timidus</i>	Omolon River Site 2, Russia	Far East Russia	38401	UAM80537	timidus ww	AY422321
<i>L. timidus</i>	Chukotka Peninsula, Russia	Far East Russia	A	—	timidus aa	AY422322
<i>L. timidus</i>	Chukotka Peninsula, Russia	Far East Russia	B	—	timidus bb	AY422323
<i>L. timidus</i>	Magadan, Russia	not used	C	—	timidus gg	AY422324
<i>L. timidus</i>	Chukotka Peninsula, Russia	Far East Russia	D	—	timidus yy	AY422325
<i>L. timidus</i>	Chukotka Peninsula, Russia	not used	E	—	timidus zz	DQ067369
<i>L. timidus</i>	Magadan, Russia	not used	NED 25	—	timidus aaa	DQ067370
<i>L. timidus</i>	Magadan, Russia	not used	NED 42	—	timidus x	DQ067371
<i>L. timidus</i>	Ekaterinburg Region, Russia	Central Russia	52380	—	timidus ll	DQ067372
<i>L. timidus</i>	Ekaterinburg Region, Russia	Central Russia	52381	—	timidus m	DQ067373
<i>L. timidus</i>	Ekaterinburg Region, Russia	Central Russia	52382	—	timidus p	DQ067374
<i>L. timidus</i>	Ekaterinburg Region, Russia	Central Russia	52383	—	timidus q	DQ067375
<i>L. timidus</i>	Ekaterinburg Region, Russia	Central Russia	52384	—	timidus b	DQ067376
<i>L. timidus</i>	Chita Region, Russia	not used	52385	—	timidus ddd	DQ067377
<i>L. timidus</i>	Chita Region, Russia	not used	52386	—	timidus y	DQ067378
<i>L. timidus</i>	Chita Region, Russia	not used	52387	—	timidus h	DQ067379
<i>L. timidus</i>	Novosibirsk Region, Russia	Central Russia	52355	—	timidus tt	DQ067380
<i>L. timidus</i>	Novosibirsk Region, Russia	Central Russia	52338	—	timidus fff	DQ067381
<i>L. timidus</i>	Novosibirsk Region, Russia	Central Russia	52326	—	timidus xx	DQ067382
<i>L. timidus</i>	Novosibirsk Region, Russia	Central Russia	52337	—	timidus d	DQ067383
<i>L. timidus</i>	Novosibirsk Region, Russia	Central Russia	52342	—	timidus j	DQ067384
<i>L. timidus</i>	Omolon River, Siberia	Far East Russia	52323	—	timidus dd	DQ067385
<i>L. timidus</i>	Omolon River, Siberia	Far East Russia	52327	—	timidus dd	DQ067386
<i>L. timidus</i>	Omolon River, Siberia	Far East Russia	52325	—	timidus qq	DQ067387
<i>L. timidus</i>	Altai Region, Russia	Central Russia	52330	—	timidus ee	DQ067388
<i>L. timidus</i>	Altai Region, Russia	Central Russia	52352	—	timidus n	DQ067389
<i>L. timidus</i>	Altai Region, Russia	Central Russia	52356	—	timidus n	DQ067390
<i>L. timidus</i>	Altai Region, Russia	Central Russia	52340	—	timidus n	DQ067391
<i>L. timidus</i>	Altai Region, Russia	Central Russia	52349	—	timidus f	DQ067392
<i>L. timidus</i>	Taimyr Peninsula, Russia	Central Russia	52334	—	timidus i	DQ067393
<i>L. timidus</i>	Taimyr Peninsula, Russia	Central Russia	52354	—	timidus o	DQ067394
<i>L. timidus</i>	Taimyr Peninsula, Russia	Central Russia	52339	—	timidus hh	DQ067395
<i>L. timidus</i>	Taimyr Peninsula, Russia	Central Russia	52343	—	timidus hh	DQ067396
<i>L. timidus</i>	Taimyr Peninsula, Russia	Central Russia	52348	—	timidus pp	DQ067397
<i>L. timidus</i>	Tuva Region, Russia	South-central Siberia	52335	—	timidus r	DQ067398
<i>L. timidus</i>	Tuva Region, Russia	South-central Siberia	52336	—	timidus eee	DQ067399

Appendix *Continued*

Species	Collection locality	Population	ID #	Catalogue #	Haplotype	GenBank#
<i>L. timidus</i>	Tuva Region, Russia	South-central Siberia	52344	—	timidus ccc	DQ067400
<i>L. timidus</i>	Tuva Region, Russia	South-central Siberia	52324	—	timidus ggg	DQ067401
<i>L. timidus</i>	Tuva Region, Russia	South-central Siberia	52332	—	timidus ggg	DQ067402
<i>L. timidus</i>	Tuva Region, Russia	South-central Siberia	52328	—	timidus hhh	DQ067403
<i>L. timidus</i>	Tuva Region, Russia	South-central Siberia	52341	—	timidus rr	DQ067404
<i>L. timidus</i>	Tumen Region, Russia	not used	52353	—	timidus ss	DQ067405
<i>L. timidus</i>	Buriatia Region, Russia	not used	52346	—	timidus kk	DQ067406
<i>L. timidus</i>	Krasnoyarsk Region, Russia	not used	52351	—	timidus s	DQ067407
<i>L. timidus</i>	Ekaterinburg Region, Russia	Central Russia	62376	UAM84417	timidus k	DQ067408
<i>L. timidus</i>	Ekaterinburg Region, Russia	Central Russia	62377	UAM84415	timidus v	DQ067409
<i>L. timidus</i>	Ekaterinburg Region, Russia	Central Russia	62378	UAM84416	timidus bbb	DQ067410
<i>L. timidus</i>	Ekaterinburg Region, Russia	Central Russia	62366	UAM84418	timidus t	DQ067411
<i>L. timidus</i>	Ekaterinburg Region, Russia	Central Russia	62367	UAM84419	timidus p	DQ067412
<i>L. timidus</i>	Ekaterinburg Region, Russia	Central Russia	62368	UAM84420	timidus ff	DQ067413
<i>L. timidus</i>	Udmurtia Region, Russia	E Europe	62369	UAM84421	timidus l	DQ067414
<i>L. timidus</i>	Udmurtia Region, Russia	E Europe	62370	UAM84422	timidus l	DQ067415
<i>L. timidus</i>	Udmurtia Region, Russia	E Europe	62371	UAM84423	timidus uu	DQ067416
<i>L. timidus</i>	Udmurtia Region, Russia	E Europe	62372	UAM84424	timidus g	DQ067417
<i>L. timidus</i>	Udmurtia Region, Russia	E Europe	62373	UAM84425	timidus u	DQ067418
<i>L. timidus</i>	Udmurtia Region, Russia	E Europe	62374	UAM84426	timidus u	DQ067419
<i>L. timidus</i>	Udmurtia Region, Russia	E Europe	62375	UAM84427	timidus e	DQ067420
<i>L. townsendii</i>	Summit County, Utah	not used	FXG229	BYU15993	townsendii a	AY422327
<i>L. townsendii</i>	Sevier County, Utah	not used	FXG231	BYU15986	townsendii b	AY422328