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Spatial structure of lemming populations (*Dicrostonyx groenlandicus*) fluctuating in density

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Abstract

The pattern and scale of the genetic structure of populations provides valuable information for the understanding of the spatial ecology of populations, including the spatial aspects of density fluctuations. In the present paper, the genetic structure of periodically fluctuating lemmings (*Dicrostonyx groenlandicus*) in the Canadian Arctic was analysed using mitochondrial DNA (mtDNA) control region sequences and four nuclear microsatellite loci. Low genetic variability was found in mtDNA, while microsatellite loci were highly variable in all localities, including localities on isolated small islands. For both genetic markers the genetic differentiation was clear among geographical regions but weaker among localities within regions. Such a pattern implies gene flow within regions. Based on theoretical calculations and population census data from a snap-trapping survey, we argue that the observed genetic variability on small islands and the low level of differentiation among these islands cannot be explained without invoking long distance dispersal of lemmings over the sea ice. Such dispersal is unlikely to occur only during population density peaks.

Keywords: Canadian Arctic, *Dicrostonyx groenlandicus*, dispersal, gene diversity, gene flow, small rodent cycles

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Introduction

Populations may be structured on a small scale with very little interbreeding among local units separated by a few kilometers (Aars *et al*. 1998), or they can be structured on a much larger scale with regular dispersal occurring over considerable distances (e.g. Petit & Mayer 1999). In principle, different scaling and levels of gene flow may be investigated with genetic markers. However, it is necessary to be cautious when linking gene flow to actual movement (Whitlock & Mccauley 1999). A small number of effective migrants per generation is sufficient to prevent strong genetic differentiation among populations. In a continuous habitat, gene flow may take place over large distances without individual long distance movement through stepping-stone dispersal (Kimura & Weiss 1964). In a fragmented area it is different; little genetic differentiation among habitat patches implies migration among these patches. In an isolated population, genetic variability will be maintained against random genetic drift only if the effective population size is large and mutation rates are high.

The genetic structure of populations reflects many aspects of their ecology, including past and present demography, interactions with habitat and landscape, social structure and migration. Knowledge about the genetic structure can, therefore, contribute new insight in the functioning of populations in general and the spatial aspects of population processes in particular. The spatial aspects of population density fluctuations have recently been addressed through theoretical examination and empirical description (Bjørnstad *et al*. 1996, 1999; Steen *et al*. 1996; Stenseth *et al*. 1998). The marked density fluctuations typical of small rodents should have a strong effect on the genetic structure, as during the low phases of the cycle populations experience repeated bottlenecks and their long-term genetically effective size is thus considerably reduced (e.g. Motro & Thomson 1982). In turn knowledge of the genetic structure of fluctuating or cyclic species may contribute to the understanding of the mechanisms underlying their dynamics and notably the role dispersal

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plays in synchronizing density fluctuations in space (Stacy *et al*. 1997).

The focus of the present paper is to examine the genetic population structure of a species well known for its multiannual density fluctuations, the North American collared lemming, *Dicrostonyx groenlandicus* (Traill, 1823) (Finerty 1980; Krebs 1993; Stenseth & Ims 1993a), in order to better understand its spatial ecology. This arctic microtine rodent typically experiences fluctuations in amplitude from 25 to 200-fold over a period of 3–5 years (Pitelka 1973; Krebs 1996). These periodic multiannual fluctuations have an impact on many other organisms (e.g. Hansson & Henttonen 1988; Underhill *et al*. 1993) and lemmings may, therefore, play a key role in the arctic ecosystem (e.g. Stenseth & Ims 1993b). The phenomenon of cyclic density fluctuations have long attracted the attention of biologists, and the discussion on the mechanism(s) underlying them is still ongoing (e.g. Stenseth & Ims 1993c; Krebs 1996; Stenseth 1999). Because of these population cycles, microtine rodents — and lemmings in particular — have become model organisms for theoretical research in population dynamics (e.g. May 1972; Stenseth *et al*. 1998).

Because of the very low population densities experienced by cyclic rodents in the low phase (Boonstra *et al*. 1998), one could expect reduced genetic variability and considerable local differentiation in such species. The few studies that have addressed the genetic structure of cyclic microtine rodent populations found considerable differentiation between local units separated by as little as 100 m (Plante *et al*. 1989) to a few kilometers (Stacy *et al*. 1997; Aars *et al*. 1998), in agreement with the expected effect of these low densities and presumably low average effective population size. On the other hand, in a peak year the assumed local units may expand geographically, and one could imagine more movement and contact at such times. Relative to other microtines, few data are available on the spatial aspects of lemming populations. The studies that have been performed to measure movement in lemmings were mainly designed to determine activity patterns and home range size, and were limited to the short arctic summer (Rodgers 1990; Brooks & Banks 1971; Brooks 1993). They report individual movement rarely exceeding a few hundred meters.

Here we examine the genetic structure of fluctuating collared lemming populations in the central Canadian Arctic and address the following questions: (i) how important is local differentiation in comparison to regional differentiation; (ii) is genetic diversity reduced on small islands and how isolated are small islands genetically; and (iii) how much gene flow is there in a continuous habitat and at what distance is similarity between local populations reduced? Answering these questions will enable us to further understand the spatial ecology of these lemming populations and to contribute to the understanding of spatial processes of cyclic populations in general.

Materials and methods

Study area and sample collection

Tissue samples from collared lemmings were collected at 14 localities in the Canadian Arctic in 1996 and 1997, with a few additional samples collected in 1998 (cf. Tables 3 and 4). The study area included one region in the central Canadian Arctic with two mainland localities (Walker Bay and Hope Bay) and four small islands in Bathurst Inlet (Breakwater, Cockburn, Hurd and Wilmot Islands) referred to as the Kent Region, six localities on the southern part of Victoria Island, and an island and a mainland locality situated on the Anderson Peninsula, 700 km to the west (Fig. 1). The Kent Region was chosen for its fragmented habitat, and the small islands in this region were selected for their apparent isolation. The coastal habitat of both islands and the mainland in Bathurst Inlet consists mostly of bare rock, which constitutes large inhospitable areas between suitable lemming habitats (Table 1). The sea in this area is frozen eight months of the year. The sites on the large Victoria Island, on the other hand, are in continuous tundra, and thus in a suitable setting to address on what scale distance, rather than barriers, acts to isolate populations. The Anderson Peninsula was chosen for its remoteness from the rest of the study area. In all three regions lemming populations undergo strong multiannual density fluctuations, including the small islands (see below). The fluctuations were, to a certain extent, synchronous between the Kent Region and Victoria Island, whereas on Anderson Peninsula they were out of phase (Wilson *et al*. 1999; CJ Krebs *et al*. unpublished).

Liver and kidney tissues were sampled from snap-trapped animals. In 1996, samples were packed in snow until they could be placed in a freezer. In 1997, the samples were instead stored in 70% ethanol. Total genomic DNA was isolated from the collected tissue using a standard proteinase K and phenol–chloroform extraction, or alternatively by the use of proteinase K digestion, NaCl precipitation of proteins and DNA precipitation with isopropanol (Miller *et al*. 1988).

Genetic analysis

Two types of genetic markers were used, the control region (CR) of the mitochondrial genome (mtDNA) and four nuclear microsatellite loci. The mtDNA CR is a relatively fast evolving DNA segment that has been widely used in studies of population structure (e.g. Avise 1994). In general, mtDNA is maternally transmitted, and information about population structure obtained from this marker refers to females only. 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 9–13 individuals from each locality as described in Ehrich *et al*. (2000).

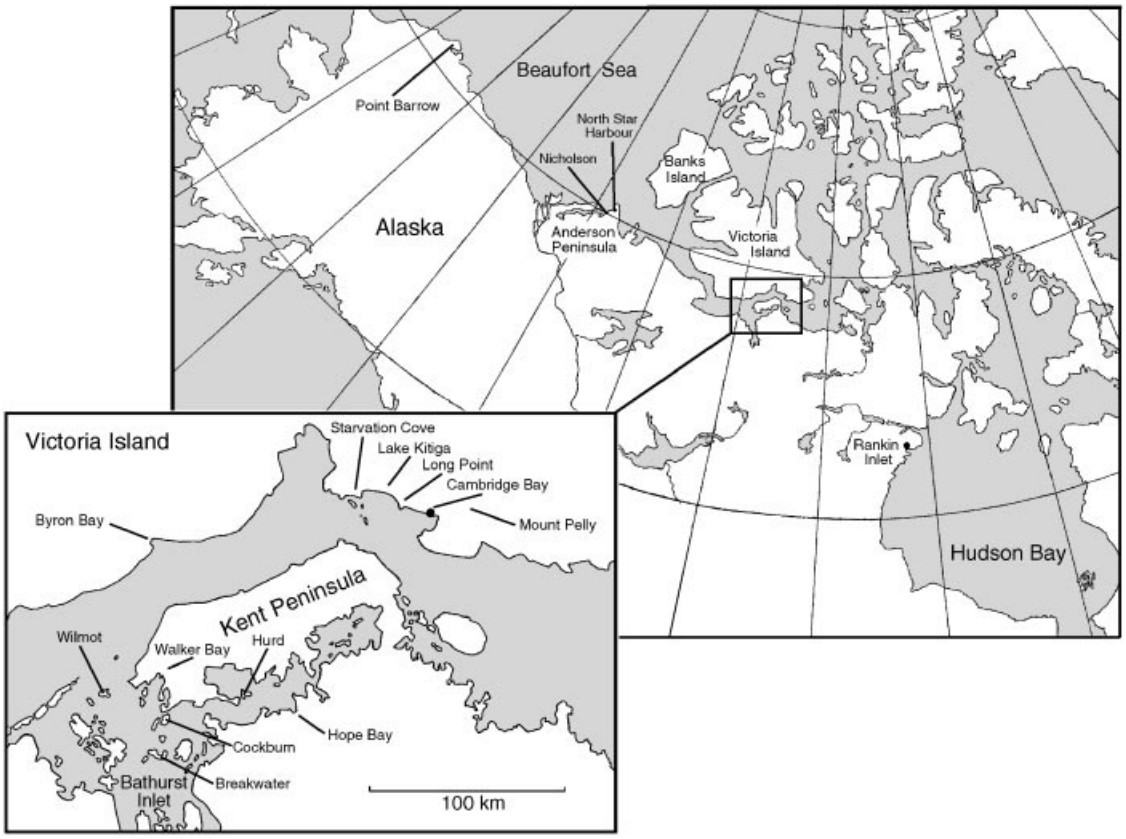


Fig. 1 Map of the study area in the central Canadian Arctic (North-west Territories). Coordinates of the localities where the samples were collected: Walker Bay, 68°22′ N/108°08′ W; Hope Bay, 68°55′ N/108°30′ W; Breakwater Isl., 68°06′ N/106°43′ W; Cockburn Isl., 68°05′ N/108°18′ W; Hurd Isl., 68°13′ N/107°20′ W; Wilmot Isl., 68°12′ N/109°05′ W; Mount Pelly, 69°12′ N/104°45′ W; Cambridge Bay, 69°07′ N/105°05′ W; Long Point, 69°06′ N/105°26′ W; Lake Kitiga, 69°10′ N/105°37′ W; Starvation Cove, 69°09′ N/105°57′ W; Byron Bay, 68°45′ N/109°04′ W; North Star Harbour, 70°15′ N/127°37′ W; Nicholson Isl., 69°55′ N/128°59′ W.

Table 1 Characteristics of the four islands in Bathurst Inlet where samples were collected. The total area of each island is given along with an estimate of the area of suitable lemming habitat. Approximate peak and low population sizes for the collared lemming are estimated for each island based on a range of 1–4 lemmings/10 ha in the low phase and 100–300 lemmings/10 ha in the peak of the cycle

Island	Total area (ha)	Lemming habitat (ha)	Estimated number of lemmings		Distance to nearest lemming habitat
			Low phase	Peak phase	
Breakwater	2180	331	33–132	3300–10000	10 km to another island 20 km to the mainland
Cockburn	1767	353	35–140	3500–10500	2.3 km to either
Hurd	1580	632	63–252	6300–19000	2.5 km to another island 10 km to the mainland
Wilmot	1042	408	41–163	4100–12300	20 km to the mainland

Microsatellite loci are nuclear noncoding DNA segments with high mutation rates, segregating for alleles that vary in the number of tandem repeats of motifs that are a few base pair long (Jarne & Lagoda 1996; Goldstein & Schlötterer 1999). As microsatellite primers have been reported to amplify polymorphic loci in closely related species (e.g. Ishibashi *et al*. 1997 for small rodents), we tested 20 primer sets published for other microtine rodents. Four of them, MSCRB-5A, MSCRB-6, AV-9 and AV-15 (Ishibashi *et al*. 1997; Stewart *et al*. 1998; Table 2), gave a polymorphic product in *Dicrostonyx groenlandicus* and could be scored reliably. The forward primer was end-labelled with [γ^{32}P]-ATP.

Table 2 Species of origin, reference, repeat motif, PCR conditions and total number of alleles identified for the four microsatellite loci that were reliably amplified in *Dicrostonyx groenlandicus*. The repeat motif is given as described for the source species

Locus	Source	Repeat motif	Annealing temp.	No of alleles
MSCRB-5A	*Clethrionomys rufocanus* (Ishibashi *et al*. 1997)	mixture of CA, ATAC and ATGT	54 °C	19
MSCRB-6	*C. rufocanus* (Ishibashi *et al*. 1997)	mixture of AC and AG	54 °C	28
AV-9	*Arvicola terrestris* (Stewart *et al*. 1998)	GATA	52 °C	14
AV15	*A. terrestris* (Stewart *et al*. 1998)	GATA	54 °C	15

The following primer sets were tested but could not be used: MSCRB-2, MSCRB-3, MSCRB-4 and MSCRB-7 (*C. rufocanus*, Ishibashi *et al*. 1997); MSCg-9, MSCg-15, MSCg-19, MSCg-20 (*C. glareolus*, Gockel *et al*. 1997); MSMM-2, MSMM-3, MSMM-4, MSMM-6 (*Microtus montbelli*, Ishibashi *et al*. 1999); AV-7, AV-12, AV-13, AV-14 (*A. terrestris*, Stewart *et al*. 1998).

Polymerase chain reaction (PCR) amplifications were carried out in a total volume of 10 μL, which contained 0.5 μM of each primer, a small amount of template DNA, 75 mM Tris-HCl (pH 8.8), 20 mM $(NH_4)_2SO_4$, 0.2 mM dNTP, 2.5 mM $MgCl_2$ and 0.25 units *Taq* polymerase (Advanced Biotechnologies, Surrey, UK). The PCR programme was 5 min at 94 °C, followed by 30–35 cycles of 30 s at 94 °C, 30 s at the annealing temperature (Table 2) and 1 min at 72 °C, then a final 5 min at 72 °C. The fragments were resolved by electrophoresis on 6% polyacrylamide gels, and exposed to X-ray films. Microsatellites were analysed for 7–24 individuals from each locality.

Statistical analysis

mtDNA data. The amount of genetic variability (H_S) was estimated as unbiased haplotype diversity using ARLEQUIN 1.1 software (Schneider *et al*. 1997). Genetic variability patterns across localities and larger regions were assessed by F_{ST} values estimated in an analysis of molecular variance (AMOVA; Excoffier *et al*. 1992) using Arlequin 1.1. The analysis was carried out disregarding haplotype nucleotide differences, yielding estimates of F_{ST}, and including the number of pairwise nucleotide differences among haplotypes, estimating Φ_{ST} (Excoffier *et al*. 1992). Genetic variation was partitioned into components accounting for variability among the three regions (Kent Region, Victoria Island and Anderson Peninsula: F_{RT}), among localities within each regions (F_{SR}), and within localities. The estimates were tested against the null-hypothesis of no differentiation by means of a permutation test exchanging haplotypes between populations or populations between regions (10 000 replicates). In addition F_{ST} values were calculated for pairs of localities within Victoria Island, the only region where mtDNA variability was sufficient to examine the intraregional structure (Table 3). In order to obtain estimates comparable to the estimates based on microsatellite data (see below), the number of nucleotide differences between haplotypes was not taken into account in this part of the analysis. Genetic divergence was analysed spatially by plotting pairwise estimates of $F_{ST}/(1 - F_{ST})$ against the logarithm of geographical distances among sites (Rousset 1997). A Mantel test was performed to test for significance of the correlation between genetic differentiation and the logarithm of geographical distance matrix using the program GENEPOP 3.1 (Raymond & Rousset 1995). In addition probabilities of identity among individuals within and among localities (F_d; Stacy *et al*. 1997) were calculated for the Victoria Island sites and plotted against geographical distance.

Microsatellite data. Average expected heterozygozyties (H_E, unbiased estimate; Nei 1987 p. 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 the *P*-value by the Markov chain method with GENEPOP 3.1. 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 using sequential Bonferoni correction (Rice 1989). Genetic population structure was characterized from allele frequencies by means of AMOVA estimates of *F*-statistics as for the mtDNA data. Pairwise F_{ST} values were calculated according Weir & Cockerham (1984) among all pairs of localities with GENEPOP 3.1 and used to examine isolation by distance as above.

Estimation of island population size

On the four small islands in Bathurst Inlet (Fig. 1, Table 1) collared lemming populations were censused over 6 years. The census was carried out with snap-trap lines using a standard protocol (Krebs & Wingate 1985) once each year in spring, starting in 1994. Six lines of 285 m length were surveyed with 20 stations spaced at 15 m intervals. Three Museum Special snap traps baited with peanut butter and

Table 3 Number of mtDNA control region haplotypes observed in *Dicrostonyx groenlandicus* at each locality and haplotype diversity H_S (standard deviation) according to Nei (1987). H_T: total gene diversity

Region	Locality	Sample year	*n*	No of haplotypes	H_S
Kent Region	Walker Bay	1996	10	1	0
	Hope Bay	1996	10	2	0.20 (0.15)
	Breakwater Isl.	1996	9	1	0
	Cockburn Isl.	1996	9	1	0
	Hurd Isl.	1996	10	3	0.38 (0.18)
	Wilmot Isl.	1996	10	1	0
			Average	1.5	0.10 (0.16)
Victoria Island	Mount Pelly	1997	11	3	0.73 (0.07)
	Cambridge Bay	1997	12	3	0.55 (0.15)
	Long Point	1997	12	2	0.30 (0.15)
	Lake Kitiga	1997	12	2	0.30 (0.15)
	Starvation Cove	1997	13	3	0.41 (0.15)
	Byron Bay	1996	11	4	0.78 (0.07)
			Average	2.8	0.51 (0.21)
Anderson Peninsula	North Star Harbour	1996	11	1	0
	Nicholson Isl.	1996–97	11	1	0
			Average	1	0
				Average H_S	0.20 (0.27)
				Average H_T	0.70 (0.02)

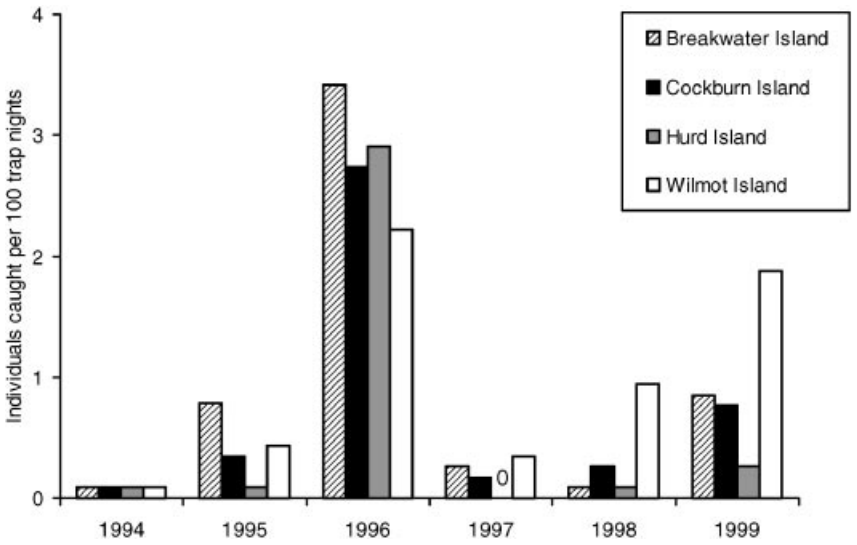


Fig. 2 Collared lemming trapping indices for 1994–1999 from the four small islands in the Kent Region.

raisins were set at each station within a 2-m radius. Separate lines were located at least 100 m apart and the total area covered by the lines was at least 10 hectares. Traps were checked once a day for three days. Populations fluctuated clearly on all four islands. Trapping indices (number of animals caught per 100 trap nights) are shown in Fig. 2. A relation between the number of animals caught in snap-trap lines and densities was estimated at Walker Bay (Fig. 1), where lemming populations were studied using live trapping and densities were estimated from mark recapture data on grids adjacent to snap-trap lines set up as mentioned above (CJ Krebs *et al*. unpublished; Wilson *et al*. 1999). The amount of lemming habitat (defined as habitat in which lemmings were captured in snap-trap lines) was estimated for each island from aerial photographs, and approximate peak and low population sizes were estimated from snap-trap catches (Table 1).

Results

mtDNA

Nine different haplotypes were found among the 151 individuals analysed (Appendix I; EMBL Database Accession

Table 4 Genetic differentiation among regions and between localities within regions. *F* values were estimated using AMOVA. The significance level was determined as the proportion of 10 000 permutation results larger than the observed estimate, $P > 0.1$ is not mentioned. A rough 94% confidence intervall (CI) was estimated as the second smallest and the second largest value of all 35 possible 'bootstrap' resampling arrangements across the four analysed loci

		mtDNA control region				Microsatellites		
		F		Φ (pairwise differences)		*F* multilocus		CI
Among Regions F_{RT}		0.664	$P < 0.001$	0.781	$P < 0.001$	0.074	$P < 0.001$	0.019–0.125
Among localities	Kent Region	0.012		−0.019		0.047	$P < 0.001$	0.032–0.059
within regions F_{SR}	Victoria	0.135	$P = 0.001$	0.073	$P = 0.016$	0.03	$P < 0.001$	0.027–0.034
	Anderson	—		—		0.035	$P = 0.025$	0.024–0.051

nos AF121820–AF121828). Each of the three geographical regions was characterized by a prevailing haplotype, with a few rarer types occurring in the Kent Region and on Victoria Island. Most haplotypes differed from their nearest neighbour by one substitution and provided too little phylogenetic information to permit a detailed phylogeographic analysis within the study area. In a wider area, however, covering most of North America, more mtDNA haplotypes were found and a phylogeographic analysis of *Dicrostonyx groenlandicus* is presented by Ehrich *et al*. (2000).

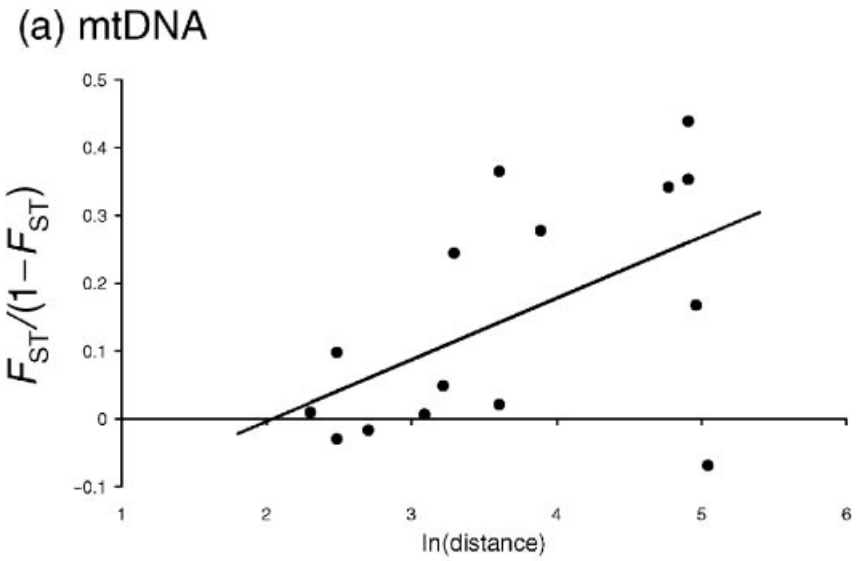
Overall genetic variability in the mtDNA CR was low with only a single haplotype detected in six out of the 14 localities (Appendix I). Lemmings from Victoria Island appeared more variable than those from the other two regions, with an average within-locality haplotype diversity (H_S) of 0.51 (Table 3). Because a different common haplotype occurred in each region, differentiation was strong and highly significant between regions ($F_{RT} = 0.664$; Table 4). Differentiation among localities within regions was weaker and significant only on Victoria Island ($F_{SR} = 0.135$; Table 4) due to lack of variation in the other regions. Taking into account nucleotide differences among haplotypes in the AMOVA, an even larger proportion of genetic variability (78%; $\Phi_{SR} = 0.781$) could be attributed to differences between regions, indicating that closely related haplotypes were grouped regionally.

On Victoria Island pairwise estimates of $F_{ST}/(1 - F_{ST})$ values for mtDNA increased significantly with the logarithm of geographical distance (Fig. 3a; Mantel test $P = 0.04$) indicating increasing genetic differentiation with distance. At the same time, the probability of identity among individuals decreased with distance (Spearman's $r = -0.86$, $P = 0.001$) and reached a low value at about 50 km (Fig. 4). The sites did not, however, consistently group according to geographical proximity, because lemmings from Mount Pelly and Byron Bay (the most distant localities) did not differ from each other but were different from all the other localities (although Mount Pelly did not differ significantly from the neighbouring Cambridge Bay).

Microsatellites

The analysed microsatellite loci were very variable with between 14 and 28 alleles per locus (Table 5, Appendix II). Genetic variability was high in all localities with an average of 8.6 alleles per locus and an average within locality H_E of 0.78 (Table 5). No significant difference in number of alleles per locality or in gene diversity (H_E) was detected between small island and mainland populations in the Kent Region and on Anderson Peninsula (the average number of alleles in the Kent Region was 10.4 and average H_E was 0.83 on the four small islands; Table 5). There were no significant deviations from Hardy–Weinberg genotype proportions at any locus in any locality. Linkage disequilibrium was significant for nine of the 84 within locality locus comparisons but linkage could not be attributed to a particular pair of loci as significant values occurred for most pairs. Hence, physical linkage seemed an unlikely explanation for the observed disequilibrium. Significant disequilibrium values were not particular to any locality, however, among the nine observed cases, six occurred on small islands (Breakwater, Cockburn and Hurd).

Differentiation between regions was significant, but the estimated F_{RT} of 0.074 was much lower than for the mtDNA data (Table 4) and estimates varied considerably among loci (data not shown). Among localities within regions differentiation seemed weaker than among regions, in concordance with the findings from mtDNA, and estimates varied less among loci. As indicated by the 94% confidence interval (Table 4; estimated as the second smallest and the second largest value of all 35 possible 'bootstrap' resampling arrangements across the four analysed loci), intraregional F_{SR} values did not differ between regions. The F_{SR} estimates tended however, to be highest in the fragmented Kent Region and lowest on Victoria Island. Whereas in the Kent Region all pairwise F_{ST} estimates were significantly different from zero ($P \leq 0.01$ in a permutation test), only seven of the 15 locality pairwise comparisons gave an estimate that was significant at this level on Victoria Island. The observed overall F_{SR} of 0.047



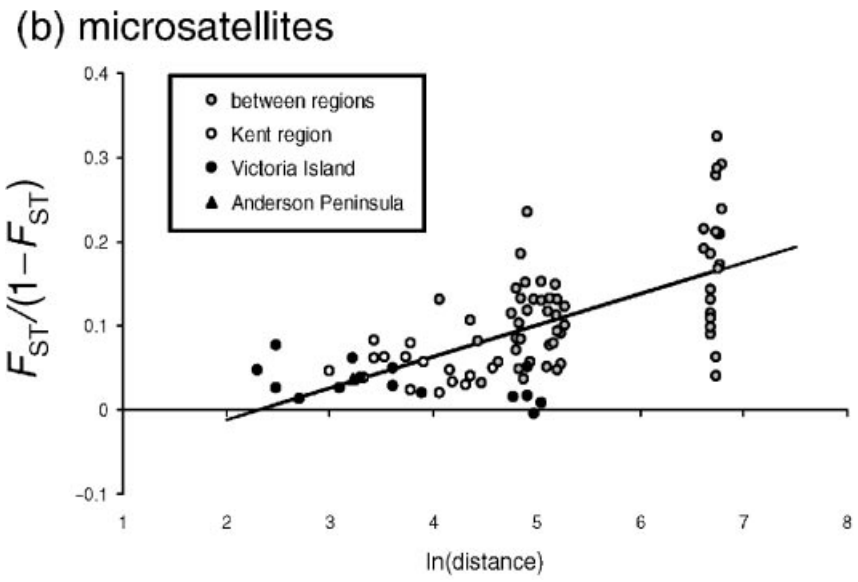


Fig. 3 Differentiation with distance among pairs of localities. (a) Pairwise differentiation estimates from mtDNA CR haplotypes between the six localities from Victoria Island are plotted against logarithm of geographical distance. The fitted regression is $F_{ST}/1 - F_{ST} = -0.18 + 0.09$ ln(distance). (b) Multilocus pairwise differentiation estimates from microsatellite data between all 14 localities are plotted against logarithm of geographical distance. The fitted regression is $F_{ST}/1 - F_{ST} = -0.086 + 0.037$ ln(distance).

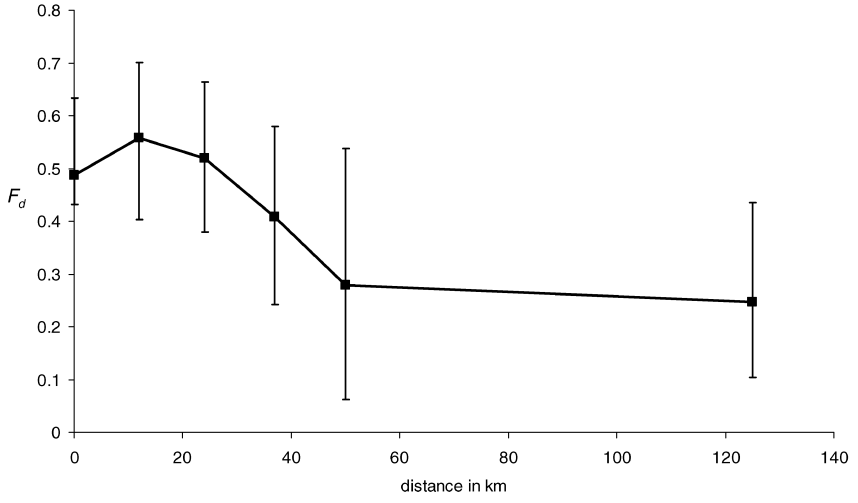


Fig. 4 Probabilities of mtDNA haplotype identity (F_d) for individuals separated by various geographical distances. The error bars represent 95% confidence intervals for the point estimates, based on bootstrap replicates resampled among the individual haplotypes from each locality.

Table 5 Genetic diversity at four microsatellite loci in *Dicrostonyx groenlandicus*. The number of alleles per locus, the expected (H_E) heterozygozity (non biased estimate, Nei 1987 p.178) with standard deviation, as well as the inbreeding coefficient *f* are given for each population. Average values are shown for each region as well as an overall average (calculated as average of the 3 regional values). Samples include those screened for mtDNA and additional ones collected in the same year, as well as a few sampled in 1998 at the localities indicated by *

			Alleles per locus		Heterozygozity		
Region	Locality	*n*	Number	Range	H_E (SD)	Range	*f*
Kent Region	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
	Breakwater Isl.	24	10.8	7–14	0.86 (0.03)	0.81–0.88	0.05
	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
	Wilmot Isl.*	24	9.3	6–14	0.79 (0.08)	0.71–0.89	0.079
	Average		10.3		0.83		overall F_{IS} 0.029
Victoria Island	Mount Pelly	11	7.8	4–15	0.72 (0.32)	0.24–0.94	0.131
	Cambridge Bay	16	9	4–12	0.78 (0.16)	0.55–0.89	−0.024
	Long Point	17	8.3	5–12	0.79 (0.11)	0.69–0.84	−0.082
	Lake Kitiga	17	6.5	6–12	0.68 (0.18)	0.48–0.86	0.041
	Starvation Cove	17	9	4–8	0.74 (0.22)	0.41–0.89	0.07
	Byron Bay	17	9	6–11	0.77 (0.22)	0.44–0.93	0.044
	Average		8.3		0.75		overall F_{IS} 0.021
Anderson	North Star Harbour	17	8	6–12	0.74 (0.18)	0.49–0.89	0.026
Peninsula	Nicholson Isl.	7	6.3	5–8	0.80 (0.1)	0.7–0.91	−0.026
	Average		7.2		0.77		overall F_{IS} 0.01
	Average		8.6		0.78		overall F_{IS} 0.025

among localities in the Kent Region was nevertheless quite low and implies a considerable amount of gene flow (see below).

In contrast to the findings for mtDNA, for microsatellites no pattern of isolation with distance was found within either region (Fig. 3b; Mantel test $P = 0.9$ in the Kent Region and $P = 0.95$ on Victoria Island). Only when including all pairs of populations, also those of different regions, there was a significant correlation between the geographical distance and the degree of genetic differentiation (Fig. 3b; Mantel test $P = 0.0004$). This correlation results from the higher differentiation estimates among localities from different regions, which are separated by larger geographical distances, and thus confirms the stronger differentiation among regions found for the mtDNA data.

Discussion

The general pattern of spatial genetic structure revealed by our study is clearly hierarchical, consisting of three large genetically differentiated regions, in which the local populations are relatively more similar to each other. This pattern was evident from mtDNA as well as from microsatellite data, although interregional differentiation was weaker for microsatellites. Levels of variation at the mtDNA control region were generally low compared to other small rodents, in particular in the Kent Region and on Anderson Peninsula (cf. Table 3; Jaarola & Tegelström 1995; Stacy *et al*. 1997). Microsatellites, on the other hand, were highly variable in all regions and localities, even on small islands. The observed pattern suggests well-isolated regions with considerable gene flow within them acting to maintain genetic variation within localities against drift and to homogenize allele frequencies among localities. We attribute the low mtDNA variability to a possible historical bottleneck in parts of the range of this species, as discussed in detail by Ehrich *et al*. (2000), and presume that the microsatellites have regained their high variability from mutations since this time. Because of the low mtDNA variability, we base the following discussion on the microsatellite data only.

Isolation and dispersal in island populations: theoretical considerations

Here, we evaluate what implications the genetic statistics estimated from microsatellite data have for the lemming populations on the small islands of the Kent Region. In this region the fragmented landscape comes close to the theoretical 'island model' and allows us to analyse local populations that are clearly separated (Fig. 1, Table 1).

Levels of genetic variation. The microsatellite data show strikingly high levels of genetic variability on each small island, both with respect to number of observed alleles and to gene diversity (H_E) estimates (Table 5). To evaluate the possibility that mutations could be responsible for the high observed levels of genetic variation we tentatively adopt

one of the highest reported mutation rates for microsatellite loci, $v = 5*10^{-3}$ (humans; Satoh *et al*. 1996), typical estimates being 10 times lower (cf. Goldstein & Schlötterer 1999). Assuming a closed population, the genetically effective population size required to balance H_E against loss due to drift can be calculated from the expected equilibrium relationship (Crow & Kimura 1970; p. 323):

$$E(H) = \frac{M}{M+1} \quad (1)$$

where $M = 4N_e v$, N_e is the long-term average effective population size and v is the mutation rate. Substituting the observed average $H_E = 0.83$ (Table 5) for its expectation into eqn 1 and solving for M yields $4N_e v = 4.9$, implying an effective size in the order of $N_e = 245$ on average per generation for the assumed mutation rate.

Another way of assessing the required effective population size for mutations to balance loss of genetic variation due to drift is to focus on the number of alleles, using Ewens' sampling formula (Ewens 1972) for the expected number of alleles:

$$E(a) = \frac{M}{M} + \frac{M}{M+1} + \frac{M}{M+2} + \ldots + \frac{M}{M+2n-1} \quad (2)$$

where $M = 4N_e v$ as before and n is the number of sampled individuals from each locality ($n = 22$; Table 4). Substituting the observed average of $a = 10.4$ for its expectation into eqn 2 yields $M = 4$, corresponding to an effective size of about $N_e = 200$, in reasonably good agreement with the previous result.

The above calculations indicate that if genetic variation is maintained through high mutation rates in isolated populations, the genetically effective size of the island populations must be at least 200–250. As the average effective size of a fluctuating population is usually close to the numbers during the low density phase (Motro & Thomson 1982), which are estimated to be approximately 50 for these islands (Table 1), it seems unlikely that mutation alone can explain the high observed genetic variability. This point is highlighted by the finding that the genetically effective size of a population is generally considerably smaller than the actual number of individuals (e.g. Frankham 1995).

If high mutation rates do not seem to explain the high observed genetic variability, they are even less likely to explain the relative similarity of allele frequencies among the localities. Rather, the low F_{SR} found represents evidence for considerable gene flow among localities. Thus, in the case of the Kent Region, migration to and among islands seems necessary to explain the observed genetic patterns.

Required amount of migration. An indication of the required level of gene flow (m) to maintain an $F_{SR} = 0.047$ (Table 4) may be obtained from the recurrent relation of F (cf. Crow & Kimura 1970; p. 269):

$$F_t = \left(\frac{1}{2N_{t-1}} + \left(1 - \frac{1}{2N_{t-1}}\right)F_{t-1}\right)(1 - m_{t-1})^2 \quad (3)$$

where m_t is the rate of exchange of migrants in generation t and N_t is the effective population size in that generation. The required proportion of migrants (m) per generation can be found by iterating eqn 3 until an equilibrium F value corresponding to the observed one is found. Migration among localities might occur either every year, only at peak densities, or only during the low phase of the population cycle. Based on the estimates from Table 1 and the fact that the genetically effective size is generally less than the actual number of individuals (e.g. Frankham 1995), we assumed a population of 50 in three consecutive low years and 5000 in the fourth year, the peak year.

As long as m is much smaller than unity, only the product Nm (i.e. the number of migrants) affects the equilibrium value of F (Crow & Kimura 1970). Assuming migration every year, to reach the observed $F_{SR} = 0.047$ (94% CI: 0.032–0.059) $Nm = 4.4$ migrants (CI: 3.5–6.3) is required every generation. If migration occurs only during low years, the number of migrants required per generation is about the same ($Nm = 4.5$). If local population sizes during the low phase is as small as estimated for the islands (Table 1), the result of $Nm = 4$ implies that an appreciable proportion of animals must be exchanged every generation. Assuming that migration occurs only in years of peak density, a substantially larger number of migrants estimated as 1150 individuals (i.e. more than 20% of the population) would have to be exchanged among localities during every peak in order to compensate for genetic drift and divergence during the low years.

While subject to a number of simplifying assumptions, such as selective neutrality, numerical iterations indicate that these values are quite robust to assumptions about generation time, population density and shape of the cycle. If the effective population size in the low years is, for example, assumed to be 200 instead of 50, $Nm = 4.8$ migrants is needed in every generation in order to maintain F_{SR} as low as observed over a longer period of time. Mutation could also interfere with the estimation of gene flow from F_{ST} values. In fact F_{ST} is always lower than $1 - H_E$, the expected heterozygozity, which in turn is determined by N_e and the mutation rate as in eqn 1 (Hedrick 1999). In the case of our small island populations, however, the incorporation of mutation into the recurrent relation of F (replacing $(1 - m_{t-1})^2$ by $(1 - m_{t-1} - v)^2$ in eqn 3 does not change the resulting estimate of Nm in a significant way: for migration every year, the previously assumed effective population sizes ($N_e = 50$ in low years and 5000 in peak years) and a mutation rate of $5*10^{-3}$, $Nm = 4.1$ effective migrants per generation would be needed to keep the small populations at the observed low level of divergence. In addition, because of the repeat structure of microsatellites (Goldstein & Schlötterer 1999), mutation at these loci often does not create distinguishable new alleles but alleles identical to those present

or having been present in the population. For microsatellites, mutation can thus, to a certain extent, reduce differentiation resulting from genetic drift. In the case of the Kent Region however, for a mutation rate as assumed above, this effect does not seem sufficient to explain the low observed differentiation without migration.

A largely independent method for estimating the number of migrants on the basis of genetic data uses the frequency of private alleles (Barton & Slatkin 1986; calculated in GENEPOP 3.1). For the Kent Region it results in an estimate of $Nm = 3.5$, in reasonably good agreement with the estimates derived above from the recurrent relation of F.

Regular extinction of local populations and recolonization of the islands could also explain the observed pattern and be considered an extreme case of migration limited to certain years. The frequency of such events required to explain the low observed differentiation depends critically on the effective population size during the low phase of the cycle. If the effective population size gets as low as a few tens (cf. Table 1), recolonization in every other peak would be required to maintain the low differentiation we have observed. With the numbers assumed above ($N_e = 50$ in low years and 5000 in peak years) F_{ST} would increase from almost no differentiation ($F_{ST} = 0.01$) to a clearly higher differentiation than the observed value ($F_{ST} = 0.1$) in 14 generations. If, on the other hand, the effective size during the low phase was 200, instead of 50, it would take 50 generations to reach this level of differentiation. In any case recolonization would have to be relatively frequent to explain the observed low differentiation.

Long distance dispersal among small islands

Our genetic data imply movement over quite large distances between small islands that are separated by up to 20 km of rocks and sea (Fig. 1, Table 1). These distances are an order of magnitude larger than movements documented for individual collared lemmings. Movement pattern of collared lemmings have been studied using live trapping or telemetry only in summer, and reported movements were mostly under 1 km (Brooks & Banks 1971; Rodgers 1990; Brooks 1993). Brooks & Banks (1971) observed, however, that one of their radio-collared males moved over 3 km in a period of 24 h and concluded that, in general, movements in collared lemmings tend to be much larger than for other microtines. There are no data on spring or autumn migration in *Dicrostonyx*, but it is assumed to be of less importance than, for example, in the Norwegian lemming, *Lemmus lemmus* (Chernyavski & Tkachev 1982; Henttonen & Kaikusalo 1993).

Long distance dispersal among islands does probably not occur during the summer. Rather movements are most likely to occur during winter or spring, when the sea is frozen. Collared lemmings are particularly well adapted to life at high latitude and they are the only small rodents changing to nearly white fur in winter. Relative to their body size, they are particularly resistant to low temperatures and have been observed active on snow and ice during the winter (Ferguson & Folk 1970). Chernyavski *et al*. (1981), observed tracks reflecting movements of up to 1 km on the snow in spring; individuals were also found on the ice 1.5 km off Wrangel Island (Chernyavski & Tkachev 1982). Hart (1962) mentions observations of collared lemming tracks as far as 12 km from the shore near Barrow, Alaska. It seems plausible, therefore, that collared lemmings are physically able to disperse over 20 km of hostile habitat. There are, however, virtually no observations of large numbers of lemmings on the ice in the Bathurst Inlet in peak years, and we are nearly certain that migration cannot occur at the predicted high rate in high density years. Long distance migration is probably an infrequent event and such undirected movement will only occasionally result in effective dispersal. Most individuals will probably not arrive at a suitable habitat and die without reproducing.

Gene flow and isolation by distance

In the continuous tundra habitat on Victoria Island, lemming populations were found to be structured at a larger scale than expected. Microsatellite data revealed only weak differentiation among sites separated by up to 156 km (Fig. 1). For mtDNA, differentiation was more marked and a pattern consistent with isolation by distance was found, but the probability of identity among individuals (F_d) markedly decreased only for localities beyond about 50 km (Fig. 4). These findings imply considerable gene flow, which can either result from frequent short distance movement or rarer long distance movement. Movement may also be different between the sexes as there is a strong sex bias in dispersal potential in collared lemmings. The general model of their social organization is of large movements (several km) of adult males and very local movements (100 m) of adult females (Brooks 1993). The few comparable studies available for other fluctuating small rodent populations report differentiation on much smaller scale than that observed herein. Stacy *et al*. (1997) studied genetic differentiation in bank vole populations in the boreal forest in Norway using the same mtDNA sequence and, comparing F_d with distance, concluded that local populations typically extend over less than about 8.5 km. The F_d value beyond 16 km was significantly smaller than the within site probability of identity. Aars *et al*. (1998), also using mtDNA CR sequences and F_d, found significant structuring on an even smaller scale for bank voles in a one-dimensional habitat (i.e. river banks) with high similarity only within sites and between sites 1 km apart. Plante *et al*. (1989) studied the genetic variation among meadow voles (*Microtus pennsylvanicus*) on four grids separated by less than 100 m, using restriction fragment length polymorphism (RFLP) of

the mitochondrial genome. Differentiation among the four grids was only slightly lower (F_{ST} = 0.119 in the decreasing phase of the population cycle; recalculated from the data) than among the six Victoria Island localities reported herein (F_{ST} = 0.135, Table 5).

Conclusions

Our study indicates that in a continuous as well as in a fragmented habitat there is gene flow between local populations of periodically fluctuating lemmings, and that these lemming populations are structured on quite a large geographical scale. The geographical setting of our sampling localities in the Kent Region, with separated small islands and mainland sites, allowed us to make inferences about dispersal from genetic data. The regular, but infrequent, long distance dispersal events required to explain the genetic structure would be very difficult to observe directly with conventional methods to study migration. Combining genetic methods with ecological data allowed us to contribute new information about dispersal and the spatial ecology of lemmings.

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This paper will be a part of D. Ehrich's PhD thesis on the genetic structure of fluctuating lemming populations. P. E. Jorde is presently a postdoc at the University of Oslo, working on genetic monitoring. C. J. Krebs and A. J. Kenney are working on ecological dynamics of terrestrial vertebrates, including lemmings, hares and lynx in Canada. J. E. Stacy's research interests are in population structure and DNA sequence evolution. N. C. Stenseth's research programme focuses on the spatio-temporal variation in northern mammals.

Appendix I

Absolute frequencies of mtDNA control region haplotypes in *Dicrostonyx groenlandicus* at each locality. *n*: sample size

		Haplotypes								
Locality	*n*	a	b	c	d	e	f	g	h	i
Walker Bay	10	10								
Hope Bay	10	9	1							
Breakwater Isl.	9	9								
Cockburn Isl.	9	9								
Hurd Isl.	10	8	1	1						
Wilmot Isl.	10	10								
Mount Pelly	11	4		4		3				
Cambridge Bay	12	2		8	2					
Long Point	12	2		10						
Lake Kitiga	12			10			2			
Starvation Cove	13			10			1		2	
Byron Bay	11	3		3		4		1		
North Star Harbour	11									11
Nicholson Isl.	11									11

Appendix II

Allele frequencies at four nuclear microsatellite loci in *Dicrostonyx groenlandicus* at each locality. The alleles are designated by the length of the amplified fragment in base pairs

Locus: MSCRB-5A		Alleles																		
Localities	*n*	134	136	138	140	142	144	146	148	150	152	154	156	158	160	162	164	168	170	172
Walker Bay	24	0.21			0.21	0.04	0.02	0.02				0.13	0.27	0.02			0.06		0.02	
Hope Bay	22	0.02		0.07	0.05	0.2	0.09	0.18	0.05	0.09		0.11	0.09		0.02				0.02	
Breakwater Isl.	24	0.27	0.08	0.04	0.06	0.06		0.08	0.19		0.08		0.04				0.02	0.02	0.04	
Cockburn Isl.	20	0.18	0.03		0.05	0.13	0.03	0.15	0.05		0.05	0.1	0.1			0.03	0.03	0.03	0.08	
Hurd Isl.	20	0.5			0.03	0.03	0.08	0.1	0.08		0.05	0.05	0.1							
Wilmot Isl.	24	0.23			0.02	0.02		0.19	0.02	0.08	0.06	0.08	0.13	0.04	0.04	0.02			0.02	0.04
Mount Pelly	12	0.88	0.04	0.04			0.04													
Cambridge Bay	16	0.66		0.06	0.06	0.13	0.09													
Long Point	17	0.5	0.06		0.24	0.12	0.06						0.03							
Lake Kitiga	17	0.71	0.03		0.09		0.18													
Starvation Cove	17	0.76	0.03		0.09	0.06	0.03		0.03											
Byron Bay	17	0.74			0.12	0.12	0.03													
North Star Harbour	17				0.03	0.06	0.03	0.03	0.03	0.15	0.21	0.18	0.18	0.06	0.03	0.03				
Nicholson Isl.	7						0.07	0.07	0.07	0.07		0.36		0.14	0.14	0.07				

Locus: MSCRB-6		Alleles																											
Localities	*n*	167	173	179	181	183	185	187	189	191	193	195	205	209	211	213	215	217	219	221	223	225	227	229	231	233	235	237	239
Walker Bay	24				0.44		0	0.06	0.06						0.06	0.08	0.04	0.04	0.02	0.02	0.02	0.15						
Hope Bay	21				0.29		0.19	0.05					0.02				0.05	0.1		0.05		0.12	0.02	0.1		0.02			
Breakwater Isl.	22			0.02	0.25	0.05	0.02								0.05	0.02	0.16	0.05	0.14	0.14	0.05	0.02	0.02	0.02					
Cockburn Isl.	22			0.09	0.3		0	0.14	0.07				0.02			0.02	0.05		0.05				0.14	0.07	0.02		0.05		
Hurd Isl.	21			0.05	0.36		0.05	0.05		0.02	0.02			0.02			0.02	0.12	0.05		0.02	0.02	0.05	0.1	0.05				
Wilmot Isl.	24				0.4		0.1		0.13							0.04		0.15			0.02	0.13	0.02				0.02		
Mount Pelly	11				0.05		0.05	0.18	0.05	0.09		0.09					0.05	0.09		0.09	0.09		0.14	0.05					
Cambridge Bay	15						0	0.03	0.3		0.03	0.03					0.03		0.17	0.1	0.03	0.03	0.1		0.07		0.03	0.03	
Long Point	17				0.03		0	0.09	0.12					0.03			0.09		0.06	0.06	0.15	0.06	0.18	0.03		0.12			
Lake Kitiga	17	0.03					0	0.18											0.12	0.09	0.38	0.03	0.15	0.03					
Starvation Cove	16						0.03		0.06	0.13									0.03	0.16	0.22	0.16	0.03	0.03		0.06	0.09		
Byron Bay	17						0	0.18	0.06	0.03	0.03							0.03	0.12	0.09	0.06	0.06	0.06	0.03	0.12	0.03	0.09		0.03
North Star Harbour	17	0.06	0.24		0.03		0.47	0.06										0.15											
Nicholson Isl.	7	0.07		0.29	0.07		0.5																				0.07		

Locus: AV-9		Alleles													
Localities	*n*	216	220	222	223	224	228	232	236	240	244	248	252	256	260
Walker Bay	23	0.09	0.33			0.07		0.17	0.04	0.17	0.07	0.04	0.02		
Hope Bay	22	0.05	0.34		0.02	0.23	0.07	0.02	0.05	0.07	0.11	0.02	0.02		
Breakwater Isl.	24	0.02	0.29			0.23	0.21				0.08	0.1	0.06		
Cockburn Isl.	22	0.05	0.16			0.45	0.02			0.16	0.02	0.02		0.05	0.07
Hurd Isl.	21		0.24		0.02	0.29	0.17	0.02		0.07	0.1	0.02	0.07		
Wilmot Isl.	24	0.06	0.02		0.04	0.48	0.25	0.04		0.08	0.02				
Mount Pelly	9	0.06	0.06		0.06	0.39		0.28	0.06	0.11					
Cambridge Bay	17	0.03	0.21		0.03	0.38	0.21	0.06	0.03		0.06				
Long Point	17		0.15		0.03	0.5	0.15	0.06	0.12						
Lake Kitiga	16		0.03	0.03	0.22	0.63	0.03				0.06				
Starvation Cove	17	0.06	0.06		0.03	0.29	0.15	0.09	0.21	0.03	0.03	0.06			
Byron Bay	17	0.06	0.18			0.32	0.24	0.06	0.06	0.03	0.06				
North Star Harbour	17		0.71			0.09	0.03				0.09		0.09		
Nicholson Isl.	7		0.5			0.21				0.14	0.07		0.07		

Locus: AV-15		Alleles														
Localities	*n*	201	205	209	213	217	221	225	229	233	237	241	245	249	253	257
Walker Bay	24				0.31	0.1	0.08	0.38	0.02	0.04					0.06	
Hope Bay	21	0.05	0.1		0.12		0.19	0.21	0.17	0.12		0.02		0.02		
Breakwater Isl.	24	0.08	0.02	0.08	0.25	0.13	0.06	0.1	0.17	0.08	0.02					
Cockburn Isl.	22	0.05			0.09	0.18	0.41	0.07	0.11	0.07						0.02
Hurd Isl.	21	0.02	0.05		0.05	0.17	0.24	0.14	0.07	0.14	0.02	0.07	0.02			
Wilmot Isl.	23				0.04	0.13		0.41	0.17	0.17		0.07				
Mount Pelly	11		0.05	0.05	0.14	0.09	0.14	0.23	0.23						0.09	
Cambridge Bay	17		0.03	0.03	0.12	0.12	0.18	0.18	0.15	0.03		0.12		0.06		
Long Point	17			0.03	0.26	0.03	0.24	0.09	0.21	0.06	0.06			0.03		
Lake Kitiga	17				0.03	0.21	0.18	0.09	0.12	0.21			0.15			0.03
Starvation Cove	17			0.06	0.38	0.06	0.15	0.21	0.03		0.03	0.06	0.03			
Byron Bay	17		0.03	0.12	0.12	0.21	0.18	0.15	0.15	0.03	0.03					
North Star Harbour	17			0.03	0.06	0.21	0.24	0.18	0.12	0.12	0.03	0.03				
Nicholson Isl.	7				0.21	0.07	0.14	0.14				0.14	0	0.14	0.14	

