

Comparing the genetic population structure of two species of arctic lemmings: more local differentiation in *Lemmus trimucronatus* than in *Dicrostonyx groenlandicus*

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Collared and brown lemmings (*Dicrostonyx groenlandicus* and *Lemmus trimucronatus*) are two largely sympatric and ecologically comparable species of arctic microtine rodents, differing however in some respects which allow us to hypothesise differences in the genetic structure of their populations. Collared lemmings are particularly well adapted to life at high latitude, they occasionally emerge to the surface of the snow and may disperse over larger distances than brown lemmings – possibly even over snow and ice. This should result in more local differentiation among populations of brown lemmings than among populations of collared lemmings. We compared the genetic population structure between the two lemming species in a fragmented landscape with small islands in the central Canadian Arctic using four microsatellite loci and partial mitochondrial control region sequences. Both types of genetic markers showed higher differentiation (F_{ST} values) among local populations for brown lemmings than for collared lemmings. We discuss to what extent the observed genetic differences may be explained by differences in dispersal rates in addition to differences in average effective population size.

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The purpose of this study is to compare the population genetic structure of brown lemmings (*Lemmus trimucronatus*, Richardson, 1825) and collared lemmings (*Dicrostonyx groenlandicus* Traill, 1823). In an earlier study (Ehrich et al. 2001) we have described the genetic structure of populations of collared lemmings in a landscape characterised by small islands in the central Canadian Arctic: despite low long-term effective population sizes, the island populations were highly variable at four microsatellite loci, and differentiation among local populations was relatively weak. The resulting pattern could be explained only by regular gene flow, leading us to hypothesise some long distance dispersal of individual collared lemmings to and possibly among

small islands separated by considerable inhospitable areas of rock, snow and ice. Building upon our earlier study on collared lemmings, we here present comparable data on the brown lemming for the same geographic region. We ask in particular whether observed differences between the two species may be attributed to differences in dispersal rates.

Collared lemmings and brown lemmings are microtine rodents distributed sympatrically over large parts of the North American Arctic. Both species typically exhibit strong cyclic density fluctuations (e.g. Krebs 1993, Stenseth and Ims 1993a). Fluctuations of particularly high amplitude characterised by very low densities during the low phase have been described for brown

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lemmings (Bunnell et al. 1975, Stenseth and Ims 1993b), and non-cyclic populations have not been reported for this species (Stenseth and Ims 1993a). For collared lemmings, on the other hand, non-cyclic populations have been reported (Krebs et al. 1995, Reid et al. 1997). The density fluctuations are often synchronous between species in a particular geographic area (e.g. Rodgers and Lewis 1986, Negus and Berger 1998), although asynchrony has been observed (Pitelka and Batzli 1993). The two lemming species share the same functional role as herbivores in the arctic ecosystem, but their food and microhabitat preferences differ: collared lemmings prefer well-drained habitat and feed mostly on dicotyledonous herbs and shrubs whereas brown lemmings prefer wet habitats and consume mostly sedges, grasses and some mosses (Rodgers and Lewis 1986, Batzli 1993).

Collared lemmings are particularly well adapted to life at high latitude; during winter they have a nearly white fur. Relative to their body size, they are particularly resistant to low temperatures, and have been observed on snow and ice during the winter (Hart 1962, Ferguson and Folk 1970). Brown lemmings on the other hand are not to the same extent specialised for the arctic environment: they are not as cold resistant (Ferguson and Folk 1970), are brown all year round, and do not occur on the northern islands of the Canadian Arctic or on Greenland, areas occupied by collared lemmings (e.g. Hall 1981). It is thus a priori less likely that brown lemmings will emerge to the surface of the snow or undertake long-distance dispersal in winter or spring (while the sea is frozen) as it was inferred for collared lemmings (Ehrich et al. 2001). Collared lemmings have also during the summer been

reported to move longer distances than brown lemmings (Brooks and Banks 1971); however, Rodgers (1990) did not observe any difference in individual movement distances between the two lemming species.

These two closely related species are thus ecologically largely comparable but, nevertheless, different in some respects, allowing us to expect differences in the genetic structure of their populations. Particularly in a landscape with a multitude of small islands, there may be less dispersal among local populations of brown lemmings resulting in more isolated populations on the islands. Less dispersal would imply less gene flow, and greater genetic differentiation of island populations might thus be expected for brown lemmings than for collared lemmings. In the present study we compare the genetic structure and the level of genetic differentiation between the two lemming species at the same island and mainland sites in Bathurst Inlet (Northwest Territories, Canada; Ehrich et al. 2001), in order to contribute to a better understanding of the ecology of the two species in such an island landscape.

Material and methods

The study area and the samples

The study area in Bathurst Inlet (Kent region, central Canadian Arctic; Fig. 1) was chosen for its fragmented habitat, and the islands were chosen for their apparent isolation. The total area of the islands is in the order of 1–2 km², but suitable lemming habitat covers less than half of the total area (see Ehrich et al. 2001 for details). The coastal habitat of both the islands and the main-

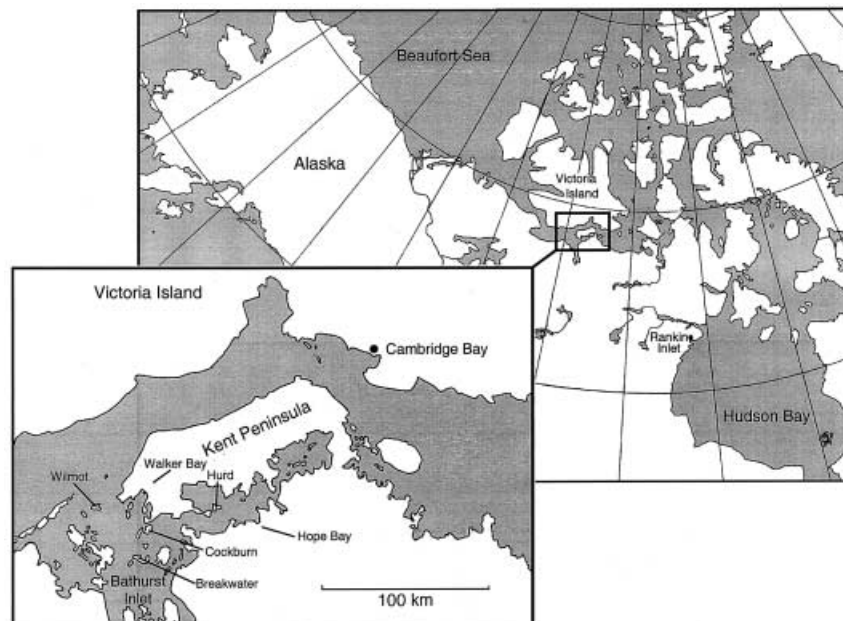
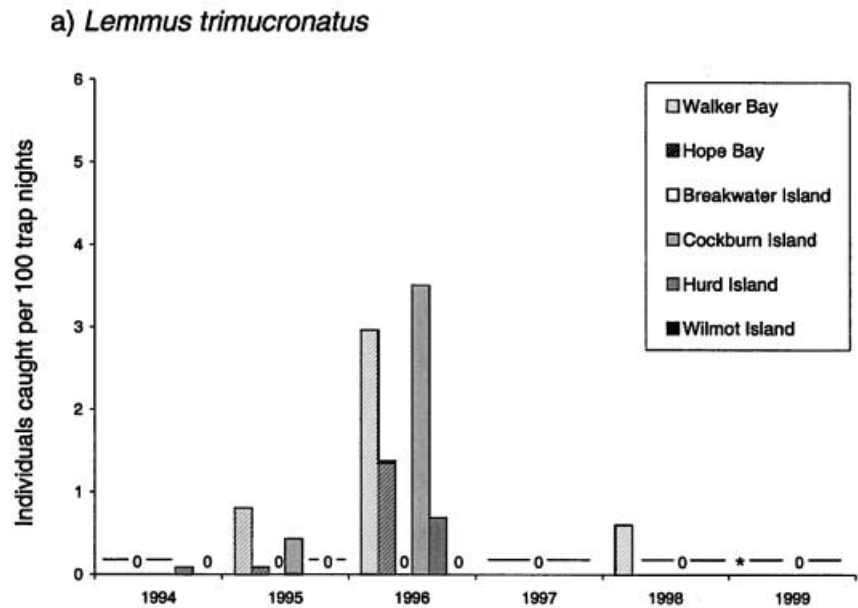
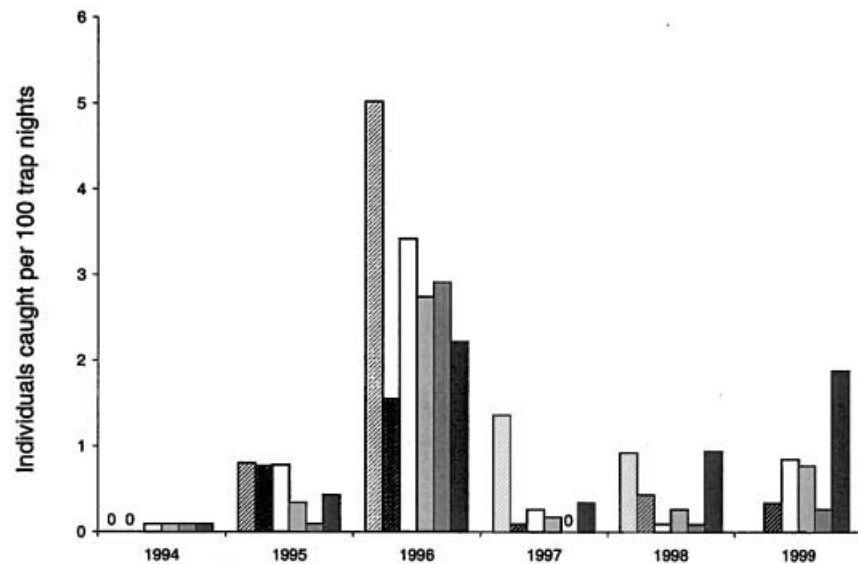


Fig. 1. Map of the study area in the central Canadian Arctic (Northwest Territories). Coordinates of the localities where the samples were collected: Walker Bay, 68°22' N/108°08' W; Hope Bay, 68°55' N/108°30' W; Breakwater Isl., 68°06' N/106°43' W; Cockburn Isl., 68°05' N/108°18' W; Hurd Isl., 68°13' N/107°20' W; Wilmot Isl, 68°12' N/109°05' W.

Fig. 2. Trapping indices for 1994–1999 from the six studied localities in Bathurst Inlet. '0' indicates no animals trapped at a particular locality and '*' represents a missing value.



b) *Dicrostonyx groenlandicus*



land consists mostly of bare rock, which constitutes large inhospitable areas between lemming habitats. Breakwater and Wilmot Islands are separated from lemming habitat on the mainland by 20 km, Hurd by 10 km and Cockburn by 2.3 km. The sea in this region is frozen eight months of the year. Tissue samples from collared lemmings were collected at six localities in the Kent Region in 1996 (a few additional

individuals were collected in 1998). Brown lemming samples could be obtained only at four localities in 1996 (Cockburn Island, Hurd Island, Hope Bay and Walker Bay; Fig. 1). The sample collection and DNA isolation were carried out as described in Ehrich et al. (2001). For the six studied localities, census data from six years were available for both lemming species (Fig. 2).

Genetic and statistical analysis

Two types of genetic markers were used, four nuclear microsatellite loci and a sequence fragment of the control region (CR) of the mitochondrial genome (mtDNA). For *Lemmus trimucronatus*, four out of the 19 microsatellite primer sets published for other microtine rodents which we tested (MSCRB-5A, Ishibashi et al. 1997; MSCg-9, Gockel et al. 1997; MMSM-4, Ishibashi et al. 1999 and AV-13, Stewart et al. 1998), gave a polymorphic product and could be scored reliably (Table 1). One of them (MSCRB-5A) was also used for collared lemmings. Eight to 15 individuals were genotyped for each locality. The PCR amplification and electrophoresis of the fragments was carried out as in Ehrich et al. (2001). A 250-bp-long fragment of the first hypervariable part of the mtDNA CR (corresponding to positions 15417–15667 in *Mus*) has been sequenced for 8 to 14 brown lemmings from each locality as described in Ehrich et al. (2000) (Genebank Accession Nos AF323042–AF323046). The collared lemming data are the same as presented in Ehrich et al. (2001). From each locality, 21 to 24 individuals were scored at four microsatellite loci and mtDNA CR sequences were determined for 9 to 10 individuals; data about number of alleles, number of haplotypes, and gene diversity for the four localities from which both lemming species were available are given for comparison in Tables 2 and 3.

For microsatellites, average expected heterozygosities (H_S , unbiased estimate; Nei 1987: 178) and inbreeding coefficients (f) were calculated for each locality using the program Genetix (Belkhir 1999). For each locality and locus, observed genotype proportions were tested against Hardy-Weinberg expectations performing an exact test and estimating a P value by the Markov chain method with GENEPOP 3.1 (Raymond and Rousset 1995). Linkage disequilibrium between all pairs of loci at each locality was tested for using Genetix. For both series of tests the significance level was adjusted through sequential Bonferroni correction (Rice 1989). The genetic population structure was characterised from allele frequen-

cies by estimates of F_{ST} calculated in an analysis of molecular variance (AMOVA) using the Arlequin1.1 software (Schneider et al. 1997). The estimates were tested for significant difference from zero by means of a permutation test exchanging genotypes between populations (10000 replicates).

For mtDNA, the amount of genetic variability was estimated as unbiased haplotype diversity (H_S) and as nucleotide diversity (π) in Arlequin1.1. Genetic differentiation among local populations was assessed by F_{ST} estimates calculated in an AMOVA as for microsatellite data. The analysis was carried out disregarding haplotype nucleotide differences, yielding estimates of F_{ST} corresponding to Weir and Cockerham's (1984) θ (Excoffier et al. 1992). The F_{ST} estimates obtained for brown lemmings from the two types of genetic markers were compared to estimates from the same localities and corresponding genetic markers for the collared lemming.

Results

The microsatellite loci analysed for brown lemmings showed considerable variability in all localities with an average of 5.3 alleles per locus and an average within locality H_S of 0.71 (Table 2). No clear difference in number of alleles per locality or in gene diversity was found between island and mainland populations, although both measures of variability were slightly lower on the two islands. After sequential Bonferroni correction, there were no significant deviations from Hardy-Weinberg genotype proportions in any locality. On Hurd Island, however, a large f -value of 0.27 (Table 2) reflected a homozygote excess, which was significant before performing the Bonferroni correction. Linkage disequilibrium was significant for seven out of 30 intra-population locus comparisons but linkage could not be attributed to a particular pair of loci as significant linkage occurred for most pairs. Hence, physical linkage seemed an unlikely explanation for the observed disequilibrium. Five out of seven cases of significant linkage disequilibrium were found on Hurd island, which can be

Table 1. Reference and species of origin, repeat sequence, total number of identified alleles and PCR conditions for the four microsatellite loci reliably amplified in *Lemmus trimucronatus*. The repeat sequence is given as described for the source species.

Locus	Source	Repeat motif	No. of alleles	MgCl ₂ (mM)	Annealing temp. (°C)
MSCRB-5A	<i>Clethrionomys rufocanus</i> (Ishibashi et al. 1997)	mixture of CA, ATAC and ATGT	12	2.5	54
MSCg-9	<i>C. glareolus</i> (Gockel et al. 1997)	CA (interrupted)	16	1.5	58
MMSM-4	<i>Microtus montbelli</i> (Ishibashi et al. 1999)	CA	13	1.5	52
AV-13	<i>Arvicola terrestris</i> (Stewart et al. 1998)	GATA	10	1.5	52

Table 2. Genetic diversity at four microsatellite loci in *Lemmus trimucronatus* and *Dicrostonyx groenlandicus* (data from Ehrich et al. 2001). The average, minimal and maximal number of alleles per locus, the expected heterozygosity (H_S ; non-biased estimate, Nei 1987) as well as standard deviation, maximal and minimal values, and the inbreeding coefficient f are given for each population.

Species	Locality	n	Alleles		Heterozygosity			f
			Number	Range	H_S	(SD)	Range	
<i>Lemmus trimucronatus</i>	Walker Bay	15	6.3	4–10	0.72	(0.08)	0.6–0.78	–0.068
	Hope Bay	15	7	5–9	0.79	(0.07)	0.7–0.85	–0.02
	Cockburn Isl.	15	4.5	4–5	0.71	(0.08)	0.59–0.76	0.033
	Hurd Isl.	8	3.5	3–4	0.63	(0.05)	0.59–0.69	0.268
	Average		5.3		0.71			overall f : 0.019
<i>Dicrostonyx groenlandicus</i>	Walker Bay	24	9.3	7–10	0.80	(0.04)	0.71–0.83	–0.069
	Hope Bay	22	10.8	9–12	0.86	(0.03)	0.82–0.9	0.074
	Cockburn Isl.	22	10.8	8–14	0.83	(0.08)	0.75–0.92	0.017
	Hurd Isl.	21	11	9–15	0.82	(0.06)	0.73–0.88	0.017
	Average		10.5		0.83			overall f : 0.013

explained by the considerable deviation from Hardy-Weinberg genotype proportions in this small sample.

Five mtDNA CR haplotypes were found among the 50 brown lemmings analysed (Table 3). Most haplotypes differed from their closest neighbour by one base pair change, and provided thus little phylogenetic information and did not warrant further phylogenetic analysis. Genetic variability in the mtDNA CR was relatively low compared to other microtine rodents (e.g. Plante et al. 1989, Stacy et al. 1997) with one to three haplotypes per locality, an average within locality haplotype diversity of 0.25 and an average nucleotide diversity of 0.21 (Table 3).

Both microsatellites and mtDNA revealed significant genetic differentiation in *L. trimucronatus* among the four localities studied with F_{ST} estimates of 0.124 and 0.534, respectively (Table 4). For both types of genetic markers differentiation estimates were clearly higher in brown lemmings than in collared lemmings, for which F_{ST} was 0.047 for microsatellite data and 0.011 for mtDNA (Table 4). The particularly high F_{ST} value for mtDNA in brown lemmings reflects mostly the high frequency of a private haplotype (i.e., haplotype e, a haplotype found only in this locality; Table 3) on Hurd Island. Differentiation among the three other localities was much lower with an F_{ST} of 0.084 ($p = 0.053$). For microsatellite data the 94% confidence intervals of the F_{ST} estimates were mutually exclusive between the two species (Table 4; estimated as the second smallest and the second largest value of all 35 possible ‘bootstrap’ resampling arrangements across the four analysed loci). Pairwise F_{ST} estimates among localities (not reported) showed that also on the basis of microsatellite data, the sample from Hurd was most clearly differentiated. Differentiation was however significant for all pairs of localities with pairwise F_{ST} estimates ranging from 0.082 to 0.226 ($p = 0.001$ or less).

Discussion

The observed difference in mtDNA differentiation between the two species cannot readily be attributed to contemporary ecological factors. The high F_{ST} value observed for brown lemmings (Table 4) is due to the fact that the sample from Hurd Island differed from the three other samples, among which little variation was found (Table 3). The very low F_{ST} estimate for mtDNA data in collared lemmings, on the other hand, is due to an almost complete lack of variability in the sequenced CR fragment among individuals from Kent Region (Table 3), which can be explained by a regional bottleneck during a warmer climatic period in the Holocene, when forested and humid habitat advanced north and resulted in the tundra covering smaller areas (Ehrich et al. 2000).

In general, the magnitude of F_{ST} estimates depends not only on the level of differentiation among subpopulations but also on the total amount of variation and notably the intra-population variability. Variability in mtDNA sequences is strongly influenced by population history, particularly by long-term effective population size (Avice 1994) and thus in some cases fails to give information about contemporary ecological processes. At the studied microsatellite loci, high levels of genetic variability were found within the studied populations for both species. At such intermediate to high levels, higher intra-population variability will lead to lower F_{ST} estimates (e.g. Hedrick 1999). In fact, for the microsatellite loci studied, genetic variability was lower in brown lemmings than in collared lemmings: an average of 5.3 alleles were found per locality and locus for brown lemmings compared to 10.5 for collared lemmings in the same localities and within-locality average gene diversity was 0.71 compared to 0.83 (Table 2).

The level of genetic variability within a population is determined by two factors, mutation rate and effective

population size. To a certain extent both factors also affect the level of differentiation among local populations. High mutation rates may decrease AMOVA F_{ST} estimates by increasing the intra-population variance component more than the inter-population component (Hedrick 1999). Ehrich et al. (2001) demonstrated, however, that a high mutation rate in the order of 5×10^{-3} does not substantially reduce differentiation in local populations of so small effective sizes as estimated for collared lemmings on the small islands in Bathurst Inlet. Hence, differences in mutation rates between the microsatellite loci analysed in both species (which most probably occurred in the present study as different loci were analysed for the two species) are not likely to affect our conclusions regarding differentiation. Smaller populations will on the other hand, in the absence of migration, diverge faster under the action of genetic drift than larger populations.

Brown lemmings were clearly less numerous than collared lemmings in the studied area (Fig. 2). Whereas collared lemmings were captured on all four small islands every year (except on Hurd in 1997), brown lemmings were caught only on Hurd and Cockburn in some years, and did not occur on the two other islands. In the entire region (Kent Peninsula as well as on the small islands) the habitat is relatively dry with only a few wetter areas where the brown lemmings' preferred sedge and grass vegetation is abundant. The observed low numbers of brown lemmings may thus be explained by the low prevalence of wet habitat in the area. Wet habitat is notably absent from Breakwater and Wilmot islands, where no brown lemmings were caught. Populations of both species fluctuated in abundance (Fig. 2). The

average effective size of a fluctuating population (being relevant for the level and distribution of genetic variability) can be approximated by the geometric mean and is thus close to the numbers during the low phase (e.g., Motro and Thomson 1982). In our study, densities seemed particularly low for brown lemmings during the low phase with no individuals trapped in several years at each locality (Fig. 2). In fact population fluctuations of high amplitude and very low densities during the low phase seem to be more typical for brown lemmings than for collared lemmings (Bunnell et al. 1975, Stenseth and Ims 1993b). Such a difference in the pattern of density fluctuations between the two species would result in an additional reduction of the average effective population size for brown lemmings.

Hence, stronger genetic differentiation among populations of brown lemmings observed in this study may, in part, be due to lower average effective population sizes for that species. With even smaller local populations than those estimated for collared lemmings on the islands (Ehrich et al. 2001), genetic differentiation will increase under the action of drift. Also assuming a comparable migration rate (i.e., a comparable proportion of individuals inclined to undertake risky long-distance dispersal), the absolute number of dispersers, which mainly affects the equilibrium value of F_{ST} (Crow and Kimura 1970), will be lower among smaller populations, which again will contribute to increased differentiation. The differences in average effective population size between the two species, make it difficult to assess to what extent the observed higher genetic differentiation in brown

Table 3. Number of mtDNA CR haplotypes, haplotype diversity (H_S) and nucleotide diversity (π in %) with standard deviations observed in *Lemmus trimucronatus* and *Dicrostonyx groenlandicus* (data from Ehrich et al. 2001) at each locality. n : sample size. The sequences are accessible in the Genebank (Accession Nos AF323042–AF323046 and AF121820–AF121822).

<i>Lemmus trimucronatus</i>								
Locality	n	Haplotypes					H_S (SD)	π in % (SD)
		a	b	c	d	e		
Walker Bay	14	10	2	2			0.48 (0.14)	0.32 (0.28)
Hope Bay	14	12			2		0.26 (0.14)	0.32 (0.28)
Cockburn Isl.	14	14					0	0
Hurd Isl.	8			1		7	0.25 (0.18)	0.2 (0.22)
						Average	0.25	0.21
<i>Dicrostonyx groenlandicus</i>								
Locality	n	Haplotypes			H_S (SD)	π in % (SD)		
		a	b	c				
Walker Bay	10	10			0	0		
Hope Bay	10	9	1		0.20 (0.15)	0.08 (0.06)		
Cockburn Isl.	9	9			0	0		
Hurd Isl.	10	8	1	1	0.38 (0.18)	0.16 (0.08)		
					Average	0.15	0.06	

Table 4. Genetic differentiation among the four localities in Kent Region for which samples from both lemming species were available. F_{ST} was estimated using AMOVA (Excoffier et al. 1992). The significance level was determined as the proportion of 10 000 permutation results larger than the observed estimate, $p > 0.1$ is not mentioned. An exact 94% confidence interval was estimated for the microsatellite data resampling across the four loci.

Species	Microsatellites (multilocus estimate)		mtDNA CR
	F_{ST}	CI	F_{ST}
<i>Lemmus trimucronatus</i>	0.124 $p < 0.0001$	0.074–0.17	0.534 $p < 0.0001$
<i>Dicrostonyx groenlandicus</i>	0.047 $p < 0.0001$	0.027–0.062	0.011

lemmings implies a lower migration rate in this species. As the brown lemmings' habitat is more scarce in the studied area, the habitat patches probably have to be considered even more isolated for this species than for collared lemmings. It is thus very unlikely for a potential migrant brown lemming to move from one habitat patch to another.

Although collared lemmings inhabit the islands in Bathurst Inlet permanently, it is possible that the rarer brown lemming only occasionally establishes small populations on those islands, experiencing strong genetic drift and relatively soon going extinct. The sample from Hurd, which was clearly different from the three other samples on the basis of both genetic marker types, may represent a particularly isolated small population founded by a few individuals. The considerable excess of homozygotes and significant linkage disequilibrium in five out of six pairwise loci comparisons observed in this sample, may also be an indication that the effective size of this population is very small. The sample from Cockburn might represent a more recently established island population.

To conclude, it is likely that – in the case of our study – the stronger genetic differentiation among local populations of brown lemmings than among populations of collared lemmings reflects both a lower average effective population size and a lower absolute number of migrants among localities. Because of differences between species in effective population size and habitat availability our data do not allow us to draw any firm conclusions about differences in migration rate and about the relative importance of migration versus effective population size in shaping the observed genetic structures. However, circumstantial evidence suggests that differences in dispersal behaviour might indeed be one of the causal factors.

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