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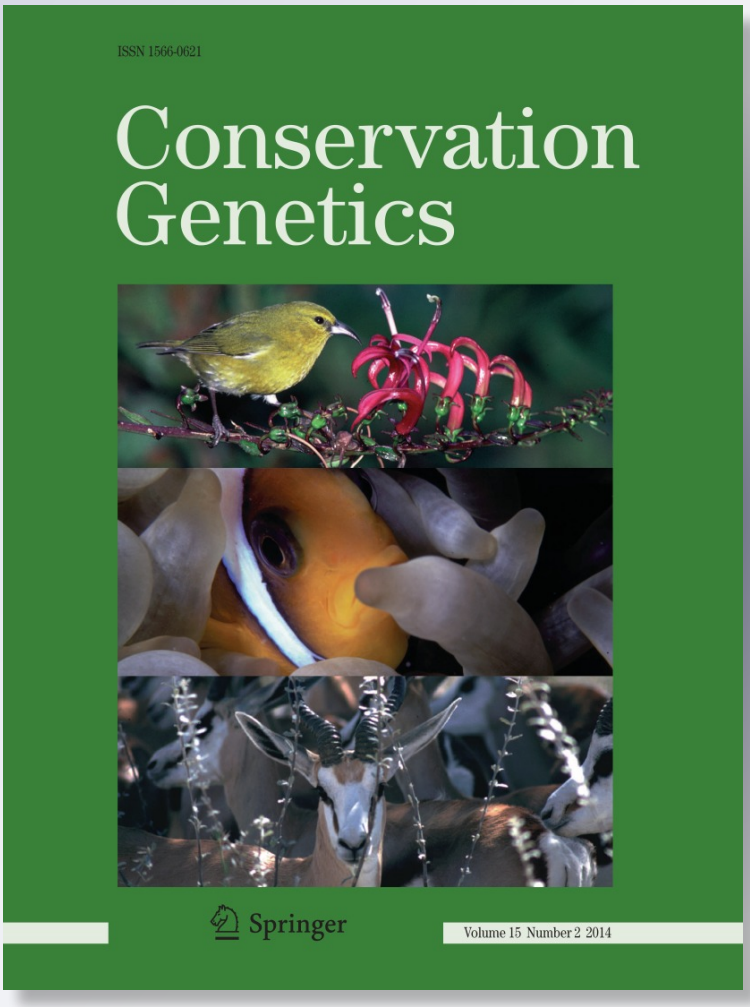

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RESEARCH ARTICLE

Evidence for genetic differentiation among Caspian tern (*Hydroprogne caspia*) populations in North America

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Abstract The Caspian tern (*Hydroprogne caspia*) is a globally distributed seabird that breeds throughout North America, generally in low numbers. Many colonies are threatened by habitat loss and pollution. Additionally, adult terns compete directly with salmonid stocking programs on the west coast, where a large proportion of the fish they feed their young are stocked salmon smolts. North America colonies have been classified into five 'breeding groups' based on banding data and geography. To help delineate effective management units, we characterized variation in mitochondrial DNA (488 base pair fragment of cytochrome b) and five microsatellite loci among 111 terns from six sites representing three of the North American breeding areas. We found significant range-wide population differentiation (cytochrome b: global $\Phi_{ST} = 0.12$, $P < 0.01$; microsatellites: global $F_{ST} = 0.094$, $P < 0.001$). Pacific Coast sites differed genetically from sites east of the Rocky Mountains, and sites in Central Canada differed from those in the Great Lakes region. Gene flow among these three regions appears to be restricted. Thus, our results indicate that at least three of the breeding regions delineated using banding data and geography should be treated as separate management units.

Keywords Breeding groups · Caspian tern · Conservation genetics · *Hydroprogne caspia* · Management units · Population genetic structure

Introduction

Caspian terns (*Hydroprogne caspia*) are colonial waterbirds that are globally distributed but uncommon throughout their range (Wires and Cuthbert 2000). Populations in North America have been increasing since the 1960's, but have been decreasing across the rest of their global range (Cuthbert and Wires 1999). In North America, Caspian tern colonies range in size from <100 to >10,000 breeding pairs; however, colonies are generally on the smaller end of this size spectrum (Cuthbert and Wires 1999). Given the variable size of colonies, many of which are quite small, Caspian Terns are vulnerable to stochastic events and human disturbance (Wires and Cuthbert 2000). Caspian terns also present a management conflict on the Pacific Coast of North America, where consumption of stocked salmon smolts by waterbirds appears to be inhibiting the recovery of endangered salmonid populations (Roby et al. 2002). This conflict has lead to colony relocation (Roby et al. 2002). Understanding patterns of genetic differentiation and gene flow among colonies is

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important for management and conservation of this species (Moritz 1994; Haig et al. 1998). For example, if dispersal and gene flow occur among colonies at large spatial scales, colony relocation may not adversely affect the population genetic structure of the species in the Pacific Northwest. Similarly, in regions where colony persistence is threatened by habitat loss or pollution, high gene flow could indicate that evolutionary potential may be retained in the face of some colony loss. Currently no genetic information exists for this species, thus, genetic data are needed to help define management units (Moritz 1994), and to identify isolated or vulnerable populations that should be prioritized for protection.

The North American distribution of Caspian terns has been divided into five breeding groups based on banding data and geography: Pacific Coast, Central Canada, Gulf Coast, Atlantic Coast, and Great Lakes (Wires and Cuthbert 2000; Fig. 1). Within each group significant dispersal occurs between breeding sites (Gill and Mewaldt 1983; L'Arrivée and Blokpoel 1988), but little dispersal appears to occur among groups. During one monitoring period, 15 % of banded individuals moved to non-natal sites within the Pacific Coast breeding population, but no evidence of dispersal between breeding groups was found (Gill and Mewaldt 1983; L'Arrivée and Blokpoel 1988). Furthermore, the Pacific Coast and Great Lakes groups have non-overlapping breeding and wintering ranges. However, the genetic connectivity among these breeding groups is not known. For example, even rare successful dispersal can result in genetic panmixia; in contrast, if immigrants do not breed successfully, populations that appear to be demographically connected may be genetically isolated (Wright 1931). The Rocky Mountains have been implicated as a physical barrier to gene flow leading to east–west population genetic differentiation in many avian species (e.g., Ruegg and Smith 2002; Lovette et al. 2004) but their importance in waterbirds is unclear (e.g., Peters et al. 2005 vs. Mercer 2008; Oomen et al. 2011; Reudink et al. 2011).

Here we examine variation in microsatellite loci and mitochondrial DNA (mtDNA) among North American Caspian terns to test two predictions. First, given that Pacific Coast and Great Lakes breeding groups appear demographically isolated, we predict significant genetic differentiation between regions. Second, if the Rocky Mountains are a barrier to gene flow, then the Central Canada group will be more closely related to the Great Lakes group than to the Pacific Coast.

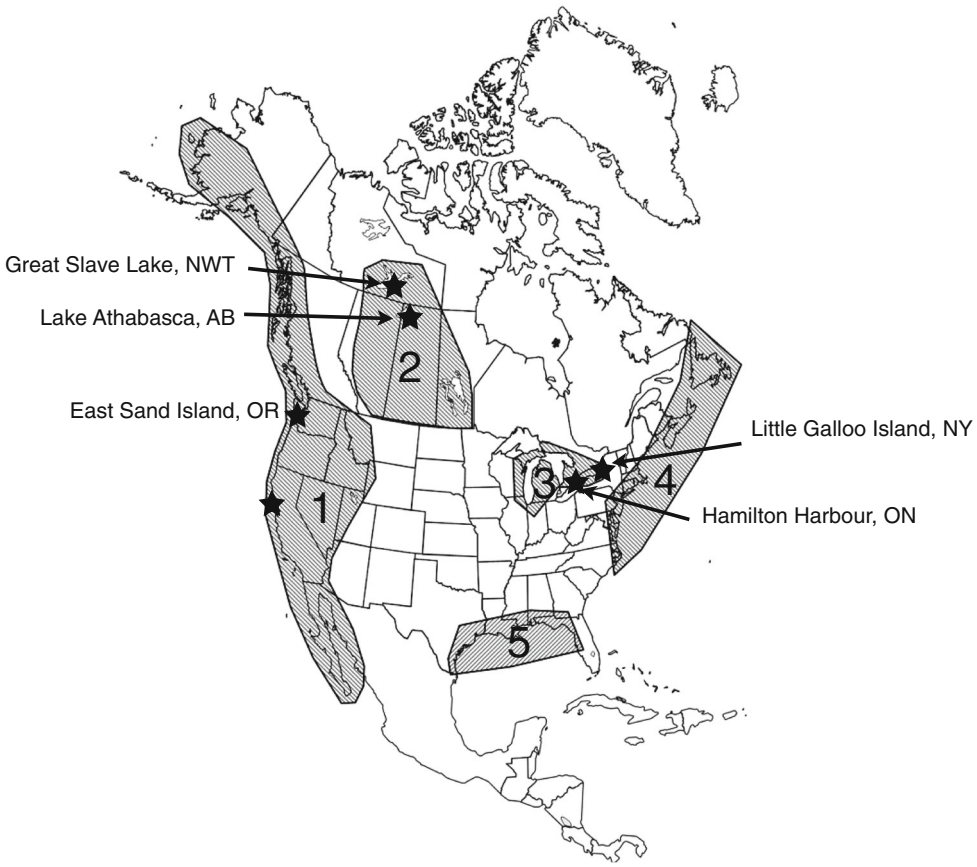

Fig. 1 Sample sites (*black stars*) and breeding groups (*shaded areas*, as defined by Wires and Cuthbert 2000) for Caspian terns in North America. *1* Pacific Coast, *2* Central Canada, *3* Great Lakes, *4* Atlantic Coast, *5* Gulf Coast

Methods

Sample collection and laboratory methods

Tissue samples were collected from six breeding sites: two each from the Pacific Coast, Central Canada (although sample sizes were small), and Great Lakes breeding groups (Fig. 1; Table 1). Sampling more than one adult or chick from any one nest was avoided. DNA was extracted from tissue using a standard phenol/chloroform procedure (Sambrook and Russell 2001). Length variation in five microsatellite loci (RBG18, RBG27, RBG29 [Given et al. 2002], Scaac20 and Sdaat20 [Szczys et al. 2005]) and sequence variation in a 488 base pair fragment of the mitochondrial cytochrome b were assayed following standard conditions (Online Resource 1). Although cytochrome b is not as variable as other mitochondrial genes such as the control region, it is easily amplified using generic primers, is less vulnerable to homoplasy and duplication (e.g., Friesen and Anderson 1997), and has been used successfully to assay population genetic structure in other species of birds (e.g., thick-billed murres *Uria lomvia* Birt-Friesen et al. 1992).

Tests of assumptions and estimates of genetic variation

MICROCHECKER (van Oosterhout et al. 2004) was used to test for null alleles. Allele frequencies and allelic richness (R) were calculated using FSTAT (version 2.9.3; Goudet 2001). For most population-level analyses, Lake Athabasca and Great Slave Lake samples were combined into "Central Canada" (CC) to increase sample size, given the geographic proximity of sampling sites and low pairwise F_{ST} ($F_{ST} = 0.04$, $P = 0.37$). Differences in allelic richness among sites were analyzed using a one-way analysis of variance (ANOVA; Microsoft Excel 2010). ARLEQUIN (version 3.1; Excoffier et al. 2005) was used to calculate observed (H_O) and expected (H_E) heterozygosities for each site, as well as to test for deviations from Hardy–Weinberg and genotypic equilibrium. Hardy–Weinberg equilibrium was tested for all loci using an exact test and randomization with 100,000 Markov chain steps and 1,000 dememorisation steps, and genotypic equilibrium was evaluated by randomization with 10,000 permutations. Tajima's D and Fu's F tests of selective neutrality (Tajima 1989; Fu 1997) were conducted on mitochondrial cytochrome *b* variation using ARLEQUIN.

Estimates of population differentiation and gene flow

To estimate the extent of genetic differentiation among sites, ARLEQUIN was used to perform global and pairwise analyses of molecular variance (AMOVAs) on all microsatellite loci, each microsatellite locus alone, and cytochrome *b* alone. F_{ST} was estimated for microsatellite variation using the "number of different alleles" option, and Φ_{ST} was estimated for cytochrome *b* variation using Kimura's two-parameter nucleotide substitution model (Kimura 1980) with the shape parameter (α) of the gamma distribution determined empirically using MRMODELTEST (version 2.3; Nylander 2004). Tests for isolation by distance were precluded by the small number of sampling sites and the presence of major potential barriers to dispersal (e.g., Rocky Mountains, large breaks in geographic distribution).

The most likely number of genetic clusters (K) in the microsatellite data set was inferred using STRUCTURE (version 2.3; Pritchard et al. 2000). For each value of K between one and seven, 20 runs were performed using an admixture model with allele frequencies correlated among sites, a burn-in of 30,000 generations, and an additional 100,000 generations. In separate analyses, sampling location was either used or not used as prior information. The most likely number of genetic clusters was evaluated using both the method of Pritchard et al. (2000) and ΔK (Evanno et al. 2005). CLUMPP (version 1.1; Jakobsson and Rosenberg 2007) was used to average assignment probabilities across the 20 runs. The "FullSearch" method was specified ($M = 1$) and other parameters were set to default values.

Contemporary gene flow between regions was estimated from microsatellite variation using BAYESASS (version

Table 1 Sample sites and codes, locations, sample sizes (N) and tissue types for Caspian terns

Sample site	Code	Breeding group	Location	N	Tissue
Brooks Island, CA	BI	Pacific Coast	37°53′47.33″N,122°21′18.82″W	30	Feather
East Sand Island, OR	ESI	Pacific Coast	46°15′28.80″N,123°59′12.60″W	30	Muscle
Lake Athabasca, AB	ATH	Central Canada	58°58′51.60″N, 110°26′20.40″W	5	Egg contents
Great Slave Lake, NWT	GSL	Central Canada	62°13′0.00″N, 114°40′60.00″W	8	Egg contents
Hamilton Harbour, ON	HH	Great Lakes	43°17′36.26″N, 79°49′51.11″W	26	Blood
Little Galloo Island, NY	LGI	Great Lakes	43°53′9.21″N, 76°23′43.13″W	12	Blood

Breeding groups are from Wires and Cuthbert (2000)

1.3; Wilson and Rannala 2003). Model parameters were set to default values, and the MCMC was run for 3,000,000 iterations, with a burn-in of 999,999 iterations and a sampling frequency of 2,000.

Results

Genetic variability

In total, 111 individuals from six sample sites were genotyped at five microsatellite loci and sequenced for 488 base pairs of cytochrome *b*. Deviations from Hardy–Weinberg and gametic equilibrium were present in three and one sites, respectively (Online Resources 2). Results from MICROCHECKER suggested that the heterozygote deficiency for locus RBG29 in Central Canada might be due to null alleles. However, deviations from both Hardy–Weinberg and linkage equilibrium could also result from genetic differentiation between the pooled Central Canada sites. Since these deviations were not consistent across sites or loci, all loci were used in subsequent analyses. However, we also explored the effect of individual loci by excluding each locus from each analysis (STRUCTURE, BAYESASS, AMOVA): with the exception of diminished power for one STRUCTURE analysis, all results were qualitatively similar. The number of microsatellite alleles per locus ranged from three for Sdaat20 and Scaac20 to eight for RBG27. No evidence was found that allelic richness differed among sites (ANOVA, $F_{5,24} = 0.19$, $P = 0.96$) (Online Resources 3).

Only two cytochrome *b* haplotypes were found (GenBank accession nos. KC241873- KC241874), and one of these was found only in the Great Lakes and only at low frequency (haplotype B; 5 % of all individuals; Online Resources 2). There was no evidence that cytochrome *b* variation deviated from selective neutrality (Tajima's D, all $P > 0.17$; Fu's F, all $P > 0.13$).

Population differentiation

Unique microsatellite alleles were found within some sites and regions, and some occurred at high frequency (Online Resources 2). For example, allele 220 for locus RBG27 was exclusive to the Central Canada sites, where it occurred in 23 % of chromosomes sampled.

Global F_{ST} based on microsatellite loci indicated significant differentiation among the five Caspian tern breeding sites ($F_{ST} = 0.094$, $P < 0.001$). Significant differentiation was also found for each microsatellite locus alone ($F_{ST} = 0.05$–0.14, all $P < 0.01$). Pairwise F_{ST} estimates within regions were not significant, but were high and statistically significant between sites from different breeding groups (Table 2). Although cytochrome *b* variation was low, the global Φ_{ST} indicated significant population structure ($\Phi_{ST} = 0.12$; $P < 0.01$; Table 2). This pattern appeared to be driven entirely by the presence of haplotype B in the Great Lakes sites but nowhere else (Online Resources 2).

Results from STRUCTURE supported either two or three genetic clusters (Fig. 2). When location was not used as prior information, posterior probabilities and ΔK all indicated that 2 was the most likely number of clusters ($P[K = 2] > 0.9999$; Online Resource 4). However, using the "locprior" model, posterior probabilities indicated that 3 was most likely ($P[K = 3] = 0.982$), whereas ΔK suggested 2 was most likely (Online Resource 4).

Given the results from AMOVA and STRUCTURE, analyses in BAYESASS were performed under both $K = 2$ and $K = 3$. For $K = 2$, Pacific Coast sites were treated as one group, and the other sites as another. In this scenario, individuals assigned to their region of origin on average 95.8 % of the time (which exceeds the estimated rate of 83.3 % expected for non-informative data), and the 95 % confidence intervals for rates of gene flow between regions included zero (Table 3a). For $K = 3$, sites were grouped by breeding group. Individuals assigned to their breeding group on average 86.4 % of the times (which also exceeds the estimate for non-informative data). Although the origin of Central Canada individuals was less certain, the 95 % confidence intervals on rates of gene flow included zero (Table 3b).

Discussion

Results of the present study indicate that Caspian terns breeding in North America are not genetically panmictic.

Table 2 F_{ST} values based on microsatellite variation (below diagonal) and Φ_{ST} values based on cytochrome *b* variation (above diagonal) for pairwise comparisons of sample sites of Caspian terns

	Pacific Coast		Central Canada	Great Lakes	
	BI	ESI	CC	HH	LGI
BI	–	0.00	0.00	0.19*	0.09
ESI	−0.001	–	0.00	0.19*	0.09
CC	0.11*	0.10*	–	0.11	0.01
HH	0.15*	0.13*	0.06*	–	−0.01
LGI	0.16*	0.14*	0.09*	−0.02	–

CC (Central Canada) represents the pooled Lake Athabasca/Great Slave Lake sites

Given the small number of sampling sites, no corrections for multiple tests were conducted

* Significantly greater than 0 at $\alpha = 0.05$

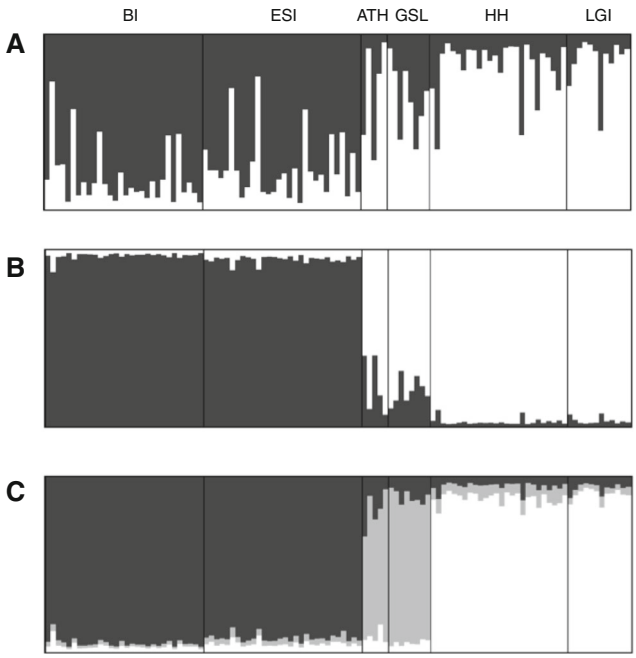

Fig. 2 Assignment probabilities for each individual Caspian tern into genetic clusters inferred by STRUCTURE (the *shades* of each *vertical bar* represent an individual's assignment probabilities to each genetic cluster) for the following scenarios: **a** K = 2, **b** K = 2 using location as prior information, **c** K = 3 using location as prior information. *Vertical black lines* separate sampled populations. See Table 1 for sample site names

Results from AMOVA and BAYESASS for microsatellites indicate that terns from Pacific Coast sites are significantly differentiated from both Great Lakes and Central Canada sites at microsatellite loci, and contemporary gene flow between Pacific Coast and other sites is apparently low (Tables 2, 3a,b). Pacific Coast sites are also significantly differentiated from Great Lakes sites at cytochrome b (Table 2). Although results from STRUCTURE with 'no locprior' were less clear, results using sampling site as prior information differentiated terns by breeding group, rather than sampling site. These findings support conclusions from banding data suggesting that little or no gene flow occurs between Caspian terns from the Pacific Coast and other breeding regions (Gill and Mewaldt 1983; L'Arrivée and Blokpoel 1988). Additionally, Caspian terns breeding in the Great Lakes and Central Canada appear to be genetically isolated from each other: any migration occurring between these regions is likely very low (Table 2; Fig. 2, Online Resources 4). Note however that estimates of genetic differentiation between the Great Lakes and Central Canada may be less accurate than between other breeding populations due to low sample size in Central Canada and the small number of colonies sampled.

East–west differentiation in Caspian terns is consistent with other North American avian taxa (e.g., northern flicker *Colaptes auratus*, Moore and Buchanan 1985; indigo *Passerina cyanea* and Lazuli buntings *P. amoena*, Harrison 1993; yellow-breasted chat *Icteria virens*, Lovette et al. 2004). The Rocky Mountains may be driving this pattern by limiting connectivity among breeding groups. Indeed, results indicate that the Rocky Mountains provide a contemporary physical barrier to gene flow in Caspian terns, and this has been confirmed by low dispersal estimates from band returns (Gill and Mewaldt 1983; L'Arrivée and Blokpoel 1988).

Eastern and western breeding groups of Caspian terns may also have been isolated historically by Pleistocene glaciations. Pleistocene glaciations had significant impacts on the genetic signatures of numerous organisms in North America (Hewitt 2004). With ice as a barrier to gene flow, organisms in ice-free refugia diverged genetically via drift and/or selection, and this divergence was often retained

Table 3 Estimates of contemporary dispersal using the Bayesian assignment method in BAYESASS (95 % confidence intervals) between a) the Pacific Coast and other Caspian terns in North America ("East"), and b) the Pacific Coast, Central Canada, and Great Lakes breeding groups

Recipient	Source	
	Pacific Coast	Great Lakes
a		
Pacific Coast	**0.99** (0.95, 1.0)	0.01 (0.00, 0.05)
East	0.03 (0.00, 0.08)	**0.97** (0.92, 1.0)

Recipient	Source		
	Pacific Coast	Central Canada	Great Lakes
b			
Pacific Coast	**0.99** (0.96, 1.0)	0.01 (0.00, 0.04)	0.01 (0.00, 0.03)
Central Canada	0.06 (0.00, 0.16)	**0.88** (0.76, 0.98)	0.06 (0.00, 0.18)
Great Lakes	0.01 (0.00, 0.05)	0.00 (0.00, 0.02)	**0.98** (0.92, 1.0)

Values represent proportions of individuals in a population that are immigrants. Values in bold are self-recipient (non-dispersal) rates

when the glaciers receded (Hewitt 2004). Isolation in multiple refugia has been invoked to explain the marked east–west genetic differentiation in wood ducks (*Aix sponsa*, Peters et al. 2005) and some neotropical migrant birds (e.g., Ruegg and Smith 2002; Lovette et al. 2004). Since Caspian terns display similar differentiation patterns, they also may have occupied multiple refugia during the late Pleistocene. However we were unable to estimate a divergence time between eastern and western Caspian terns due to the low level of cytochrome *b* variation.

The east–west divergence seen in Caspian terns is not common to all North American waterbird species. Draheim et al. (2010) did not find strong genetic differentiation between western, interior and eastern subspecies of least terns (*Sterna antillarum*). Instead, subspecies appeared to be highly connected, with evidence of isolation by distance (Draheim et al. 2010). Isolation by distance was also implicated in double-crested cormorants (*Phalacrocorax auritus*), though the Pacific region may remain genetically distinct from eastern regions (Mercer 2008). Similarly, American white pelicans in North America were found to be panmictic ($\Phi_{ST} = 0.00$; $P = 0.341$; $F_{ST} = 0.0016$; $P = 0.13$), with significant dispersal across the Rocky Mountains (Anderson and Anderson 2005; Oomen et al. 2011; Reudink et al. 2011). The existence of population genetic structure in North American Caspian terns suggests that gene flow in this species is influence by factors other than, or additional to, those affecting other waterbirds. For example, the Central Canada breeding group may overwinter in an area distinct from Great Lakes terns (Friesen et al. 2007), but this possibility needs to be explored with additional molecular, banding or stable isotope data.

Conclusions and future prospects

Our results suggest that at least three of the breeding groups of Caspian terns described by Wires and Cuthbert (2000) should be protected as independent management units (sensu Moritz 1994). However, due to extremely low levels of cytochrome b variation, we cannot conclude whether these populations also represent evolutionarily significant units (sensu Moritz 1994). Analysis of birds from other regions, and denser sampling within Central Canada, would create a more complete picture of genetic differentiation throughout North America and enable tests of isolation by distance. Eastern breeding populations have suffered the largest declines of the five breeding populations and have not recovered in most locations (Cuthbert and Wires 1999). Thus, determining if these population are genetically distinct is especially important for conservation and management. Results from this study also suggest that migration routes for the lesser-studied regions should be investigated (e.g., Central Canada). These data would provide a more integrated picture of demographic connectivity throughout North America. Ecological and behavioural data, as well as loci under selection, should also be examined to test whether populations are ecologically exchangeable, especially given the species' broad geographic range (Crandall et al. 2000).

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