Conserv Genet (2009) 10:923–933
DOI 10.1007/s10592-008-9581-6

SHORT COMMUNICATION

No phylogeographic structure in the circumpolar snowy owl (*Bubo scandiacus*)

Gunnhild Marthinsen · Liv Wennerberg · Roar Solheim · Jan T. Lifjeld

Received: 31 March 2007 / Accepted: 26 March 2008 / Published online: 9 April 2008

Abstract The snowy owl (*Bubo scandiacus*) is a nomadic species with a circumpolar distribution. It has recently declined in the western Palearctic and may thus be worthy of special consideration for conservation. We investigated genetic structure in three well separated geographic regions within the snowy owls' breeding range. We sequenced two mitochondrial genes; the control region and cytochrome *b*, and two Z-chromosome introns; VLDLR-9 and BRM-15. We found no phylogeographic structure among the sampled regions, indicating high levels of gene flow in the recent past and possibly still today. Intra-population diversity did not vary between regions for the control region, but for Cyt *b*, North American birds had higher haplotype diversity than Scandinavian and eastern Siberian birds. Western Palearctic birds do not seem to be genetically deprived or inbred. Genetic diversity in the snowy owl was not lower than Scandinavian populations of three other owl species: tawny owls (*Strix aluco*), Tengmalm's owls (*Aegolius funereus*) and eagle owls (*Bubo bubo*).

Keywords Genetic structure · Gene flow · mtDNA control region · Phylogeography · Population genetics · Z-chromosome intron

G. Marthinsen (✉) · L. Wennerberg · J. T. Lifjeld
National Centre for Biosystematics, Natural History Museum, University of Oslo, P.O. Box 1172, Blindern, 0318 Oslo, Norway
e-mail: g.m.marthinsen@nhm.uio.no

R. Solheim
Agder Museum of Natural History, P.O. Box 1887, Gimlemoen, 4686 Kristiansand S, Norway

Introduction

The snowy owl has a circumpolar distribution and breeds mainly on the arctic tundra (Cramp and Simmons 1994). It is a food specialist, preying on rodents with fluctuating population cycles, such as lemmings (*Lemmus* and *Dicrostonyx* spp.) and voles (*Microtus* and *Clethrionomys* spp.). Consequently, snowy owls migrate to places where there are peak densities of these rodents, and thus show large fluctuations in local breeding populations (Alerstam 1990; Cramp and Simmons 1994). Snowy owls have declined in numbers in the western Palearctic in the 20th century due to illegal hunting and possibly reduction in rodent densities (Portenko 1972; Solheim 1994, 2004). In Norway, the snowy owl is listed as Vulnerable (Kålås et al. 2006), in Finland as Endangered (Rassi et al. 2001), and in Sweden as Critically Endangered (Gärdenfors 2005). World-wide, the species is not threatened (IUCN 2006), and in North America there are no indications of reduction in population sizes (del Hoyo et al. 1996). The global population of snowy owls today is estimated to about 290,000 individuals, and is reported to be stable (BirdLife International 2004).

The snowy owls capacity for long distance dispersal was demonstrated by Fuller et al. (2003), who tracked post-breeding movements of six adult snowy owls with satellite telemetry techniques. Maximum travel distance found was about 1,300 km during 11 days. The tracked birds did not remain in the nesting area after the breeding season, and they did not return to the same nesting area the next year. The potential for movement thus appears to be considerable in the snowy owl. One would therefore expect little or no barriers to gene flow in this species and a rather homogeneous population genetic structure across the breeding range.

Here we present the first analysis of the population genetic structure in snowy owls, using samples from three widely separated regions: Scandinavia, eastern Siberia and North America. We investigated whether there is genetic differentiation between these areas, and whether snowy owls in western Palearctic are less diverse than snowy owls in other areas. In addition, we compared the level of genetic diversity in snowy owls with three other owl species breeding in Scandinavia.

Methods

Samples and DNA extraction

Blood or tissue samples were taken from 14 snowy owl individuals from Scandinavia, 14 individuals from North America, and 12 individuals from eastern Siberia. Sample details are given in the Appendix. Most sampled birds were unrelated chicks or assumed breeding birds (i.e. at age 2Y+ and caught in the period May–August at breeding grounds). Exceptions were five Norwegian birds caught outside the breeding range or in a year of no recorded breeding, and the samples from North America, which were from wintering areas. We assume the latter ones belong to the breeding population in northern North America, an assumption supported by telemetry studies from Massachusetts where snowy owls caught during winter were tracked to Maine and Quebec during spring, apparently on their ways to breeding grounds (Smith 2005). Blood samples from 10 adult tawny owls (*Strix aluco*) and 10 adult Tengmalm's owls (*Aegolius funereus*), and down samples from 10 eagle owl chicks (*Bubo bubo*), were collected in Scandinavia (Appendix). Of these species, the eagle owl is the closest relative to the snowy owl, as the two species are now considered congeneric (Wink and Heidrich 2000; Sangster et al. 2004).

DNA was extracted from blood samples using QIAamp® DNA Mini kit (QIAGEN), and from tissue and down samples using DNeasy® Tissue Kit (QIAGEN).

Sequencing

From the mitochondrial DNA (mtDNA) we sequenced a part of the control region corresponding to domain I and part of domain II (Marshall and Baker 1997), and the second half of the cytochrome *b* (Cyt *b*) gene. For the control region in the snowy owls, initial analyses with internal primers produced two sequences for each individual, differing in three sites. The occurrence of two copies of the control region in the mtDNA is known from other bird species, among them tawny owl (Brito 2005). We therefore assume the same is the case for snowy owls. With the use of the primers D11 (Barrowclough et al. 1999) and BO24 (Haig et al. 2004), we did not obtain any ambiguous bases, and thus assume that we managed to amplify only one of the copies. Initial nested sequencing analyses with external PCR primers; N1, which is placed in a tRNA region, and D16 (Barrowclough et al. 1999), amplified the same unambiguous fragment. Tengmalm's owl individuals did not amplify with BO24; the use of D11 and D16 produced unambiguous sequences.

The 5′ end of Cyt *b* was sequenced using modified versions of Sorenson et al.'s (1999) primer L15560 (5′-GCGACA AAATCCCATTCCACCC for snowy owl and eagle owl, 5′-GYGAYAARATCCCATTCCACCC for Tengmalm's owl and tawny owl), and H15646 (Sorenson et al. 1999).

We also sequenced the two introns BRM-15 and VLDLR-9, which are found on the Z-chromosome in a passerine bird (Hansson et al. 2005). In birds, Z-chromosomes are found in two copies in males, and one copy in females. In our study, individuals heterozygous for these loci were all males, and we thus assume the loci are located on the Z-chromosome in the analyzed species. We used the primers published by Hansson et al. (2005). Of the Z-introns, only VLDLR-9 displayed more than one polymorphic site; Tengmalm's owls were polymorphic at two sites (Table 1). No Tengmalm's owl males were polymorphic at both sites, and there were thus no ambiguities in any male genotype. For females of tawny owl and Tengmalm's owl, we obtained two different sequences for BRM-15, indicating that the primers also amplified a second sequence, most likely on the W-chromosome. We therefore used a specific internal forward primer (5′-AGTGTTTSAACTCTCCCTG GT) for these species and obtained single sequences for the second half of the original sequence. The Z-introns did not amplify on the eagle owl samples, probably due to low concentration of DNA extracted from the down samples.

PCR reactions were performed according to Wennerberg (2001). The cycle-sequencing reactions were carried out using the ABI PRISM BigDye Terminator v1.1 Cycle Sequencing Kit, and run on an ABI PRISM 3100 Genetic Analyzer following the manufacturer's instructions (Applied Biosystems). The sequences were aligned in SEQUENCHER 4.1.4 (Gene Codes Corporation) and edited in BIOEDIT 5.0.9 (Hall 1999). All sequences are deposited in GenBank (Accession numbers: EU410971–EU411039, EU436175–EU436319; Appendix).

Data analyses

Number of haplotypes, haplotype diversity and nucleotide diversity were calculated in ARLEQUIN 3.01. Allelic (haplotype) richness was estimated by rarefaction according to El Mousadik and Petit (1996) using the program Contrib 1.02 (Petit et al. 1998). We used a rarefaction size of 10 for the snowy owl regions and eight for the Scandinavian

Table 1 Characteristics of two mtDNA genes and two nuclear introns in four owl species

Species	Population	Control region									Cytochrome *b*								
		n chromosomes	# Bases	Polymorphic sites	# Haplotypes	Allelic richness[a]	Haplotype diversity	SE	Nucleotide diversity	SE	*n* chromosomes	Bases	Polymorphic sites	# Haplotypes	Allelic richness[a]	Haplotype diversity	SE	Nucleotide diversity	SE
Snowy owl	All	40	510	37	33		0.99	±0.001	0.012	±0.0010	40	415	5	6		0.60	±0.009	0.0026	±0.00032
	Eastern Siberia	12	510	21	11	8.32	0.99	±0.012	0.011	±0.0019	12	415	3	3	1.83	0.59	±0.032	0.0027	±0.00064
	North America	14	510	23	12	8.01	0.98	±0.009	0.012	±0.0018	14	415	4	5	3.35	0.73	±0.027	0.0028	±0.00056
	Scandinavia	14	510	28	14	9.00	1.00	±0.007	0.013	±0.0019	14	415	2	2	1.00	0.53	±0.017	0.0025	±0.00053
Eagle owl	Scandinavia	10	512	11	2	1.00	0.56	±0.024	0.012	±0.0022	10	415	0	1	0	0		0	
Tawny owl	Scandinavia	10	511	7	4	2.96	0.82	±0.022	0.006	±0.0012	10	415	0	1	0	0		0	
Tengmalm's owl	Scandinavia	9	476	21	8	6.22	0.97	±0.021	0.014	±0.0028	10	415	5	6	4.98	0.91	±0.026	0.0041	±0.00097

Species	Population	BRM-15									VLDLR-9								
		n ind	*n* chromosomes[b]	# Bases	Polymorphic sites	# Haplotypes	Haplotype diversity	SE	Nucleotide diversity	SE	*n* ind	*n* chromosomes[b]	# Bases	Polymorphic sites	# Haplotypes	Haplotype diversity	SE	Nucleotide diversity	SE
Snowy owl	All	40	63	343	1	2	0.09	±0.008	0.00027	±0.00009	40	62	354	0	1	0		0	
	Eastern Siberia	12	20	343	1	1	0		0		12	20	354	0	1	0		0	
	North America	14	23	343	1	2	0.17	±0.026	0.00048	±0.00020	14	23	354	0	1	0		0	
	Scandinavia	14	20	343	1	2	0.10	±0.024	0.00029	±0.00016	13	19	354	0	1	0		0	
Eagle owl	Scandinavia		–	–	–	–	–		–			–	–	–	–	–		–	
Tawny owl	Scandinavia	10	13	215	0	1	0		0		10	13	355	1	2	0.385	±0.042	0.00213	±0.00060
Tengmalm's owl	Scandinavia	10	14	208	0	1	0		0		10	14	351	2	3	0.560	±0.040	0.00215	±0.00060

[a] Rarefaction size for allelic richness calculations was 10 for snowy owl regions and 8 for Scandinavian populations of four owl species. Scandinavian snowy owls had an allelic richness of 7.00 for the control region, and 1.00 for Cyt *b*, with a rarefaction size of 8

[b] Number of chromosomes equals number of females (one chromosome) plus two times the number of males (two chromosomes)

populations of four owl species. Differences in nucleotide and haplotype diversity between regions and between Scandinavian populations of all four species were tested with *t*-tests, by hand, using mean and standard deviation values from ARLEQUIN (Table 1).

Median joining haplotype networks were constructed in NETWORK 4.1.1.2 (Fluxus Technology Ltd.).

We calculated both F_{ST} (Weir and Cockerham 1984) and Φ_{ST} (Excoffier et al. 1992) values among the snowy owl regions in ARLEQUIN 3.01 (Excoffier et al. 2005). For Φ_{ST} calculations we used Tamura and Nei's (1993) nucleotide substitution model for all loci, as this gave the lowest log likelihood scores in MODELTEST 3.7 (Posada and Crandall 1998) among the models available in ARLEQUIN. Tests for significance were performed with 3,000 permutations.

To test hypotheses about the phylogeographic pattern based on the control region in snowy owls statistically, we performed an automatic Nested Clade Phylogeographic Analysis (Templeton et al. 2005) using the program ANeCPA (Panchal 2007). This program incorporates TCS v1.18 (Clement et al. 2000) and GeoDis v2.2 (Posada et al. 2000).

We used the Bayesian version of LAMARC 2.1.2 (Kuhner 2006; Kuhner and Smith 2007), which assumes migration/drift equilibrium, to calculate relative estimates of gene flow between snowy owl regions (M) and population growth rates (G) based on the control region sequences. In addition, we estimated long-term effective population size for snowy owls from estimates of theta ($=2N_e\mu$, where N_e is the effective female population size and μ is the mutation rate per sequence per generation) based on the control region and Cyt *b* sequences. The obtained estimates of long-term effective population sizes are uncertain for several reasons. Divergence rate for the control region is unknown for Strigidae, and furthermore, the fact that divergence rates appear to be higher on short than on longer time scales obscure such calculations (Ho and Larson 2006). We used the minimum and maximum divergence rates found in other bird species for the control region; 4% and 14% per Myr (Wenink et al. 1996; Drovetski 2003). For Cyt *b* we used a rate of 1% per Myr (Krajewski and King 1996). We calculated μ as [divergence rate/2/10^6 * number of base pairs * generation time (in years)]. A generation time of 4 years (the birds probably do not breed until at least two-years old, Portenko 1972) and our sequence lengths (Table 1) correspond to mutation rates of 4.08 * 10^{-5} mutations per sequence per generation (4% divergence rate) and 1.43 * 10^{-4} (14% divergence rate) for the control region, and 8.3 * 10^{-6} for Cyt *b* (1% divergence rate).

We ran three replicates for each run in LAMARC, with a burn-in of 1,000 steps, followed by one initial chain of 10,000 steps; sampling 500 trees every 20 steps, and one final chain of 200,000; sampling 10,000 trees per 20 steps. We performed three runs and used the median values for the final estimates.

Results

Marker characteristics

We amplified a 510 base pair long fragment of the control region for snowy owl, in which 37 sites were polymorphic. In eagle owl, 11 of 512 sites were polymorphic, in tawny owl, 7 of 511 sites were polymorphic, and in Tengmalm's owl, 21 of 276 sites were polymorphic. All variable sites represented transitions except one A/C transversion in snowy owl. The different primer sets used for snowy owl, as described in Sect. 'Methods', amplified identical sequences. All individuals of each investigated species were similar in the conserved F block (as defined in Baker and Marshall 1997), which occurs at the end of the fragments used in the analyses. The investigated species differed by 3.3–20% in the F block, which is in the lower range of differences between more distantly related bird species (e.g. 10–25%, Baker and Marshall 1997; 7–59%, Ruokonen and Kvist 2002).

Base composition in the snowy owl control region was similar to other investigated bird species (Baker and Marshall 1997; Ruokonen and Kvist 2002), except for an unexpected high ratio of A compared to C (33.9% A, 28.6% C, 11.4% G and 26.1% T). All variable sites were found within domain I in snowy owl, eagle owl and tawny owl. Tengmalm's owl had one variable site within the start of domain II.

From the 5′ end of Cyt *b*, a 415 base pair fragment was amplified for all species. The sequences did not contain stop codons or indels. Snowy owl and Tengmalm's owl had five variable sites, all transitions in third codon position. There was no amino acid variation within the two species. Tawny owl and eagle owl were monomorphic. Snowy owl differed from eagle owl by nine (6.6%) amino acid substitutions, from tawny owl by 13 (9.4%) and from Tengmalm's owl by 18 (13.1%) amino acid substitutions, which is what we expect for species within the same order (Haring et al. 2001).

Based on these characteristics and comparisons, we are confident that the mitochondrial markers were of truly mitochondrial and not nuclear origin, and that the amplified fragments in the different species were homologous.

There were 33 control region haplotypes, six Cyt *b* haplotypes, two BRM-15 haplotypes and one VLDLR-9 haplotype among the 40 snowy owl individuals (Table 1).

Genetic structure

Median joining haplotype networks given in Fig. 1 for snowy owls for the three variable loci (the control region, Cyt *b* and BRM-15) revealed no phylogeographic structure. The nested clade analysis confirmed the result of no

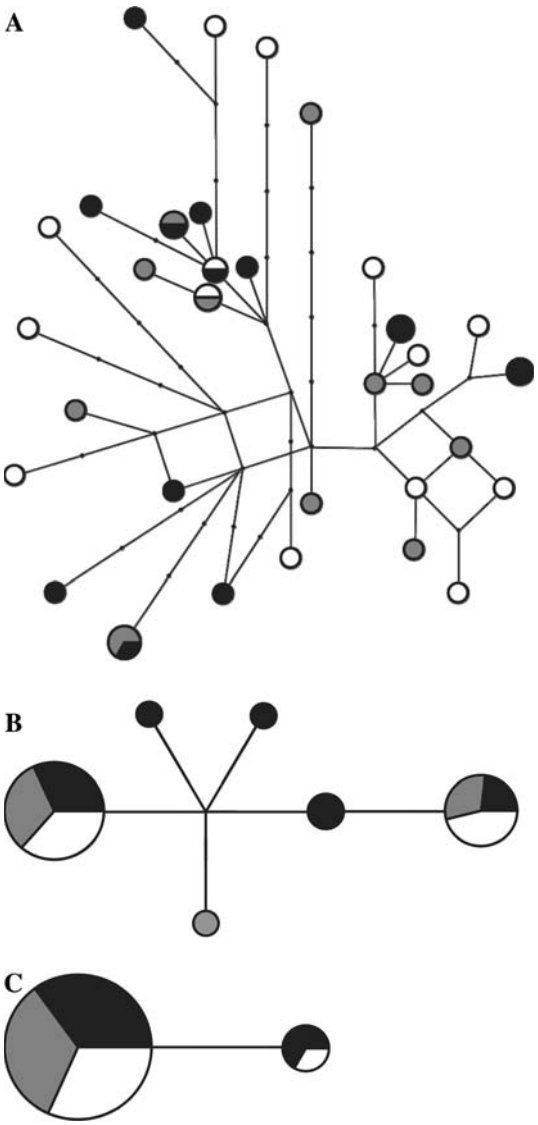

Fig. 1 Median joining haplotype networks for snowy owls revealing low levels of phylogeographic structure among three sampled regions (*black* = North America, *grey* = eastern Siberia and *white* = Scandinavia). (**a**) The mitochondrial DNA control region, (**b**) cytochrome *b* and (**c**) the Z-chromosome intron BRM-15. Sizes of pies indicate relative number of individuals with that haplotype. Black points on the branches in (**a**) represent hypothetical, non-sampled haplotypes. All lines in (**b**) and (**c**) represent single mutations

phylogeographic structure; there was no significant association between haplotype and geographic location in any clade, in any of altogether six nesting levels (all *P*-values > 0.20). The null hypothesis of no genetic structure could not be rejected, and there was no evidence of historical fragmentation, range expansion, long-range colonization or restricted gene flow.

Also *F*-statistics revealed low levels of phylogeographic structure. F_{ST} and Φ_{ST} values for all loci comparing the snowy owl regions were similar; only F_{ST} values are given. Overall F_{ST} values were low and non-significant (-0.001 for the control region, -0.033 for Cyt *b* and 0.002 for BRM-15). Pairwise F_{ST} values were also non-significant, and all were negative except for the values comparing North America with eastern Siberia for two loci ($F_{ST} = 0.020$ for the control region, 0.077 for BRM-15).

Gene flow and long term effective population size

Gene flow estimated by LAMARC varied between runs, but was consistently lowest across the Atlantic Ocean. Median values of the gene flow parameter M was 853 (Credibility Interval: 279–1,014) from Scandinavia to eastern Siberia, 361 (24–1,048) from eastern Siberia to Scandinavia, 218 (27–483) from Scandinavia to North America, 166 (20–360) from North America to Scandinavia, 732 (246–1016) from North America to eastern Siberia, and 433 (119–944) from eastern Siberia to North America. One should however bear in mind that estimates of migration rates from LAMARC may not be accurate if population genetic structure is weak (LAMARC documentation), as is the case in this study.

These high gene flow estimates indicate that snowy owl constituted one panmictic population in the recent past and possibly still today (see Discussion). Therefore, we estimated the long term effective population size for all samples pooled. Theta was estimated to 0.332 (CI: 0.137–1.147), corresponding to a long-term effective population size of about 4,100 (1,700–14,100) females with 4% divergence rate, and 1,200 (500–4,000) females with 14% divergence rate. Based on Cyt *b*, theta was estimated to 0.0044 (0.0011–0.022), corresponding to a long-term effective population size of about 270 (70–1,330) females. The high diversity of estimates highlights the uncertainty of these calculations.

Genetic diversity and population growth

There was no difference between the snowy owl sampling regions in nucleotide diversity for either mitochondrial marker, nor in haplotype diversity for the control region (all tests non-significant) (Table 1). North America had significantly higher Cyt *b* haplotype diversity than eastern Siberia and Scandinavia ($t = 3.40$, df $= 24$, $P < 0.01$ and $t = 6.3$, df $= 26$, $P < 0.01$, respectively). Allelic richness was highest for Scandinavia for the control region, whereas North America had higher allelic richness for Cyt *b* (Table 1).

The Scandinavian snowy owl population had higher control region nucleotide and haplotype diversity than tawny owl ($t = 2.78$, df $= 22$, $P < 0.01$, and $t = 8.71$, df $= 22$, $P < 0.01$, respectively), and higher control region haplotype diversity than eagle owl ($t = 20.33$, df $= 22$, $P < 0.01$). In Cyt *b*, eagle owl and tawny owl were not polymorphic. Tengmalm's owl did not differ significantly

from snowy owl in nucleotide or haplotype diversities for mitochondrial loci ($t = 0.30$, df $= 21$, $P > 0.05$, and $t = 1.57$, df $= 21$, $P > 0.05$, respectively). Allelic richness showed the same pattern; Tengmalm's owl and snowy owl had the highest values (Table 1). For the Z-introns, all species showed too little variation for any comparisons to be relevant (Table 1). In summary, snowy owls from the different regions did not differ much in genetic diversity, and the snowy owl seemed to be more diverse than eagle owl and tawny owl, but at the same level as Tengmalm's owl.

The growth rate parameter (G) estimated based on control region sequences for all snowy owl individuals pooled was positive and relatively large (630, CI: 357–972), which is a strong indication of population growth (LAMARC documentation: http://evolution.gs.washington.edu/lamarc/). Of the Scandinavian populations of four species, snowy owl and Tengmalm's owl showed indications of population growth (G = 913, CI: 413–1,000 and G = 592, CI: 197–968, respectively), whereas tawny owl and eagle owl showed indications of a stable population, and population decline, respectively (G = 51, CI: −455–911, for tawny owl, G = −212, CI: −487–142, for eagle owl).

Discussion

Analyses of two mitochondrial and two nuclear loci provided no evidence of phylogeographic structure among snowy owls from Scandinavia, eastern Siberia and North America as shown by minimum spanning networks, low F_{ST} values and a nested clade analysis. Furthermore, no reduction in genetic diversity was revealed in Scandinavia compared to the other two investigated regions. Snowy owls in western Palearctic, where the species has declined the last 100 years, do thus not seem to suffer from inbreeding or reduced genetic diversity.

LAMARC analyses indicated high levels of gene flow, especially across the Palearctic and the Bering Strait. This is not surprising, given the snowy owls high potential for long distance flights (Fuller et al. 2003), and the Atlantic Ocean probably being the greatest barrier to gene flow. It is however difficult to assess whether gene flow occurs at present, or whether the estimated levels mirror historical events. The LAMARC analyses indicated that the snowy owl regions have been exchanging individuals at least recently.

Our inclusion of samples from non-breeding individuals (Appendix) could potentially lead to erroneous results since these may have been breeding in other areas than assumed. However, analyses excluding samples from non-breeding birds in Scandinavia did not change the results (not shown), and it seems unlikely that the North-American samples did not belong to the Nearctic breeding population (see Smith 2005). The fact that North American samples were from wintering birds, and so may represent a more widespread sample of the breeding population than the Palearctic samples, may explain why the North American population had the highest Cyt *b* haplotype diversity. However, this hypothesis assumes some level of genetic structure, which we did not detect in our study.

The long-term effective population size estimates were low; the maximum estimate was 14,000 snowy owl females (upper credible interval limit for 4% divergence rate for the control region dataset). Although this number excludes males, juveniles and not-reproducing adults, this is far lower than today's census size of 290,000 individuals. However, the result corresponds well with the population expansion indicated in the LAMARC analyses.

Genetic analyses of other species with Holarctic distributions have also revealed recent population expansions. Reindeer (*Rangifer rangifer*) and Arctic fox (*Alopex lagopus*), particularly the 'lemming ecotype', have both been hypothesised to have been restricted to several refugia during the last interglacial period, when their tundra habitat was restricted (Flagstad and Røed 2003; Dalén et al. 2005). When the last glacial period started, their habitat increased, and the populations expanded and spread, creating a pattern of low genetic structure and relatively high levels of genetic diversity seen today. The haplotype networks of both of these species lack, similar to the snowy owl control region network, a central haplotype, and have several clades (Flagstad and Røed 2003; Dalén et al. 2005). The history of the three species may thus be parallel. Particularly the lemming-ecotype of Arctic fox resembles the snowy owl in habitat and prey choice. The snowy owls higher potential for dispersal through flights may have taken the mixing process farther than for Arctic fox and reindeer, and our results of no phylogeographic structure support this hypothesis.

Despite the restricted number and spread of samples for the other investigated owl species, the differences between species in levels of genetic diversity fit well with differences in phylogeographic history and behaviour. Tawny owl and eagle owl, which had the lowest diversity levels, and low or negative growth parameter estimates, are both relatively resident (Cramp and Simmons 1994). In addition, the sampled populations probably originate from a range expansion from a Pleistocene refugium in the Balkan region, as was suggested for Norwegian tawny owls (Brito 2005). Founder events during the expansion would have lead to lower genetic diversity. The diversity level in Tengmalm's owl, on the other hand, was about the same as in snowy owl. Tengmalm's owls have, like snowy owls, a nomadic behaviour due to the cyclic abundance of their prey (Mysterud 1970; Cramp and Simmons 1994). In contrast to snowy owl, however, Tengmalm's owls in

North America and Eurasia are genetically differentiated (Koopman et al. 2005). The North Pacific may function as a larger barrier to gene flow between the continents in this species, than does the Bering Strait for the snowy owl.

In conclusion, our results indicate no phylogeographic structure across the entire circumpolar breeding range of the snowy owl. The decline in breeding numbers seen in western Palearctic is not associated with reduced genetic diversity. Given the species' potential for long-distance breeding dispersal and lack of phylogeographic structure, it seems as if snowy owls can be considered as one global panmictic population from a genetic perspective.

Acknowledgements The study received financial support from the Norwegian Ornithological Society and the Research Council of Norway. We thank the Field Museum in Chicago, the Swedish Museum of Natural History, the Zoological Museum at the University of Oulu, Tromsø Museum, Lista Bird Observatory, the Swedish Polar Research Secretariat, colleagues at the Dept of Animal Ecology at Lund University, C. Steel and E. Dahl for samples, and D. Ehrich, J. Johnson, four anonymous referees and colleagues at NHM, for valuable comments on the manuscript.

Appendix: Information on samples from four owl species

Species	Region	Locality	Source[a]	Voucher no.[b]	Sex[c]	Age	Date	GenBank accession no.			
								Control region	Cyt *b*	BRM-15	VLDLR-9
Snowy owl	Scandinavia	Värmland, Sweden	NRM	966087	F	–	1 February 1996	EU411003	EU436207	EU436255	
		Värmland, Sweden	NRM	976241	M	–	1 May 1997	EU411004	EU436208	EU436256, EU436257	
		Dalarne, Sweden	NRM	996648	M	–	1 November 1999	EU411005	EU436209	EU436258, EU436259	
		Västernorrland, Sweden	NRM	20006286	F	–	1 June 2000	EU411006	EU436210	EU436260	
		Norrbotten, Sweden	NRM	20006304	M	–	1 July 2000	EU411007	EU436211	EU436261, EU436262	
		Finnmark, Norway	TM	TM6	F	2Y	17 April 2000	EU411010	EU436214	EU436265	
		Finnmark, Norway	TM	TM117	F	3Y+	14 July 2003	EU411009	EU436213	EU436264	
		Finnmark, Norway	ANM	1100 (*17811*)[d]	M	2Y	July 2001	EU410983	EU436187	EU436246, EU436247	
		Captive, Norway	ANM	1619 (*17812*)[d]	F	–	2003	EU410984	EU436188	EU436248	
		Norway	ANM	1085 (*17813*)[d]	M	1Y	1997	EU410985	EU436189	EU436249, EU436250	
		Hedmark, Norway	ANM	1101 (*17814*)[d]	F	–	2000	EU410986	EU436190	EU436251	EU436291[f]
		Finnmark, Norway	ANM	1572 (*17815*)[d]	F	–	1 July 2000	EU411008	EU436212	EU436263	
		Lapland, Finland	ZUO	31500	M	–	14 June 2000	EU411001	EU436205	EU436252, EU436253	
		Lapland, Finland	ZUO	970509	–	–	9 May 1997	EU411002	EU436206	EU436254	
Snowy owl	Eastern Siberia	Lopatka peninsula	SRE	–	M	Pullus	15 July 1994	EU410971	EU436175	EU436226, EU436227	
		Wrangel Island	SRE	–	M	Pullus	25 July 1994	EU410972	EU436176	EU436228, EU436229	
		Wrangel Island	SRE	–	F	Pullus	25 July 1994	EU410973	EU436177	EU436230	
		Wrangel Island	SRE	–	M	Pullus	25 July 1994	EU410974	EU436178	EU436231, EU436232	
		Wrangel Island	SRE	–	M	Pullus	25 July 1994	EU410975	EU436179	EU436233, EU436234	
		Wrangel Island	SRE	–	M	Pullus	25 July 1994	EU410976	EU436180	EU436235, EU436236	
		Wrangel Island	SRE	–	M	Pullus	25 July 1994	EU410977	EU436181	EU436237, EU436238	

Appendix continued

Species	Region	Locality	Source[a]	Voucher no.[b]	Sex[c]	Age	Date	GenBank accession no.			
								Control region	Cyt *b*	BRM-15	VLDLR-9
		Wrangel Island	SRE	–	M	Pullus	25 July 1994	EU410978	EU436182	EU436239, EU436240	
		Wrangel Island	SRE	–	F	Pullus	25 July 1994	EU410979	EU436183	EU436241	
		New Siberian Islands	SRE	–	F	Pullus	–	EU410980	EU436184	EU436242	
		New Siberian Islands	SRE	–	M	Pullus	1 August 1994	EU410981	EU436185	EU436243, EU436244	
		Wrangel Island	SRE	–	F	Pullus	25 July 1994	EU410982	EU436186	EU436245	
Snowy owl	North America	Illinois, USA	FMNH	334760[e]	F	–	10 December 1987	EU410987	EU436191	EU436266	
		Minnesota, USA	FMNH	356917[e]	M	–	27 April 1992	EU410988	EU436192	EU436267, EU436268	
		Wisconsin, USA	FMNH	384651[e]	F	–	30 November 1993	EU410989	EU436193	EU436269	
		Illinois, USA	FMNH	384661[e]	M	–	29 November 1996	EU410990	EU436194	EU436270, EU436271	
		Minnesota, USA	FMNH	385467[e]	M	–	24 April 1997	EU410991	EU436195	EU436272, EU436273	
		Illinois, USA	FMNH	386069[e]	M	–	11 December 1996	EU410992	EU436196	EU436274, EU436275	
		Minnesota, USA	FMNH	396989[e]	F	–	23 November 1999	EU410993	EU436197	EU436276	
		Minnesota, USA	FMNH	430331[e]	M	–	29 November 2000	EU410994	EU436198	EU436277, EU436278	
		Minnesota, USA	FMNH	430332[e]	F	–	3 November 2000	EU410995	EU436199	EU436279	
		Illinois, USA	FMNH	430528[e]	M	–	28 October 2001	EU410996	EU436200	EU436280, EU436281	
		Minnesota, USA	FMNH	435689[e]	M	–	–	EU410997	EU436201	EU436282, EU436283	
		Minnesota, USA	FMNH	436414[e]	M	–	–	EU410998	EU436202	EU436284, EU436285	
		Captive, USA	FMNH	437421[e]	M	–	–	EU410999	EU436203	EU436286, EU436287	
		Minnesota, USA	FMNH	438319[e]	F	–	–	EU411000	EU436204	EU436288	
Eagle owl	Scandinavia	Nordland, Norway	NHMO	*18681*	–	Pullus	May/June 2005	EU411030			
		Nordland, Norway	NHMO	*18682*	–	Pullus	May/June 2005	EU411031			
		Nordland, Norway	NHMO	*18684*	–	Pullus	May/June 2005	EU411032			
		Nordland, Norway	NHMO	*18685*	–	Pullus	May/June 2005	EU411033			
		Nordland, Norway	NHMO	*18687*	–	Pullus	May/June 2005	EU411035			
		Nordland, Norway	NHMO	*18689*	–	Pullus	May/June 2005	EU411034			
		Nordland, Norway	NHMO	*18690*	–	Pullus	May/June 2005	EU411036			
		Nordland, Norway	NHMO	*18693*	–	Pullus	May/June 2005	EU411037			
		Nordland, Norway	NHMO	*18696*	–	Pullus	May/June 2005	EU411038	EU436215[f]		
		Nordland, Norway	NHMO	*18699*	–	Pullus	May/June 2005	EU411039			

Appendix continued

Species	Region	Locality	Source[a]	Voucher no.[b]	Sex[c]	Age	Date	GenBank accession no.			
								Control region	Cyt *b*	BRM-15	VLDLR-9
Tengmalm's owl[e]	Scandinavia	Vest-Agder, Norway	NHMO	*7531*	F	2Y+	13 October 2003	EU411011	EU436217	EU436290[f]	EU436306
		Vest-Agder, Norway	NHMO	*7532*	F	1Y	13 October 2003	EU411012			EU436307
		Vest-Agder, Norway	NHMO	*7533*	M	1Y	13 October 2003	EU411013	EU436219		EU436308, EU436309
		Vest-Agder, Norway	NHMO	*7534*	M	1Y	13 October 2003	EU411014	EU436220		EU436310, EU436311
		Vest-Agder, Norway	NHMO	*7535*	F	2Y+	13 October 2003	EU411015	EU436221		EU436312
		Vest-Agder, Norway	NHMO	*7536*	M	1Y	13 October 2003	EU411016	EU436222		EU436313, EU436314
		Vest-Agder, Norway	NHMO	*7538*	F	1Y	14 October 2003	EU411017	EU436223		EU436315
		Vest-Agder, Norway	NHMO	*7539*	F	1Y	14 October 2003		EU436224		EU436316
		Vest-Agder, Norway	NHMO	*7540*	F	1Y	14 October 2003	EU411018	EU436225		EU436317
		Vest-Agder, Norway	NHMO	*7541*	M	1Y	14 October 2003	EU411019	EU436218		EU436318, EU436319
Tawny owl	Scandinavia	Telemark, Norway	NHMO	*6506*	M	1Y+	5 November 1999	EU411023	EU436216[f]	EU436289[f]	EU436292, EU436293
		Akershus, Norway	NHMO	*7017*	F	Pullus	20 May 2004	EU411020			EU436294
		Akershus, Norway	NHMO	*7018*	F	Pullus	20 May 2004	EU411025			EU436295
		Akershus, Norway	NHMO	*7019*	M	Pullus	20 May 2004	EU411026			EU436296, EU436297
		Akershus, Norway	NHMO	*9394*	M	Pullus	22 May 2005	EU411027			EU436298, EU436299
		Akershus, Norway	NHMO	*9395*	F	Pullus	22 May 2005	EU411022			EU436300
		Akershus, Norway	NHMO	*9396*	F	Pullus	22 May 2005	EU411024			EU436301
		Aust-Agder, Norway	NHMO	*19127*	F	2Y	18 April 1994				EU436302
		Aust-Agder, Norway	NHMO	*19128*	F	3Y	18 April 1994	EU411028			EU436303
		Aust-Agder, Norway	NHMO	*19129*	F	3Y	18 April 1994	EU411021			EU436304
		Aust-Agder, Norway	NHMO	*19130*	F	3Y	18 April 1994	EU411029			EU436305

[a] NRM: Swedish Museum of Natural History; TM: Museum of Tromsø, Norway; ANM: Agder Museum of Natural History, Norway, ZUO: Zoological Museum at the University of Oulu, Finland, SRE: Swedish-Russian tundra expedition 1994, FMNH: The Field Museum of Natural History, Chicago, NHMO: Natural History Museum of Oslo, Norway

[b] Journal numbers from the DNA/tissue collection of NHM Oslo given in italic

[c] Sex was determined genetically with the primers 2500F/2718R which has been shown to produce two bands for females (W + Z) and one for males (Z) on Tengmalm's owls (Fridolfson and Ellegren 1999). We tested snowy owl and tawny owl individuals with known sex (determined from morphological characters, Cramp and Simmons 1994) and found the expected pattern. We could not amplify any Z chromosome fragments for the eagle owl samples, probably due to low concentration of DNA extracted from the down samples, and could thus not determine their sex

[d] Non-breeding bird (non-breeding year, or outside breeding season)

[e] Birds caught on migration

[f] All individuals of the species have the same haplotype

References

Alerstam T (1990) Bird migration. Cambridge University Press, Cambridge

Baker AJ, Marshall HD (1997) Mitochondrial control region sequences as tools for understanding evolution. In: Mindell DP (ed) Avian molecular evolution and systematics. Academic Press, San Diego

Barrowclough GF, Gutierrez RJ, Groth JG (1999) Phylogeography of spotted owl (*Strix occidentalis*) populations based on mitochondrial DNA sequences: gene flow, genetic structure, and a novel biogeographic pattern. Evolution 53:919–931

BirdLife International (2004) *Nyctea scandiaca* In: IUCN 2006. 2006 IUCN red list of threatened species. http://www.iucnredlist.org. Downloaded on 07 February 2007

Brito PH (2005) The influence of Pleistocene glacial refugia on tawny owl genetic diversity and phylogeography in western Europe. Mol Ecol 14:3077–3094

Clement M, Posada D, Crandall KA (2000) TCS: a computer program to estimate gene genealogies. Mol Ecol 9:1657–1659

Cramp S, Simmons MP (eds) (1994) Handbook of the birds of Europe, the Middle East and North Africa. The birds of the Western Palearctic. Oxford University Press, London

Dalén L, Fuglei E, Hersteinsson P et al (2005) Population history and genetic structure of a circumpolar species: the arctic fox. Biol J Linn Soc 84:79–89

del Hoyo J, Elliott A, Sargatal J (eds) (1996) Handbook of the birds of the world. Hoatzin to Auks, vol 3. Lynx Edicions, Barcelona

Drovetski S (2003) Plio-Pleistocene climatic oscillations, Holarctic biogeography and speciation in an avian subfamily. J Biogeogr 30:1173–1181

El Mousadik A, Petit RJ (1996) High level of genetic differentiation for allelic richness among populations of the argan tree [*Argania spinosa* (L.) Skeels] endemic to Morocco. Theor Appl Genet 92:832–839

Excoffier L, Laval G, Schneider S (2005) ARLEQUIN ver. 3.0: an integrated software package for population genetics data analysis. Evol Biol Online 1:47–50

Excoffier L, Smouse PE, Quattro JM (1992) Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. Genetics 131:479–491

Flagstad Ø, Røed KH (2003) Refugial origins of reindeer (*Rangifer tarandus* L.) inferred from mitochondrial DNA sequences. Evolution 57:658–670

Fridolfson A, Ellegren H (1999) A simple and universal method for molecular sexing of non-ratite birds. J Avian Biol 30:116–121

Fuller M, Holt D, Schueck L (2003) Snowy owl movements: variation on the migration theme. In: Berthold P, Gwinner E, Sonnenschein E (eds) Avian migration. Springer-Verlag, Berlin Heidelberg, pp 359–366

Gärdenfors U (ed) (2005) Rödlistade arter i Sverige 2005—The 2005 red list of Swedish species. ArtDatabanken, SLU, Uppsala

Haig SM, Mullins TD, Forsman ED et al (2004) Genetic identification of spotted owls, barred owls, and their hybrids: legal implications of hybrid identity. Conserv Biol 18:1347–1357

Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symp Ser 41:95–98

Hansson B, Åkesson M, Slate J et al (2005) Linkage mapping reveals sex-dimorphic map distances in a passerine bird. Proc R Soc Lond B 272:2289–2298

Haring E, Kruckenhauser L, Gamauf A et al (2001) The complete sequence of the mitochondrial genome of *Buteo buteo* (Aves, Accipitridae) indicates an early split in the phylogeny of raptors. Mol Biol Evol 18:1892–1904

Ho SYW, Larson G (2006) Molecular clocks: when times are a-changin'. Trends Ecol Evol 22:79–83

IUCN (2006) 2006 IUCN red list of threatened species. http://www.iucnredlist.org. Downloaded on 22 November 2006

Kålås JA, Viken Å, Bakken T (eds) (2006) Norwegian red list. Artsdatabanken, Norway

Koopman ME, McDonald DB, Hayward GD et al (2005) Genetic similarity among Eurasian subspecies of boreal owls *Aegolius funereus*. J Avian Biol 36:179–183

Krajewski C, King DG (1996) Molecular divergence and phylogeny: rates and patterns of cytochrome *b* evolution in cranes. Mol Biol Evol 13:21–30

Kuhner MK (2006) LAMARC 2.0: maximum likelihood and Bayesian estimation of population parameters. Bioinformatics 22:768–770

Kuhner MK, Smith LP (2007) Comparing likelihood and Bayesian coalescent estimation of population parameters. Genetics 175:155–165

Marshall HD, Baker AJ (1997) Structural conservation and variation in the mitochondrial control region of fringilline finches (*Fringilla* spp.) and the greenfinch (*Carduelis chloris*). Mol Biol Evol 14:173–184

Mysterud I (1970) Hypotheses concerning characteristics and causes of population movements in Tengmalm's owl (*Aegolius funereus* (L.)). Nytt Magasin For Zoologi 18:49–74

Panchal M (2007) The automation of nested clade phylogeographic analysis. Bioinformatics 23:509–510

Petit RJ, Mousadik AE, Pons O (1998) Identifying populations for conservation on the basis of genetic markers. Conserv Biol 12:844–855

Portenko LA (1972) Die Schnee-Eule, *Nyctea scandiaca*. A. Ziemsen Verlag, Wittenberg Luterstadt

Posada D, Crandall KA (1998) MODELTEST: testing the model of DNA substitution. Bioinformatics 14:817–818

Posada D, Crandall KA, Templeton AR (2000) GeoDis: a program for the cladistic nested analysis of the geographical distribution of genetic haplotypes. Mol Ecol 9:487–488

Rassi P, Alanen A, Kanerva T et al (eds) (2001) The red list of Finnish species. Ministry of the Environment & Finnish Environment Institute, Helsinki

Ruokonen M, Kvist L (2002) Structure and evolution of the avian mitochondrial control region. Mol Phylogenet Evol 23:422–432

Sangster G, Collinson JM, Helbig AJ et al (2004) Taxonomic recommendations for British birds: second report. Ibis 146:153–157

Smith N (2005) Snowy owl telemetry research project. http://www.massaudubon.org/Birds_&_Beyond/snowyowl/index.php, Massachusetts Audubon Society. Accessed 04 Feb 2007

Solheim R (1994) Snøugle *Nyctea scandiaca*. In: Gjershaug JO, Thingstad PG, Eldøy S, Byrkjeland S (eds) Norsk fugleatlas. NOF, Klæbu, p 272

Solheim R (2004) 30 år uten snøugle. Vår fuglefauna 27:102–108

Sorenson MD, Ast JC, Dimcheff DE et al (1999) Primers for a PCR-based approach to mitochondrial genome sequencing in birds and other vertebrates. Mol Phylogenet Evol 12:105–114

Tamura K, Nei M (1993) Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. Mol Biol Evol 10:512–526

Templeton AR, Maxwell T, Posada D et al (2005) Tree scanning: a method for using haplotype trees in phenotype/genotype association studies. Genetics 169:441–453

Weir BS, Cockerham CC (1984) Estimating *F*-statistics for the analysis of population structure. Evolution 38:1358–1370

Wenink PW, Baker AJ, Rösner H-U et al (1996) Global mitochondrial DNA phylogeography of Holarctic breeding dunlins (*Calidris alpina*). Evolution 50:318–330

Wennerberg L (2001) Breeding origin and migration pattern of dunlin (*Calidris alpina*) revealed by mitochondrial DNA analysis. Mol Ecol 10:1111–1120

Wink M, Heidrich P (2000) Molecular systematics of owls (*Strigiformes*) based on DNA-sequences of the mitochondrial cytochrome *b* gene. In: Chancellor RD, Meyburg B-U (eds) Raptors at risk: proceedings of the V world conference on birds of prey and owls, Midrand, Johannesburg, South Africa 4–11 August 1998. Hancock House Publishers, Berlin, pp 819–828