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RESEARCH ARTICLE

Dispersal promotes high gene flow among Canada lynx populations across mainland North America

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Abstract The amount and extent of dispersal can have a large effect on the evolutionary trajectory, dynamics and structure of populations. Thus, understanding patterns of genetic structure provide information about the needs and approaches for population management and species conservation. To date studies addressing the population structure of Canada lynx (*Lynx canadensis*) have been surprisingly equivocal, despite a large amount of research quantifying population cyclicity and synchrony and the species' species at-risk status in the contiguous United States and eastern provinces of Canada. Here we use 17 microsatellite loci to conduct a large-scale genetic structuring assessment for Canada lynx, including most of its geographic range from Alaska to Newfoundland. We found large differentiation between lynx populations on the island of Newfoundland and those on the mainland. Yet, contrary to previous studies we found little genetic differentiation (F_{ST}, D_{est}, R_{ST}) owing to the Rocky Mountains, but some evidence of a subtle gene flow restriction between Ontario and Manitoba as previously proposed to be the result of a climatic barrier. Bayesian clustering analysis, however, only suggested two genetic clusters, one consisting of lynx from Newfoundland, and the other consisting of lynx from the rest of the North American range. Because Canada lynx are harvested for fur across most of their range, our results are informative for effective management strategies (e.g., defining management units) aimed at ensuring long-term population connectivity and species persistence.

Keywords Bayesian clustering · Conservation · Discriminant analysis of principal components · Microsatellite · Newfoundland

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Introduction

Dispersal is a central process affecting the dynamics and evolution of populations (Hanski 1998). A variety of factors can influence patterns of dispersal, including home range attributes (Bowman et al. 2002), connectivity of landscapes or habitats (Gibbs 1998; Riley et al. 2006), and even large-scale climatic patterns (Geffen et al. 2004). Because of the importance of dispersal in maintaining genetic diversity (O'Connell et al. 2007) and population persistence (e.g. Brooker and Brooker 2002; Bonte et al. 2004), effective management and conservation strategies require an understanding of the dispersal patterns and their impact on the genetic population structure. Dispersal is difficult to observe in nature, necessitating the quantification of dispersal success through measures of gene flow (Broquet and Petit 2009). Genetic approaches have been used to identify factors that promote or impede dispersal, its extent and direction, and its overall effect on broader genetic structure of meta-populations (Manel et al. 2003; Broquet and Petit 2009).

Because of its large and cyclic fluctuations, the population dynamics and ecology of Canada lynx (*Lynx canadensis*) have long garnered the attention of population ecologists (Elton and Nicholson 1942; Moran 1953; Stenseth et al.

1998). Dispersal may be closely linked with these population fluctuations, with some studies suggesting greater dispersal rates during population crashes (Slough and Mowat 1996; Poole 1997). Through radio-telemetry, Poole (1997) also revealed extensive dispersal distances (average ~150 km and maximum ~1,100 km), with no significant difference in dispersal rates between males and females or between yearling and adults. Despite these large dispersal distances, Canada lynx have been described as habitat specialists (Murray et al. 1994; Mowat and Slough 2003; Hoving et al. 2005), which might imply limited dispersal ability, especially in portions of their geographic range where habitat may be fragmented (Murray et al. 2008).

Genetic studies that have quantified rates of dispersal and levels of population structure in lynx have provided equivocal results. Rueness et al. (2003) used 9 microsatellite loci to examine population differentiation across a large portion of their range and suggested east–west and north–south dispersal barriers imposed by the Rocky Mountains. They also suggested that climatic conditions caused by the North Atlantic Oscillation (NAO) forced an 'invisible barrier', restricting gene flow in the eastern range between Manitoba and Ontario, Canada. Follow-up work suggested that these climatic barriers do not only restrict gene flow, but also cause differential population dynamics on either side of the barriers (Stenseth et al. 1999, 2004a, b). In contrast to these results, Schwartz et al. (2002) failed to find either restricted gene flow or isolation by distance between lynx populations in the Rocky Mountains. This was further supported by Campbell and Strobeck (2006) who found that lynx in southern Alberta, Canada were largely panmictic. Thus, because of these conflicting results the linkage between lynx populations in the core of their range in Canada remains unclear.

Rueness et al. (2003) had incomplete range-wide sampling and used arbitrarily defined geographic populations, which can lead to spurious identification of genetic boundaries (Manel et al. 2004) and possibly resulted in the equivocal results of these previous studies. Thus, here we use additional microsatellite loci and range-wide sampling (Fig. 1) to quantify patterns of dispersal and population connectivity and test for the presence of large-scale continental boundaries. Given the large dispersal capacity for lynx (Poole 1997) and low F_{ST} values presented in Rueness et al. (2003) we predict that with more complete sampling these boundaries will not be apparent at a continental scale. We also include sampling from the island of Newfoundland and because of previously described morphological divergence (Van Zyll De Jong 1975) we predict a restriction in gene flow between mainland and island populations.

Materials and Methods

Sample collection and summary statistics

From fur auction houses we collected tissue samples (2.5 × 2.5 mm) cut from the hide of 298 Canada lynx

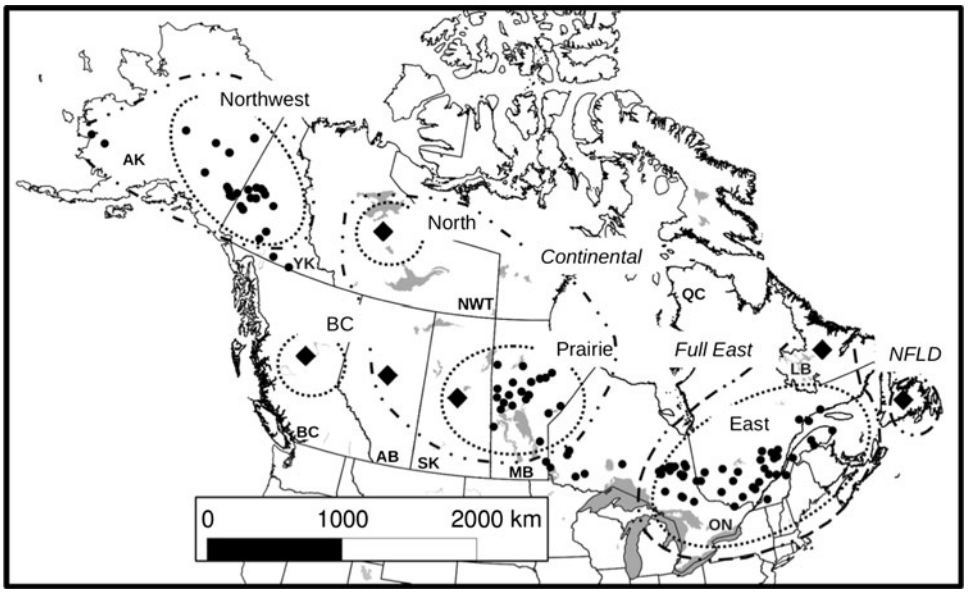

Fig. 1 Sampling locations of Canada lynx across North America. *Small black circles* are the geographic centroid of the *trap-line* where the individual was harvested and *large black diamonds* represent the centroid of the province or territory for those samples where individual harvest location was unknown. *Large open circles* with *dashed lines* are sampling divisions based on Rueness et al. (2003) used for population-level analysis and comprise subset A. Groupings with *double dashed lines* and *italic labels* (*Continental, Northwest, NFLD)* are additional groupings used in subset B (see text), and *small bolded labels* are abbreviations for sampling jurisdictions

Table 1 Sample size (n), mean observed heterozygosity (H_{obs}), mean expected heterozygosity (H_{exp}), mean number of alleles (MNA) and F_{IS} for 17 microsatellite loci within subset A and Newfoundland (see text and Fig. 1) of Canada lynx across North America

Population	n	H_{obs}	H_{exp}	MNA	F_{IS}
East	51	0.70 (0.16)	0.71 (0.14)	7.00 (2.69)	0.020 (0.06)
Prairie	59	0.70 (0.17)	0.71 (0.17)	7.47 (3.16)	0.011 (0.07)
North	30	0.71 (0.19)	0.70 (0.15)	6.76 (3.19)	0.002 (0.15)
Northwest	53	0.72 (0.16)	0.72 (0.16)	7.29 (3.57)	0.014 (0.09)
BC	30	0.71 (0.19)	0.70 (0.16)	6.47 (2.92)	−0.016 (0.09)
NFLD	25	0.38 (0.23)	0.41 (0.23)	2.94 (1.08)	0.054 (0.18)

Standard deviation is given in brackets

legally trapped during 2009 in 9 Canadian provinces/territories and Alaska, USA. We identified the trap-line or fur management unit of harvest for samples from Alaska, Yukon, Manitoba, Ontario, and Quebec. For samples from British Columbia, Alberta, Saskatchewan, and Northwest Territories, we identified the province or Territory of harvest only. Samples from the province of Newfoundland were identified as been harvested in Labrador (mainland) or the island of Newfoundland (island) (Fig. 1). We extracted DNA from tissue by first placing the tissue in lysis solution with 10 µl proteinase K (Roche, Basel, Switzerland) and placing the sample in a 65 °C water bath for ~2 h. Subsequently we added another 10 µl of proteinase K and placed it in a 37 °C incubator for at least 24 h. We vortexed the samples after each addition of proteinase K. We then processed the lysate using a Qiagen (Hilden, Germany) DNeasy Blood and Tissue kit following the manufacturer's protocols.

Initially, we genotyped the extracted DNA at 21 microsatellite loci; 6 characterized in lynx (Lc106, Lc109, Lc110, Lc111, Lc118, and Lc120; Carmichael et al. 2000) and 15 in the domestic cat (Fca008, Fca031, Fca035, Fca043, Fca045, Fca077, Fca078, Fca090, Fca096, Fca149, Fca391, Fca441, Fca559, F41, and F115; Menotti-Raymond et al. 1999). We used capillary electrophoresis on an Applied Biosystems (ABI) 3730 DNA Analyzer using GeneScan 500 ROX as a size standard. We scored genotypes manually with Genemarker version 1.7 (Softgenetics, Pennsylvania, USA). We paid particular attention to scoring, with each profile scored by two independent observers. We removed 4 loci (Fca149, F41, F115, Fca096) from further analysis because of discrepancies in allele size between our two independent observers.

Genetic diversity and differentiation

Because our sample range extended beyond the area studied by Rueness et al. (2003), we divided our samples into two subsets. To directly compare with the results of Rueness et al. (2003) the first subset (subset A) consisted of samples grouped into the same 5 spatially discrete populations (Northwest ($N = 53$), North ($N = 30$), BC ($N = 30$), Prairie ($N = 59$), East ($N = 51$); Fig. 1). We removed individual samples that were outside of the sampling region of Rueness et al. (2003)and within proposed boundaries (we omitted all samples from Alberta and the island of Newfoundland, and some individual samples from Alaska, Yukon, Ontario, and Manitoba; Fig. 1). As an additional test of the putative dispersal barriers in the Rocky Mountains (separating Continental region from BC and Northwest) and eastern Canada (separating Continental region from Full East), we re-grouped the samples (subset B) into 5 groups (Northwest ($N = 55$), British Columbia ($N = 30$), Continental ($N = 118$), Full East ($N = 62$), island of Newfoundland ($N = 25$); Fig. 1) using an extended dataset, but still based on the proposed boundaries. Individual samples in proposed boundary zones were also left out of this subset.

For each locus, we used Fisher's exact tests (100 batches with 1,000 iterations per batch) in Genepop 4.0.10. (Raymond and Rousset 1995) to test for Hardy–Weinberg equilibrium (HWE) and linkage disequilibrium within regions in subset A and the island of Newfoundland (Table 1; Fig. 1). We tested for null alleles and scoring errors using MICRO-CHECKER 2.2.3 (Van Oosterhout et al. 2004), which tests for HWE within each allele size class in each population. We also summarized the patterns of genetic diversity for all loci within each region by determining mean observed and expected heterozygosity, mean number of alleles, and mean F_{IS} using the adegenet 1.2-8 (Jombart 2008) package in R (R Development Core Team 2009).

For both subset A and subset B we compared the magnitude and statistical significance of differentiation between each group. We determined pair-wise F_{ST} (Weir and Cockerham 1984) and R_{ST} (Slatkin 1995) values using GENEPOP 4.0.10 (Raymond and Rousset 1995) (the same program used by Rueness et al. 2003) and pair-wise D_{est} (Jost 2008) values using SMOGD v 1.2.5 (Crawford 2010). We estimated the statistical significance of genetic differentiation between populations with GENEPOP 4.0.10 (100 batches with 1,000 iterations per batch) by comparing the observed grouping of populations to randomly distributed genotypes using a

Goudet's G test (Goudet et al. 1996). We also tested for isolation by distance between regions (centroids as locations) in subset A by calculating a Mantel's r and determining if it was significantly greater than 0 with 100,000 permutations using the ecodist 1.2.2 package (Goslee and Urban 2007) in R (R Development Core Team 2009).

Discriminant analysis of principal components

We used discriminant analysis of principal components (DAPC; Jombart et al. 2010) with the adegenet 1.2-8 (Jombart 2008) package in R (R Development Core Team 2009) to determine if we could genetically differentiate regions based on the suggested barriers (i.e., the Rocky Mountain barrier and climatic barrier between Manitoba and Ontario, suggested by Rueness et al. 2003). DAPC is a two-step process, which first transforms raw genetic data using principal components analysis (PCA) and then maximizes genetic differentiation between groups, without making several commonly required assumptions (e.g., Hardy–Weinberg equilibrium, linkage disequilibrium) about the underlying genetic data (Jombart et al. 2010). Because previous work on lynx (Rueness et al. 2003) did not use DAPC, a direct comparison was not possible. We therefore only used subset B, excluding Newfoundland, because of the large and obvious genetic differentiation found in the other analysis.

The number of PCA components retained for the discriminant analysis is a tradeoff between the power and consistency of assignment, with more PCA axes increasing the ability to discriminate between sampled groups, but possibly reducing the ability to correctly assign new individuals (Jombart et al. 2010). We therefore determined the optimal number of components to be retained by calculating the *a*-score as the true assignment probability of individuals to their population (Pt) minus the assignment probability for individuals from randomly permuted populations (Pr) for increasing numbers of retained PCA components (optim.a.score function in adegenet). We ran 100 permutations for each increasing number of retained PCA components and used the number of components that maximized the *a*-score. Using the optimal number of PCA components, we then determined the mean *a*-score (Pt–Pr) for each group from 10,000 permutations and calculated a *p* value as the proportion of permutations with an *a*-score greater than 0.

Bayesian clustering

Although spatial clustering can have greater power to detect spatially distributed genetic population structure (Chen et al. 2007) and genetic clines (François and Durand 2010) than their non-spatial counterparts, the absence of explicit spatial locations for some of our samples necessitated that we use non-spatial Bayesian clustering. Because previous studies did not use Bayesian clustering we used our full dataset ($N = 298$) for this analysis. We used STRUCTURE 2.3.3 (Pritchard et al. 2000) to determine the optimal number of clusters (k) by running 600,000 MCMC iterations (100,000 burnin) with 10 runs per k, for $k = 1$–5, using the admixture model with correlated allele frequencies and determined the number of clusters with ΔK, calculated using the criteria outlined in Evanno et al. (2005). We started with a maximum k of 5 because the suggested barriers would likely result in four clusters across the mainland, and then a fifth could be comprised of the samples from the island of Newfoundland.

Results

General summary statistics

We found no evidence for departures from HWE after sequential Bonferroni correction (Rice 1989), but found evidence for two loci (Fca391 & Lc110) to be in linkage disequilibrium on the island of Newfoundland. MICRO-CHECKER found no evidence of scoring errors, but potential null alleles for 1 locus (Fca441) in the Northwest population. Because of the large number of tests (11 populations at 17 loci), null alleles nor linkage disequilibrium were likely not a pervasive problem in our dataset and we used all of the remaining loci in subsequent analyses.

All measures of genetic diversity (H_{obs}, H_{exp}, number of alleles, F_{IS}) averaged across loci were similar between regions (Table 1), with the exception of the Newfoundland population. Newfoundland had lower H_{obs} and H_{exp}, as well as lower number of alleles per locus (Table 1) relative to the other populations.

Genetic differentiation

Our F_{ST} values for subset A were overall lower than those of Rueness et al. (2003) (Table 2) with comparisons involving the BC and Northwest region differing by 1–2 orders of magnitude. In our analysis, the East region was significantly differentiated from all other regions and generally had the largest D_{est}, F_{ST}, and R_{ST} values. Contrary to Rueness et al. (2003), British Columbia was not significantly differentiated from the North or Northwest regions. Consistent with Rueness et al. (2003), we found no significant difference between the Prairie and North regions. The Mantel's r was 0.80, which was significantly greater than 0 (p value = 0.016). This trend however was mainly driven by larger F_{ST} values between the EAST and all other regions.

When using subset B, we found similar results, with only British Columbia and Northwest regions not being significantly differentiated (Table 3). D_{est} (not shown) and F_{ST} between Newfoundland and all other regions were

Table 2 Pairwise F_{ST} (lower)[a] and R_{ST} (upper) between populations of Canada lynx across North America using data subset A

	East	Prairie	North	Northwest	BC
East		0.0069	0.0021	0.0004	0.0000
Prairie	0.0071***		0.0001	0.0030	0.0100
North	0.0080***	0.0018		0.00113	0.0002
Northwest	0.0069***	0.0061***	0.0035**		0.0034
BC	0.0077***	0.0034***	0.0008	0.0008	

See Fig. 1 and text for distribution of populations

[a] We used Goudet's G test (Goudet et al. 1996) in Genepop 4.0.10 (Raymond and Rousset 1995) to determine significant differentiation based on F_{ST} (* 0.05, ** 0.01, *** 0.0001)

Table 3 Pairwise F_{ST} (lower)[a] and R_{ST} (upper) between populations of Canada lynx across North America using data subset B

	East	Northwest	Continental	BC	NFLD
Full East		0.0042	0.0003	0.0009	0.2240
Northwest	0.0048***		0.0009	0.0029	0.1940
Continental	0.0070***	0.0048***		0.0107	0.2087
BC	0.0070***	0.0003	0.0019**		0.2548
NFLD	0.1876***	0.1938***	0.1800***	0.2028***	

See Fig. 1 and text for distribution of populations

[a] We used Goudet's G test (Goudet et al. 1996) in Genepop 4.0.10 (Raymond and Rousset 1995) to determine significant differences based on F_{ST} (* 0.05, ** 0.01, *** 0.0001)

significant and 2–3 orders of magnitude higher than all other values (Table 3). R_{ST} values were similar, but often slightly smaller than F_{ST} values for both comparisons. The exception was Newfoundland, where R_{ST} values were similar, but slightly higher than F_{ST} values (Table 3).

Discriminant analysis of principal components

We determined that the optimal number of PCA components to include in the DAPC analysis was 73, which accounted for 85 % of the variation within the multivariate microsatellite dataset. A scatterplot of the first two principal components suggested some separation between the East and the other three regions along the first DA component and possibly some separation between the Continental, BC, and Northwest regions along the second DA component (Fig. 2). Assignment probabilities (Pt) were higher for the East (0.82) and Continental (0.85) regions than the British Columbia (0.60) and Northwest (0.69) regions. The East region, however, had much higher *a*-scores (0.25, $p < 0.0001$) than the Continental (0.06; $p = 0.03$), Northwest (0.13; $p = 0.03$) and British Columbia (0.04; $p = 0.39$) regions.

Bayesian clustering

We used the Evanno et al. (2005) method to determine the number of genetic clusters in our data; ΔK reached a clear plateau at $k = 2$ (Fig. 3a, b), with the island of Newfoundland forming one distinct cluster and all of the mainland regions forming the other (Fig. 4a). When we increased the assumed number of clusters to $k = 3$ and above, no additional patterns of structure emerged, supporting our conclusion of $k = 2$ (Fig. 4b). Furthermore, we re-ran the analysis including only the mainland individuals with and without including a location prior (Hubisz et al. 2009) of the province, territory or state of sampling. For both of these analysis mean log-likelihood was highest for $k = 1$ (Fig. 3c, d), also supporting the mainland samples coming from the same genetic cluster.

Discussion

Using both individual and population-based analyses we found surprisingly low levels of population genetic structure across all of mainland North America for Canada Lynx, suggesting high levels of dispersal. We found no evidence that the Rocky Mountains were a barrier to gene flow, but we did find some evidence using Goudet's G test and DAPC for a subtle restriction in gene flow between Manitoba and Ontario. Levels of differentiation on either side of the putative barrier, however, were markedly low and not identified using non-spatial Bayesian clustering. In contrast, we found relatively large differentiation between

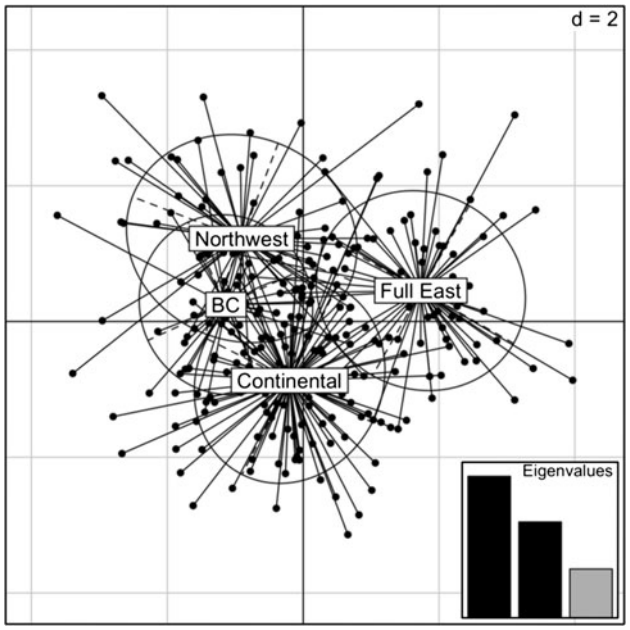

Fig. 2 Scatterplot of individual genotypes from a discriminant analysis (DA) of DA axis 1(x-axis) and DA axis 2(y-axis) of Canada lynx genotypes. *Black ovals* are 95 % inertia *ellipses* and *dots* represent individual genotypes, with *black lines* extending to the centroids of the respective populations (see text and Fig. 1 for distribution of samples). *Inset* shows a *bar chart* of the eigenvalues with corresponding components in *black*. Grid distance (*d*) corresponds to a value of 2

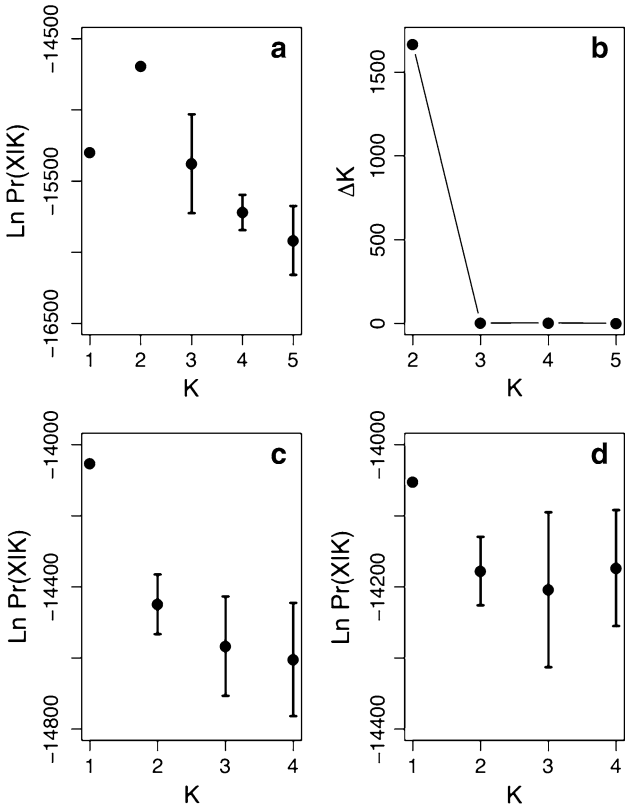

Fig. 3 Identification of the number of genetic clusters for Canada lynx across North America using Bayesian clustering with STRUCTURE: **a** mean log-likelihood (±SD) for 10 replicate runs using individuals from all regions, **b** Δ*k* for 10 replicate runs using individuals from all regions, **c** mean log-likelihood (±SD) for 10 replicate runs using individuals from mainland regions (excluding individuals from the island of Newfoundland), and **d** mean log-likelihood (±SD) for 10 replicate runs using individuals from mainland regions and using jurisdiction (State, Province or Territory) as a locational prior

the mainland and individuals on the island of Newfoundland. Our results, suggest there should be close cooperation among different jurisdictions across the lynx range to ensure continued population connectivity and further assessment of the distinctiveness of lynx on the island of Newfoundland.

Large-scale population structure

Using Bayesian clustering we found only two genetic clusters, one of which stretched across all of mainland North America. Similarly, levels of differentiation (F_{ST}, D_{est}, R_{ST}) between different regions sampled on the mainland, was exceedingly low. Very few studies that have examined large-scale genetic population structure for continuously distributed mammals at comparable scales have found such a lack of genetic structure. For example, population genetic analysis on wolves (*Canis lupus*; Carmichael et al. 2007), caribou (*Rangifer tarandus*; Ball et al. 2010), and wolverines (*Gulo gulo*; Kyle and Strobeck 2001) in North America and brown bears (*Ursus arctos*; Tammeleht et al. 2010) in Eurasia have all found greater differentiation between regions and/or a higher number of genetic clusters at comparable scales. Even the closely related Eurasian Lynx (*Lynx lynx*; reviewed in Schmidt et al. 2011) and North American bobcat (*Lynx rufus*; Croteau 2009) have much greater genetic population structure across their respective ranges.

Neutral genetic structure is generally the result of a variety of causes acting across spatial and temporal scales (Costello et al. 2003; Row et al. 2011). Indeed, in terrestrial mammals, observed genetic structure has been attributed to a variety of factors including: habitat and prey-mediated dispersal patterns and historical fragmentation during the glacial periods (wolves: Carmichael et al. 2007; Musiani et al. 2007), human mediated habitat fragmentation (wolverines: Kyle and Strobeck 2001), and demographic history and landscape barriers (brown bears: Tammeleht et al. 2010). The arctic fox (*Alopex lagopus)* is another mammalian species that has very little genetic differentiation across its continent-wide distribution, likely related to the absence of historical population fragmentation combined with high levels of recent gene flow (Carmichael et al. 2007). A similar process might be at work for mainland Canada lynx; Rueness et al. (2003) used mitochondrial

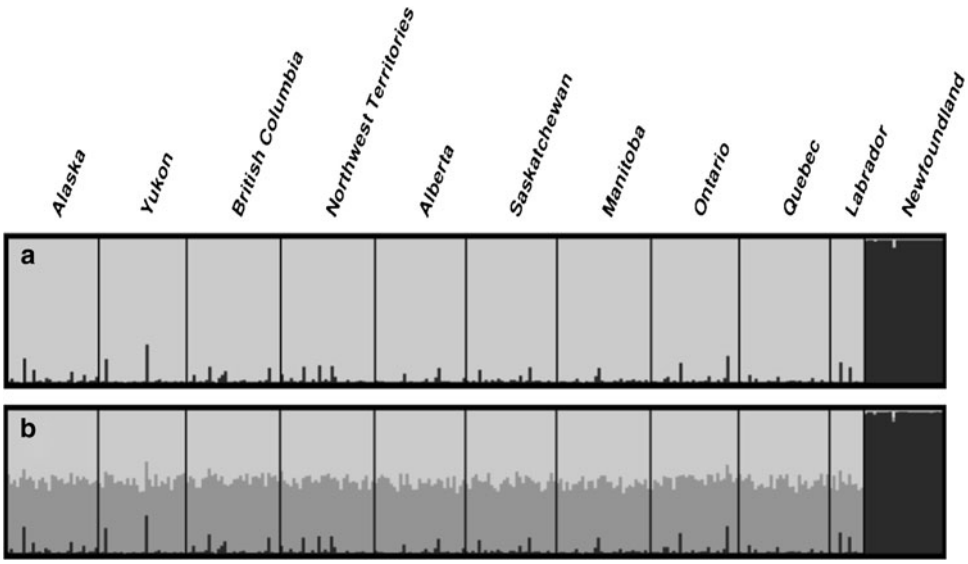

Fig. 4 Admixture coefficients for Canada lynx genotypes from a non-spatial Bayesian clustering analysis. Number of clusters (k) set to two (**a**) and three (**b**)

DNA to show that the genetic structure of Canada lynx across its range is reflective of recent expansion from a smaller number of individuals, rather than historical population fragmentation. This is also supported by the similarity of our divergence estimates when using R_{ST} and F_{ST}, which is suggestive of divergence patterns related to genetic drift rather than mutations (Hardy et al. 2003).

The possibility that lynx dispersal is more pronounced during population declines of its primary prey, the snowshoe hare (*Lepus americanus;* Slough and Mowat 1996; Poole 1997) may also contribute to the low levels of genetic differentiation in lynx. Genetic differentiation at neutral loci is the result of the diversifying effects of genetic drift and mutation, counter-balanced by the unifying effect of gene flow (Wright 1948). Small population sizes during population crashes will be subject to greater amounts of genetic drift, but will also be more affected by gene flow (i.e., less gene flow is required to unify small populations). Simulations of population cycles could provide insight into the effects of population cyclicity on genetic differentiation, although limited simulations by Stenseth et al. (2004b) suggested that genetic differentiation was lower with high gene flow during population crashes.

For the western portion of lynx distribution, our results are similar to Schwartz et al. (2002) and Campbell and Strobeck (2006) in that we found no genetic differentiation between lynx populations. In contrast to our results, Rueness et al. (2003) found significant genetic differentiation between the BC and the North (Alaska-Yukon) and Northwest (Northwest Territories) regions, despite low patterns of differentiation overall. In fact, F_{ST} values for all studies (excluding Campbell and Strobeck (2006) who used individual based analysis) varied quite substantially between studies, possibly because different microsatellite loci were used. Here we used more loci than Rueness et al. (2003) and Stenseth et al. (2004a), including 6 loci specifically developed for lynx, therefore we should have greater power to detect genetic population structure if it exists. Population definition and the distribution of samples may also affect the differences between studies (i.e. how populations are grouped is likely to have an effect on the analysis; Manel et al. 2004), although we tried to minimize this by grouping our samples the same way as Rueness et al. (2003). From a biological perspective, it is possible that samples collected at different time-points in the lynx population cycle could have significant effects on observed patterns of gene flow. Despite the differences between studies, it is clear from our results, Schwartz et al. (2002) results, and the low F_{ST} values presented in Rueness et al. (2003), that the Rocky Mountains do not provide a strong barrier to gene flow for lynx. Further analysis with geo-referenced samples may identify corridors to gene flow that allow dispersal through this region.

Similar to Rueness et al. (2003), we found that the East (Ontario-Quebec) region was significantly differentiated from all other regions. Our pairwise F_{ST} values, however, were very low (in some cases 1–2 orders of magnitude lower than Rueness et al. (2003)) and similar between all regions. The differentiation of the East region was also not supported by Bayesian clustering, but somewhat supported the DAPC results, which could assign individuals to this region significantly greater than randomly permuted clusters. These results support the possibility of a subtle restriction in gene flow between the East and Prairie regions. The 'invisible barrier' between these regions, originally proposed by Rueness et al. (2003), was later attributed to snow conditions resulting from the North

Atlantic Oscillations, resulting in different population dynamics on either side of the barrier (Stenseth et al. 1999, 2004a, b). Given the importance of snow conditions for prey capture by lynx (Stenseth et al. 2004b) and its importance for other species (Carr et al. 2007) it is possible that population dynamics differ on either side of the putative climate barrier. Direct tests of association between genetic data and landscape or environmental data (e.g. Balkenhol et al. 2009) and verification from other species that should similarly be affected by snow conditions (e.g., coyotes or fox) would provide stronger evidence.

Newfoundland differentiation

Despite morphological divergence between mainland and Newfoundland populations of Canada lynx (Van Zyll De Jong 1975), to date no study has quantified the genetic divergence between the mainland and the island. Given that Newfoundland is at least 18 km from the mainland, we do not expect regular lynx dispersal from the mainland. We therefore expected the high levels of genetic differentiation that we observed between island and mainland populations of lynx, as well as lower genetic diversity for the island population. There has been different speculation as to the initial colonization of lynx on the island, with some suggesting they arrived early in the post-glacial period (Cameron 1958) and others as late as 1861 (Dodds 1960). There are many factors that may have influenced the genetic differentiation between mainland and Newfoundland lynx, such as the level of gene flow, population size, and timing of migration. Future work using slower mutating genetic markers (e.g., mitochondrial, nuclear introns) or coalescent analysis might provide some insight into the colonization history, taxonomy, and status of Canada lynx in Newfoundland.

Conservation implications

The Canada lynx is legally trapped throughout its range and a thorough understanding of population structure is particularly important for proper management (e.g., defining management units) and conservation. Management units are generally defined as demographically independent units and provide guidance on delineating areas for monitoring and regulating human pressures on species and populations (Palsbøll et al. 2006). Currently, lynx are managed on a provincial and state level, but based on our results it is clear lynx are not confined to these boundaries. Although we are not necessarily suggesting that lynx in mainland North America should comprise a single management unit, there should be close cooperation among different jurisdictions given the patterns of population structure.

Although we found very little genetic population structure at course spatial scales, more research is required to understand patterns at finer geographic scales. Incorporating geographic locations and examining correlations between individual-based isolation by distance patterns and landscape variables may provide insight into the effects of landscape and climate on patterns of differentiation between individuals (e.g., Cushman et al. 2006). This information will assist with identifying and maintaining current patterns of connectivity across the range of lynx. This is particularly true for more southern populations, which were not examined in detail here, but are likely more at risk and possibly more fragmented (Murray et al. 2008).

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