Contrasting mitochondrial DNA diversity estimates in two sympatric genera of Arctic lemmings (*Dicrostonyx*: *Lemmus*) indicate different responses to Quaternary environmental fluctuations

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The fossil records show that since the Middle Pleistocene, lemmings (*Dicrostonyx*, *Lemmus*) have been sympatric across their ranges. I compared mitochondrial DNA (mtDNA) diversity estimates between the two genera to infer a difference in demographic history resulting from biotic responses to Quaternary environmental fluctuations. The mtDNA diversity estimates in *Lemmus* consistently exceed those in *Dicrostonyx* on regional and continental spatial scales. However, as opposed to the mainland, the diversity estimates in *Lemmus* are lower than those in *Dicrostonyx* on Wrangel Island. Under the assumption of equal mutation rates, a difference in diversity estimates reflects a difference in the historical effective size. On a regional scale, the low mtDNA diversity in *Dicrostonyx* suggests it suffered a reduction in effective population size, probably due to range contractions during warming events in the Holocene. On a continental scale, the low average divergence in *Dicrostonyx* indicates a dispersion event after the range contraction in Eurasia to a single refugium, also due to warming events in one of the interglacials. In contrast to *Dicrostonyx*, the high mtDNA diversity in *Lemmus* gives no indications for a reduction in its effective size during late Quaternary warming events. This implies that the two historically codistributed genera responded differently to Quaternary environmental changes, even if their differences in biotic responses are undetectable in the Arctic fossil record. This study demonstrates that molecular genetic data increase the resolution of palaeoecological analyses at the community level.

Keywords: *Dicrostonyx*; *Lemmus*; Arctic; Quaternary environmental changes; mtDNA variation; biotic response

1. INTRODUCTION

Species can respond to environmental fluctuations by distribution change, extinction and adaptation. Palaeoecological data indicate that species mostly responded to late Quaternary environmental oscillations by distribution change, often associated with local extinction (Bennett 1997). The fossil record of Quaternary mammals in North America demonstrates that the geographical ranges of individual species shifted at different times, in different directions, and at different rates (Faunmap Working Group 1996). Biotic responses to Quaternary climatic fluctuations are usually analysed on the scale of glacial–interglacial cycles. However, emerging evidence indicates that biotic responses to short-term, high-amplitude climatic oscillations, occurred within the glacial–interglacial periods, and are close to the limits of the resolving power of the fossil record (Roy *et al.* 1996). Nevertheless, these historical processes are recorded in genes and gene pools of extant species.

Phylogeography, the analysis of information integrating allele genealogies, allele frequencies and geographical distribution of alleles, provides an insight into the historical

factors generating the extant patterns of genetic variation (Avice 1994). This approach provides a means of detecting biotic responses to even the relatively short millennial climatic events within glacial–interglacial periods (cf. Roy *et al.* 1996). Furthermore, comparisons of genetic patterns across several codistributed species can reveal interspecific differences in biotic responses and alterations in community-level associations (Riddle 1996).

Collared lemmings (*Dicrostonyx*) and true lemmings (*Lemmus*) are arvicoline rodents sympatrically distributed over the major part of the Arctic. However, the geographical ranges of *Dicrostonyx* and *Lemmus* are not completely identical (cf. Jarrell & Fredga 1993). While the distribution of *Dicrostonyx* is restricted to the treeless tundra, *Lemmus* occurs in the boreal forest zone. The palaeontological evidence indicates that since the Middle Pleistocene *Dicrostonyx* and *Lemmus* have been typical members of the same biotic association in the Eurasian and the American Arctic (Guthrie & Matthews 1971; Agadjanian 1976; Zazhigin 1976; Kowalski 1980; Borodin 1996). Despite their codistribution in the Arctic fossil record, there is palaeontological evidence that during the early-Middle Pleistocene in Europe, these two genera were sometimes

Figure 1. Map showing the sampling localities (expedition site numbers are given in brackets): 1, Yamal (5); 2, W. Taymyr (8); 3, N. Taymyr (9); 4, E. Taymyr (10); 5, Yana (12); 6, Indigirka (14); 7, W. Kolyma (15a); 8, E. Kolyma (15b); 9, Wrangel Island (17) and Alaska. Two geographical regions, Taymyr and the mainland between the Lena and Kolyma rivers, are indicated by solid lines.

associated with different environments. *Dicrostonyx* was associated with a cold and dry environment, while the fossil record of *Lemmus* suggests it occurred in assemblages suggestive of mesic and humid environments (Kowalski 1995). This suggests the potential for a different response of each genus to the late Pleistocene–Holocene environmental changes in the Eurasian Arctic.

The processes of distribution change affect demographic history by altering the long-term effective population size. Under the assumption of equal mutation rates, a difference in genetic diversity estimates between the two genera of Arctic lemmings reflects a difference in the current and/or historical effective population size on a local spatial scale, a difference in the historical population size on a regional geographical scale (cf. Rogers & Jorde 1995) and a difference in the timing of vicariant events on a continental scale (Avice 1994). If the historically and presently codistributed genera responded differently to the environmental changes operating on different time-scales, then the mitochondrial DNA (mtDNA) diversity estimates are expected to differ between *Lemmus* and *Dicrostonyx* on local, regional and continental spatial scales.

I have previously shown that intrapopulation and intraregion mtDNA diversity estimates in each genus reflect a demographic response to the millennial environmental changes in the Holocene (Fedorov *et al.* 1999a,b). A qualitative comparison of the phylogeographical patterns between the two genera across the Eurasian Arctic revealed the geographical congruence of phylogenetic discontinuities in *Lemmus* and *Dicrostonyx* (Fedorov *et al.* 1999b). The association between observed discontinuities and probable Pleistocene glacial barriers suggests that glacial–interglacial periods were crucial in the vicariant history of both genera. In this study I compare the intrapopulation and intraregion mtDNA diversity estimates between *Lemmus* and *Dicrostonyx* to infer the

difference in demographic history resulting from biotic responses on a millennial time-scale during the Holocene. I also compare the mtDNA divergence estimates among the main phylogeographical groups in each genus so as to infer differences in the timing of vicariant events that have arisen through variation in biotic responses at the temporal scale of glacial–interglacial cycles.

2. MATERIAL AND METHODS

Two important methodical aspects were taken into consideration for direct comparisons of the mtDNA diversity estimates between the two genera of lemmings. First, to avoid the effect of geographical variation, comparisons were made between *Lemmus* and *Dicrostonyx* sampled from the same geographical localities and regions because each geographical area has a singular abiotic history. Second, to minimize the effect of intragenomic variation in the mutation rates, comparisons were made between the diversity estimates obtained with identical sets of restriction enzymes and sequencing of the same parts of the mitochondrial genome in each genus.

Lemmings were trapped during the summer of 1994 on the Swedish–Russian Tundra Ecology Expedition. The two specimens from Alaska were obtained from the Frozen Tissue Collection, University of Alaska Museum, Fairbanks.

For comparison of the intrapopulation mtDNA diversity, I selected eight localities (figure 1, locality 6 excluded) throughout the Eurasian Arctic from where both *Dicrostonyx* and *Lemmus* were sampled and the sampling size ($n = 5–11$) was adequate for diversity analyses. It has been shown that only a small amount of mtDNA variation is allocated among the populations of both *Dicrostonyx* and *Lemmus* within each of the two geographical regions (figure 1): Taymyr and the mainland between the Lena and Kolyma rivers (Fedorov *et al.* 1999a,b). This allowed me to compare total haplotype and nucleotide diversity estimates calculated for all individuals sampled in each genus within each

geographical region. One specimen of *Dicrostonyx* and six individuals of *Lemmus* from the Indigirka river (figure 1, locality 6) were included in the regional analysis. The estimates of the mtDNA diversity within the populations and the geographical regions are based on the restriction site data obtained with eight tetranucleotide restriction enzymes. The haplotype diversity (h) and the nucleotide diversity (π) within the populations and the geographical regions were calculated according to Nei (1987). The variances of nucleotide diversity estimates were obtained by using jackknifing over restriction enzymes (Nei & Miller 1990). The complete results of mtDNA diversity and phylogeographical analyses for each genus of lemmings considered separately are reported elsewhere (Fedorov *et al.* 1999a,b), and detailed information on sample sizes, localities and methods can also be found in these studies.

To compare sequence divergence and nucleotide diversity in the two genera of lemmings on a continental scale, a 915 bp fragment of the mitochondrial cytochrome *b* gene was isolated via PCR and sequenced in 12 individuals selected from the main phylogeographical groups in each genus. The sequence data for the genus *Lemmus* as well as the sequencing method are described in Fedorov *et al.* (1999b). Sequences of *Dicrostonyx* have been deposited with the GenBank data library under accession numbers AJ131439–AJ131444. For sequence data, estimates of divergence between haplotypes within each genus were calculated using Kimura's (1980) two-parameter method, and neighbour-joining (NJ) phylogenetic trees (Saitou & Nei 1987) were constructed from divergence estimates with the MEGA program (Kumar *et al.* 1993). The total nucleotide diversity and its variance were calculated from sequence data according to Nei (1987).

3. RESULTS

The intrapopulation nucleotide (π) and the haplotype diversity (h) estimates in *Lemmus* exceed those for *Dicrostonyx* in all seven localities sampled from the Siberian mainland (two-tailed Wilcoxon sign test $p = 0.02$ for both π and h ; figure 2). However, as opposed to the mainland localities, the nucleotide and haplotype diversity estimates for *Lemmus* on Wrangel Island are lower than those for *Dicrostonyx* (locality 9; figure 2), and the difference between the nucleotide diversity estimates on the island locality is significant ($0.05 \pm 0.04\%$ versus $0.22 \pm 0.08\%$ (s.e.); two-tailed Student's t -test $p < 0.05$). On a regional scale, similar to the intrapopulation comparisons on the mainland, the mtDNA diversity estimates in *Lemmus* significantly exceed those for *Dicrostonyx* within both geographical regions (two-tailed Student's t -test $p < 0.001$ for all pairwise comparisons; figure 3).

Apart from the diversity analysis, the mismatch distribution approach (Rogers & Jorde 1995) is widely used to study historical demography. This method estimates the magnitude and the timing of population expansion through the frequency distribution of the pairwise mutation differences among individuals. However, the mismatch distribution approach did not give additional resolution in the present study. Mismatch distributions in *Lemmus* within both geographical regions are ragged and multimodal (not shown) as expected for a population of constant size (Marjoram & Donnelly 1994). The occurrence of one or two most common and widespread

Figure 2. Mitochondrial DNA diversity estimates within the populations of *Lemmus* and *Dicrostonyx*. (a) Nucleotide diversity (π (%)). (b) Haplotype diversity (h). Locality numbers refer to figure 1.

haplotypes among *Dicrostonyx* populations within each geographical region, and the star-like phylogenies, result in the unimodal, left-truncated, narrow distribution of pairwise differences, reflecting the low mtDNA diversity (Fedorov *et al.* 1999a). The L-shaped frequency distribution indicates the recent bottleneck events within geographical regions (Majoram & Donnelly 1994) but does not provide an estimate with which to infer a short post-bottleneck time (Rogers & Jorde 1995).

The NJ trees (figure 4), based on Kimura's distances between haplotypes representing the main phylogeographical groups, indicate that the major phylogenetic splits in both genera are in north-eastern Siberia (figure 1) and probably resulted from isolation by intermittent inundation of the Bering Strait (Fedorov *et al.* 1999a,b).

Figure 3. Total mtDNA diversity estimates for *Lemmus* and *Dicrostonyx* within the geographical regions. (a) Nucleotide diversity (π (%)). (b) Haplotype diversity (h). Bands indicate the range (mean $\pm$ s.e.). The geographical regions are shown in figure 1.

However, the exact geographical location of the main phylogenetic splits differs between the species. On Wrangel Island, the nearctic haplotype of *Dicrostonyx* is found together with the Eurasian haplotype of *Lemmus*. Conversely, in the area east of the Kolyma river, the haplotype of *Dicrostonyx* belongs to the Eurasian clade, while the haplotype of *Lemmus* is closely related to that typical of Alaska. The phylogeny within the Eurasian *Dicrostonyx* clade is shallow compared with the phylogeny of the Eurasian clade in *Lemmus* (clades E, figure 4; average branch length, $0.37 \pm 0.12\%$ versus $1.00 \pm 0.24\%$ (s.e.); two-tailed Student's *t*-test $p < 0.05$). The average divergence among the Eurasian haplotypes, representing the main phylogeographical groups in each genus, was quantified by estimating nucleotide diversity within the Eurasian clades. Similar to intrapopulation and intraregion comparisons, the nucleotide diversity estimate in *Lemmus* significantly exceeds that in *Dicrostonyx* on a

continental scale ($3.62 \pm 0.86\%$ versus $1.18 \pm 0.30\%$ (s.e.); two-tailed Student's *t*-test $p < 0.01$).

4. DISCUSSION

This study demonstrates the contrast between mtDNA diversity estimates in two sympatric genera of Arctic lemmings. The diversity estimates in *Lemmus* consistently exceed those in *Dicrostonyx* on local, regional and continental spatial scales. Mitochondrial DNA diversity is a function of the mutation rate and the effective population size of females (Nei 1987). There is no reason to expect large variation in the mtDNA mutation rates between the two genera of arvicoline rodents with their similar body sizes and generation times (cf. Martin & Palumbi 1993). Thus, the difference in the mtDNA diversity estimates between *Lemmus* and *Dicrostonyx* reflects the difference in effective size.

In the absence of estimates of the contemporary effective population size for lemmings, it is possible to assume that differences in diversity estimates within local populations are due to differences in the effective population size in ecological time. However, on a regional geographical scale, comparisons of the total diversity between *Lemmus* and *Dicrostonyx* show significant differences of the same tendency as occurs within the local populations. This consistency between intrapopulation and intraregion comparisons, as well as the limited population structure within the regions (Fedorov *et al.* 1999a,b), implies that differences in mtDNA diversity reflect differences in long-term effective size between the two genera due to historical events operating on a regional level. The lower mtDNA diversity in *Dicrostonyx* suggests a smaller historical effective size within the regions than in *Lemmus*. Given that each geographical region has a singular abiotic history, the difference in historical demography between *Lemmus* and *Dicrostonyx* indicates different demographic responses to the same environmental factors. These historical events cannot be directly attributed to the impact of the last glaciation, since similar contrasts in mtDNA diversity were found in two geographical areas with different glaciation history. While Taymyr was covered by ice during the Pleistocene glaciations, the area between the Lena and Kolyma rivers was not glaciated (Andersen & Borns 1997).

I suggest that the intrapopulation and intraregion mtDNA diversity estimates in each genus reflect the demographic events resulting from environmental changes during the Holocene. The low mtDNA diversity in *Dicrostonyx* resulted from regional bottleneck events due to the northward expansions of the forest communities during the Holocene warming events (Fedorov *et al.* 1999a). The high mtDNA diversity and the lack of population structure in *Lemmus* suggest latitudinal distribution shifts of populations with high ancestral diversity, probably due to cold climatic periods in the Holocene (Fedorov *et al.* 1999b). Thus, the contrast in mtDNA diversity between the two genera of lemmings indicates a difference in the demographic history as a result of their different responses to millennial environmental changes during the Holocene in the Eurasian Arctic.

The significance of the Holocene environmental changes is supported by the opposite trend in the

Figure 4. NJ unrooted trees illustrating phylogenetic relationships among haplotypes representing the main phylogeographical groups observed in (a) *Lemmus* and (b) *Dicrostonyx*. The trees are based on sequences of a 915 bp segment of the mtDNA cytochrome *b* region. The Eurasian clades are designated by E. Numbers over branches indicate bootstrap support (1000 replicates). Locality numbers refer to figure 1.

diversity estimates on Wrangel Island. After the last glaciation, this non-glaciated island was isolated from the mainland by rising sea levels 11 000–9500 years BP (Elias *et al.* 1996) and was not affected by the Holocene forest expansion (Yurtsev 1982). This implies that, in contrast to the mainland, the population of *Lemmus* could not track the environment by shifting their distribution southward and the long-term population size of *Dicrostonyx* was not reduced during the Holocene. As expected, only on Wrangel Island are the diversity estimates in *Lemmus* lower than those in *Dicrostonyx*.

Despite the codistribution of the two genera in the Quaternary fossil record and the present sympatric distribution of the two genera over the major part of the Arctic, there are palaeontological, biogeographical and ecological indications suggesting the potential for different responses to environmental changes. Palaeontological data show that *Dicrostonyx*, the northernmost genus of rodents, evolved in the dry landscape of north-eastern Siberia and was always restricted to a cold and dry environment (Agadjanian 1976; Zazhigin 1976; Kowalski 1980, 1995). In contrast, *Lemmus* evolved in the boreal regions of the Western Palaearctic and was associated with a mild and mesic environment, mainly accompanied by a forest fauna during the early Middle Pleistocene in the temperate zone of Europe (Agadjanian 1976; Kowalski 1995). The present geographical ranges of *Dicrostonyx* and *Lemmus* are not completely identical (cf. Jarrell & Fredga 1993). The geographical range of *Dicrostonyx* is restricted to the treeless tundra and only this genus of rodents occurs in the polar desert of the northernmost part of the

Canadian Arctic, while the distribution of *Lemmus* extends into the boreal forest zone in Scandinavia, eastern Siberia and Alaska. Furthermore, even within their range of sympatric distribution each genus shows clearly different habitat preferences (cf. Rodgers & Lewis 1986). *Dicrostonyx* prefers dry habitats, while *Lemmus* is characteristically associated with wet, mesic habitats. Thus, it is reasonable to assume that the northward forest advances during warm and humid climate periods contracted the range and reduced the long-term effective size of *Dicrostonyx* within geographical regions, while the distribution range and the effective size of *Lemmus* were not affected by these environmental changes in the Holocene.

The contrast in the intrapopulation and intraregion mtDNA diversity estimates provides evidence of different responses to the environmental changes on a millennial time-scale during the Holocene. However, the difference between the two genera of lemmings in the average divergence estimates over the Eurasian continent indicates temporal incongruence in their vicariant history due to different responses to the climatic events in deep history. The lower average divergence between mtDNA phylogeographical groups in *Dicrostonyx* suggests a shorter time of separation by the Pleistocene glacial barriers in this genus when compared with *Lemmus*. The warming events of the interglacials strongly affected the Arctic biota (Sher 1991). There are palaeontological indications of Pleistocene reductions in the geographical range of *Dicrostonyx* in Europe during interglacial periods (Kowalski 1995). Furthermore, two *Dicrostonyx* fossil

assemblages stratigraphically separated by a fossil-wood horizon representing a pronounced warm event, were recently found on the Indigirka–Kolyma lowland (figure 1; Sher 1991). The deposits were assigned to one of the interglacials (Sher 1991). This finding provides direct palaeontological evidence that the occurrence of *Dicrostonyx* was interrupted by a forest expansion during a warm climatic event. The contraction of the distribution range of *Dicrostonyx* in Eurasia to a single refugium during one of the interglacials, the following dispersion event, and subdivision by the glacial barriers explain the shallowness of the mtDNA phylogeny in this genus. In contrast to *Dicrostonyx*, the distribution range of *Lemmus* was not contracted by warming events during the interglacial and, thus, the vicariant separation was not interrupted by climate change in this genus.

These results suggest that the two historically and presently codistributed genera of arvicoline rodents responded differently to the environmental changes resulting from the Holocene and the interglacial warming events in the Eurasian Arctic. To date, this difference among genera in biotic responses has not been detected by the Arctic fossil records. This study demonstrates that molecular genetic data can increase the resolving power of palaeoecological analyses at the community level.

I thank A. Goropashnaya for laboratory assistance, M. Lascoux and R. J. Paxton for comments on the manuscript, I. Stein for language corrections and K. Fredga for support. Specimens from Alaska were kindly provided by J. A. Cook and G. H. Jarrell. This study was financially supported by grants from the Sven and Lilly Lawski Foundation to V.B.F. and from the Royal Swedish Academy of Sciences for Research Cooperation between Sweden and the former Soviet Union to K. Fredga and V.B.F.

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