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Panmixia on a continental scale in a widely distributed colonial waterbird

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Many highly mobile species, such as migratory birds, can move and disperse over long distances, yet exhibit high levels of population genetic structuring. Although movement capabilities may enable dispersal, gene flow may be restricted by behavioural constraints such as philopatry. In the present study, we examined patterns of genetic differentiation across the range of a highly mobile, colonial waterbird. American white pelicans (*Pelecanus erythrorhynchos*) breed across continental North America and are currently experiencing a range expansion, especially on the eastern range limit. To assess patterns of genetic structuring, we sampled 333 individuals from 19 colonies across their North American range. The use of ten variable microsatellite markers revealed high levels of allelic richness with no population differentiation. Both Bayesian and frequentist approaches to examining genetic structuring revealed a single panmictic population. We found no evidence of genetic structuring across the Continental Divide or between migratory and non-migratory colonies. The lack of any genetic structure across the range indicates that, unlike other waterbirds with similar life-history characteristics, extensive gene flow and presumably low philopatry appear to preclude genetic differentiation. The lack of population genetic structure in American white pelicans provides an example of range-wide panmixia, a rare phenomenon in any terrestrial species. *Biological Journal of the Linnean Society*, 2011, **102**, 583–592.

ADDITIONAL KEYWORDS: American white pelican – gene flow – genetic structure – microsatellite – panmixia – *Pelecanus erythrorhynchos*.

INTRODUCTION

High mobility may enable long-distance dispersal (Ward, Skibinski & Woodwark, 1992), which enhances gene flow and limits population differentiation. However, movement capabilities alone may not predict patterns of genetic structure (Friesen, Burg & McCoy, 2007). Many pelagic seabirds, such as common murres (*Uria aalge* Pontoppidan, 1763; Morris-Pocock *et al*., 2008), razorbills (*Alca torda* Linnaeus, 1758; Moum & Árnason, 2001), red-legged kittiwakes (*Rissa brevirostris* Bruch, 1853; Patirana, Hatch & Friesen, 2002), and marbled murrelets (*Brachyamphus marmoratus* Gmelin, 1789; Friesen *et al*., 2005) can disperse over thousands of kilometers, yet exhibit population genetic structuring within ocean basins. This pattern of genetic structuring in species capable of long-distance dispersal may be driven by multiple mechanisms, including restricted gene flow as a result of high natal philopatry (Friesen *et al*., 2007), cryptic barriers to dispersal (Zardi *et al*., 2007), and behavioural mechanisms (Friesen *et al*., 2007). In addition, local adaptation to differing ecological conditions and strong selective pressures

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(Slatkin, 1987; Freeman-Gallant, 1996) may promote geographic patterns of differentiation. For example, Morris-Pocock *et al*. (2008) found that common murres exhibit low population genetic structuring within the Pacific Ocean but significant east–west structuring in the Atlantic Ocean. The low levels of differentiation in the Pacific were attributed to high levels of contemporary gene flow, whereas patterns in the Atlantic appear to be the result of historic population fragmentation (Morris-Pocock *et al*., 2008).

Species with movement capacities and life history characteristics similar to pelagic seabirds (e.g. colonial, *K*-selected) also inhabit terrestrial environments in continental interiors, although studies of patterns of genetic structuring over large spatial scales (e.g. continents) are limited. Goostrey *et al*. (1998) and Marion & Le Gentil (2006) detected significant genetic differentiation and patterns of genetic structure in great cormorants (*Phalocrocorax carbo* Linnaeus, 1758) across Europe. Yauk & Quinn (1999) found genetic homogeneity within Great Lakes populations of herring gulls (*Larus smithsonianus* Coues, 1862) but significant genetic divergence between the Great Lakes and eastern Canada. Although some studies have detected genetic homogeneity within part of a species range (Bates, Deyoung & Ballard, 2009), range-wide studies on continental waterbirds remain rare.

American white pelicans (*Pelecanus erythrorhynchos* Gmelin, 1789; hereafter pelicans) are highly mobile waterbirds that breed colonially at inland sites across a large portion of North America from the Pacific Coast to the Great Lakes (Knopf & Evans, 2004; Pekarik *et al*., 2009). Colonies follow a metapopulation model, ranging in size from a few individuals to more than 30 000, and experience frequent local extinction and recolonization events (Knopf & Evans, 2004; Anderson & King, 2005). Metapopulation theory assumes that local extinctions result in a loss of alleles from the extinct population, thereby facilitating divergence among groups. However, local extinctions in pelicans may instead reflect colony abandonment, resulting in a 'reshuffling' of alleles via dispersal post-abandonment (Wade & McCauley, 1988). Such a situation would enhance gene flow rather than promote differentiation, as is generally predicted by metapopulation theory (Hanski, 1999). Recent demographic history demonstrates a marked rebound in overall pelican abundance, from the 1933 estimate of only 30 000 adults (Thompson, 1933; Keith, 2005) to current estimates of approximately 134 000 breeding adults in North America (King & Anderson, 2005). As a part of this resurgence, pelicans have undergone a range expansion, including recent breeding attempts near Akimiski Island (James Bay, Nunavut), 500 km from the previous easternmost breeding population (Pekarik *et al*., 2009). Pelicans forage over hundreds of kilometers (Knopf & Evans, 2004) and can disperse long distances; yet little is known about patterns of natal or breeding philopatry, and ultimately genetic population structure. Pelicans are currently grouped into eastern and western metapopulations separated by the Continental Divide (Anderson & King, 2005), namely because of differential patterns of exchange between local and distant colonies (Anderson & Anderson, 2005), as well as frequent local extinction and recolonization events. However, band return data indicate some degree of movement across this potential barrier (Anderson & Anderson, 2005). Whether this movement is sufficient to ameliorate possible isolating effects from the Continental Divide remains unknown. However, if patterns of recapture reflect patterns of breeding dispersal, pelicans may far exceed the one-to-ten-migrant-per-generation rule, leading to genetic homogeneity (Mills & Allendorf, 1996).

The vast majority of pelican colonies are located in the northern USA and Canada where breeding adults follow a typical migration schedule, arriving at breeding colonies in early spring and departing in the autumn. Populations separated by the Continental Divide generally follow separate migratory pathways, overwintering in coastal Western Mexico and the Gulf Coast of Mexico, respectively (Knopf & Evans, 2004). However, a few small, non-migratory colonies of pelicans exist in Mexico and coastal Texas, specifically the Laguna Madre that extends from Corpus Christi, Texas, USA, to La Pesca, Tamaulipas, Mexico. In the Laguna Madre of Texas, the abundance of breeding American white pelicans has remained relatively constant at 200–500 nests since the early 20th Century (Chapman, 1988). In the Laguna Madre de Tamaulipas, unconfirmed reports of nesting pelicans have occurred ever since the 1920s but were not documented until the 1960s (Selander *et al*., 1962). In 2008, aerial surveys of all breeding colonies in the Laguna Madre de Tamaulipas yielded no confirmed nesting pelicans, although a single foraging flock of approximately 420 individuals and roosting flock of 82 individuals were photographed (C. Green, unpubl. data.). The Texas Gulf Coast, including the Laguna Madre, and Laguna Madre de Tamaulipas also contain increasing numbers of wintering pelicans (National Audubon Society, 2002; Knopf & Evans, 2004). The relationship between overwintering birds and breeding colonies in the Laguna Madre of Texas and Tamaulipas is unclear. Although the numbers have remained relatively stable, suggesting some natal site fidelity, limited banding data suggest the potential for birds fledged from colonies in the north to breed in the Laguna Madre colonies (Chapman &

Chapman, 1990). Additionally, band recovery data provide evidence for birds fledged from northern colonies to overwinter in coastal Texas (Strait & Sloan, 1975). If interbreeding between southern and northern colonies is limited, we expect that these differences in migratory behaviour will limit gene flow and promote differentiation.

In the present study, we examined variation at ten microsatellite loci in pelicans sampled from breeding colonies spanning most of their North American range. Our goals were to examine: (1) population structure across the continent; (2) patterns of differentiation between putatively non-migratory southern colonies and the rest of the migratory northern breeding range; and (3) whether the current classification of pelicans into eastern and western metapopulations is supported by variation in neutral genetic markers.

MATERIAL AND METHODS

Field methods

We collected tissue samples from 333 individuals at 19 colonies. Samples from most colonies were collected opportunistically from natural mortalities of nestling pelicans by volunteers who were either banding flightless young pelicans or surveying for disease outbreaks in colonies. Muscle or skin tissue (0.5–1.0 g) from recently dead nestlings was collected using a sterile razor blade and stored in lysis buffer (4.0 M urea, 0.2 M NaCl, 0.1 M Tris HCl, pH 8.0, 0.5% *n*-laurylsarcosine, 0.1 M 1,2-cyclohexanediamine). We took a small blood sample (< 500 μL) from the tarsal-metatarsal or brachial vein of flightless nestlings from colonies in Saskatchewan, Canada, when they were 4–10 weeks old. Similar methods were used to collect blood samples from nestlings in California colonies in the late 1980s. We extracted DNA from feathers moulted on the breeding grounds from the remaining individuals (Boles Island, Ontario, Canada). The location of study colonies and number of individuals sampled is presented in Table 1 and Figure 1.

Laboratory methods

We extracted DNA from blood and tissue samples using a Qiagen DNAeasy Tissue Extraction kit. We amplified ten polymorphic microsatellites isolated from American white pelicans (PeEr loci; Hickman *et al*., 2008) and great white pelicans (*Pelecanus onocrotalus* Linnaeus, 1758; Pel loci; de Ponte Machado *et al*., 2009) (Table 2). We created four polymerase chain reaction (PCR) reaction multiplexes: locus PeEr01, PeEr02, PeEr03, and PeEr09 (Multiplex A); locus PeEr04 and PeEr07 (Multiplex B); locus Pel149 and Pel304 (Multiplex C); and locus PeEr06, and Pel086 (Multiplex D). We amplified multiplexes A and C in a 10 μL reaction volume under the conditions: 94 °C for 5 min followed by 30 cycles of 94 °C for 30 s, 59 °C for 60 s, and 72 °C for 60 s followed by a final extension of 60 °C for 45 min. We amplified multiplexes B and D under the conditions: 94 °C for 5 min followed by 30 cycles of 94 °C for 30 s, 62 °C for 60 s, and 72 °C for 60 °C s, followed by a final extension of 60 °C for 45 min. We visualized DNA fragments using an ABI 3700 DNA analyzer (PE Applied Biosystems Inc.) and analyzed the fragments using GeneScan Analysis software (PE Applied Biosystems Inc.). PCR multiplexes A and B were visualized together, as were PCR multiplexes C and D.

Microsatellite data analysis

We tested for departures from Hardy–Weinberg equilibrium (HWE) for each of the ten loci from 333 individuals across 19 sampling locations using the exact probability test with Markov chain parameters set to 100 batches with 1000 iterations in GENEPOP, version 4.0.1 (Raymond & Rousset, 1995). We also used GENEPOP to examine genotypic linkage disequilibria (LD) among loci, calculate pairwise F_{ST} values between the eastern, western, and southern groups, and determine observed and expected heterozygosities at each sampled region. In addition, we examined whether population genetic differences could be explained by isolation by distance by conducting Mantel tests with 9999 randomizations between pairwise F_{ST} and geographical distances in R, version 2.11.0 (R Development Core Team, 2010). We examined allelic richness (R_S) and gene diversity using FSTAT, version 2.9.3 (Goudet, 1995). For R_S, we used the rarefaction method (El Mousadik & Petit, 1996), which employs resampling of the genotype data to produce sample sizes equal to the smallest population. Because some populations were represented by small sample sizes, we excluded all populations ($N = 5$) with fewer than ten individuals. We tested for differences in allelic richness, gene diversity, and observed heterozygosity among populations using one-way analysis of variance (ANOVA). We examined evidence for scoring errors, allelic dropout, and possible null alleles using MICRO-CHECKER (van Oosterhout *et al*., 2004) and examined error rates in allele scoring by re-analyzing and re-scoring alleles for 61 of 333 individuals.

We used two different individual Bayesian clustering methods to examine genetic population structure: STRUCTURE, version 2.3 (Pritchard, Stephens & Donnelly, 2000; Falush, Stephens & Pritchard, 2003) and TESS, version 2.3.1 (Francois, Ancelet & Guillot, 2006; Chen *et al*., 2007). Algorithms within these programs seek genetic structure from multi-locus

Table 1. Sample, location, and genetic diversity information for all sampled regions

Site	Region	Location	Year	East (°)	North (°)	*N*	H_O	H_E	A_{rich}	Gene diversity
CA1	West	Clear Lake, CA	2007	41.86419	−121.14487	14	0.72	0.65	5.62	0.73
CA2	West	Clear Lake, CA (historic)	1980s	41.86419	−121.14487	33	0.70	0.70	5.09	0.70
ID1	West	Blackfoot Reservation, ID	2007	43.17921	−112.28032	10	0.74	0.68	5.74	0.74
ID2	West	Minidoka NWR, ID	2007	42.66780	−113.36792	6	0.69	0.77	–	–
NV1	West	Anaho Island, NV	2007	39.95344	−119.51202	34	0.72	0.72	5.44	0.72
		All western populations				**97**	**0.71**	**0.71**	**5.47**	**0.72**
AB1	East	Pelican Lake, AB	2007	55.78816	−113.24776	12	0.72	0.70	5.39	0.72
AB2	East	Portage Lake, AB	2007	58.94363	−113.24913	19	0.69	0.73	5.01	0.69
MB1	East	Pipestone Rocks, MB	2009	51.38485	−96.55060	9	0.70	0.64	–	–
MN1	East	Marsh Lake, MN	2006–7	45.18772	−96.13020	26	0.71	0.74	5.29	0.71
MT1	East	Medicine Lake, MT	2007	48.44924	−104.38248	22	0.74	0.67	5.28	0.74
ND1	East	Chase Lake, ND	2007	47.00490	−99.43528	13	0.74	0.72	5.27	0.74
ON1	East	Boles Island, ON	2008	49.87030	−88.93913	7	0.76	0.75	–	–
SD1	East	Bitter Lake, SD	2007	45.27199	−97.33938	7	0.71	0.65	–	–
SD2	East	LaCreek NWR, SD	2007	43.12049	−101.53921	35	0.68	0.68	5.02	0.68
SK1	East	Dore Lake, SK	2006	54.72759	−107.50980	18	0.72	0.70	5.25	0.72
SK2	East	Last Mountain Lake, SK	2006	51.36396	−105.23975	24	0.69	0.68	5.11	0.69
SK3	East	Reed Lake, SK	2006	50.38707	−107.03568	24	0.70	0.65	5.11	0.70
WI1	East	Cat Island, WI	2006	47.01333	−90.55917	1	–	–	–	–
		All eastern populations				**217**	**0.71**	**0.69**	**5.19**	**0.71**
TX1	South	Padre Islands, TX	2007	27.47995	−97.31483	19	0.70	0.75	4.96	0.70
		All southern populations				**19**	**0.70**	**0.75**	**4.96**	**0.70**

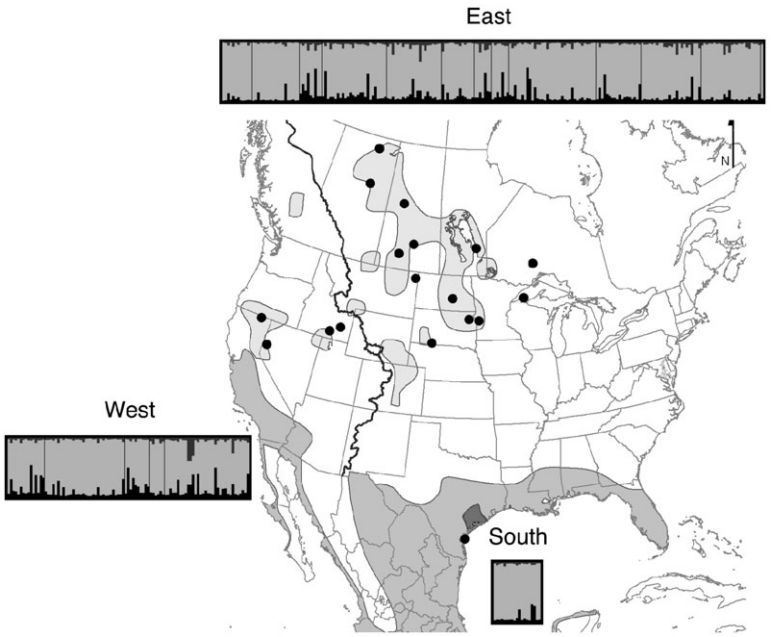

Figure 1. Map of all sampled colonies with the North American Continental Divide (black line), approximate main breeding range (light grey; Ridgely *et al*., 2007), nonbreeding range (medium grey), and year-round range (dark grey), putative eastern (east of the continental divide), western (west of the continental divide), and southern (Texas) populations. STRUCTURE results indicated that $K = 1$; however, our a priori prediction was that we would observe three genetically distinct, eastern, western and southern subunits. To illustrate the lack of support for multiple clusters, we have included bar charts alongside the putative regional populations representing probability of membership for each individual in one of three genetic clusters ($K = 3$) as calculated by the Bayesian clustering algorithm in STRUCTURE. Each stacked bar represents one individual with probability of membership into each cluster (bottom black bars = cluster 1; central light grey bars = cluster 2; top dark grey bars = cluster 3).

Table 2. Allelic information for the ten loci used in the present study, isolated from American white pelicans (PeEr01–PeEr09; Hickman *et al*., 2008) and great white pelicans (Pel086–Pel304; de Ponte Machado *et al*., 2009)

Locus	Alleles	Size range	N	H_O	H_E
PeEr01	8	139–171	332	0.67	0.67
PeEr02	10	241–268	328	0.80	0.79
PeEr03	11	227–263	325	0.81	0.80
PeEr04	11	157–201	288	0.81	0.82
PeEr06	12	186–214	330	0.76	0.77
PeEr07	4	223–235	319	0.27	0.29
PeEr09	13	136–182	321	0.83	0.86
Pel086	7	150–174	323	0.77	0.76
Pel149	19	261–341	316	0.83	0.92
Pel304	7	186–204	321	0.42	0.42

genotypes without assuming predefined populations. STRUCTURE (Pritchard *et al*., 2000; Falush *et al*., 2003; Hubisz *et al*., 2009) estimates the probability of assignment to a given number of clusters (K) and estimates the membership of each individual (q) to each cluster. In addition, STRUCTURE (Pritchard *et al*., 2000; Falush *et al*., 2003; Hubisz *et al*., 2009) uses a Markov chain Monte Carlo (MCMC) procedure that maximizes HWE and minimizes LD. Optimal K-clusters for the data set were based on a rate of change in the log probability of the data (ΔK) within each assumed K (Evanno, Regnaut & Goudet, 2005). We performed clustering under the F-model as proposed by Falush *et al*. (2003), which assumes admixture and correlated allele frequencies, and also using the inference of α for each subpopulation. Each run was set to a burn-in of 500 000 and a MCMC data collection chain of 1 000 000. We tested $K = 1$–19 replicated five times using LINUX servers.

We also used the clustering software TESS, version 2.3.1 (Francois *et al*., 2006; Chen *et al*., 2007). This Bayesian clustering program uses a MCMC approach to define genetic clusters under the assumptions of HWE to reduce inbreeding coefficients. This algorithm also uses a hidden Markov random field (HMRF) model on tessellations, allowing spatial relationships to nearest-neighbors to be defined, at the same time as assuming that spatially proximate individuals are genetically similar. Incremental increases

of the HMRF distance separating population centres value (d) from 0 (full cline) to 1 (hard clusters) permits the user to visualize genetic clustering that may be overestimated or diminished using other Bayesian clustering programs such as STRUCTURE and BAPS, version 4.1 (Bayesian analysis of population structure; Corander & Marttinen, 2006). These other approaches can have difficulties differentiating genetic clusters along a continuous cline in genetic variation, and therefore TESS analysis may provide lower error rates than alternative methods when lower levels of genetic structure are observed (Francois *et al*., 2006; Chen *et al*., 2007).

We ran TESS for 500 000 sweeps with an initial burn-in of 50 000 sweeps testing the maximal number of clusters from 1–10, with five runs per maximum cluster. Next, using three different interaction parameter settings of 0, 0.5, and 0.99, we ran five replicates at $K = 2$ with an initial burn-in of 50 000 sweeps followed by 500 000 sweeps.

Sampling regions, genetic clusters, and assignment tests

To determine the optimal number of genetic clusters, we examined ΔK (Evanno *et al*., 2005), as well as the geographic distribution of individuals with high coefficients of relationship. We did so under two thresholds ($q > 0.80$ and $q > 0.50$) from both STRUCTURE and TESS to determine whether the majority of individuals with high-ancestry coefficients could be associated with a specific geographic region. Once determined, all individuals collected within this region were used to define groups for frequency-based individual assignment (Paetkau *et al*., 1995, 2004) implemented in GENECLASS2 (Piry *et al*., 2004). We compared the results from these approaches to those generated from Bayesian clustering analyses to provide confidence in the spatial designation of genetic groupings. Also, we used this comparison to determine whether these individuals could be considered migrants among geographic areas or simply cross-assigned by chance. We set an assignment threshold of $P < 0.01$ and a default frequency for missing alleles at 0.01 for all frequency-based assignment tests within GENECLASS2.

RESULTS

Microsatellites

None of the ten loci used in the present study deviated from HWE in any of the 19 sampling locations. Genotypic disequilibrium was observed at two colonies: Anaho Island, Nevada, USA (PeEr03/Pel149), and Last Mountain Lake, Saskatchewan, Canada (Pel149/086). Because genotypic disequilibrium was not observed for these loci in several groups, it is unlikely that the loci are physically linked; thus, the loci were retained for subsequent analyses. MICRO-CHECKER revealed no evidence of scoring errors allelic dropout, nor null alleles in any loci.

Genetic diversity

We found no differences in allelic richness (ANOVA: $F_{13,\,139} = 0.12$, $P = 0.999$) or gene diversity (ANOVA: $F_{13,\,139} = 0.10$, $P = 1.00$) across the 14 populations with $N > 10$ individuals (Table 1). In addition, we found no significant heterozygote excesses or deficiencies and observed heterozygosities did not vary among the 18 sampled regions with $N > 1$ individual (ANOVA: $F_{17,179} = 0.30$, $P = 0.997$).

Genetic clustering and assignment tests

F_{ST} values for each population pair were low (East–West: $F_{ST} = 0.0016$, $P = 0.13$; East–South: $F_{ST} = -0.00123$, $P = 0.86$; South–West: $F_{ST} = -0.0029$, $P = 0.61$) and we found no evidence of isolation by distance ($r = 0.04$, $P = 0.42$). The most likely number of clusters revealed by STRUCTURE was $K = 1$, with higher values of K returning lower likelihoods (Fig. 2). Although STRUCTURE indicated $K = 1$, we were interested in further testing our a priori assumption that eastern and western metapopulations are genetically distinct sub-units. Thus, we

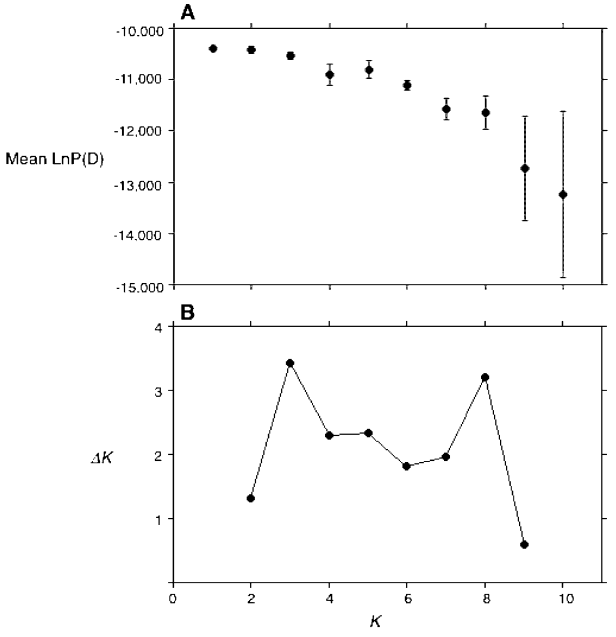

Figure 2. A, plot of the mean Ln$P(D)$ values ± 1 SD for $K = 1$ through $K = 10$ as calculated by STRUCTURE 2.3. Ln$P(D)$ is an estimate of the posterior probability for the data for each K. B, plot of ΔK versus K.

examined inferred population assignments from $K = 2$ (averaged over five iterations). In total, 321 of the 333 individuals had higher likelihoods of belonging to cluster 1 ($q > 0.5$); however, the highest likelihood for cross-assignment to cluster 2 was 0.68. Assignments of individuals using GENECLASS2 at the broadest geographic region ($K = 3$; East, West, South) were weak. Only 34.8% (116/333) of individuals were assigned to their original sampling location and < 10% of the samples (31/333) had a $q > 0.8$, suggesting a broad exchange of genes across the sampling region. Only 16% (5/31) of individuals with $q > 0.8$ were assigned to their original sampling locations. Increasing the number of populations did not improve assignment rates.

Results from TESS Bayesian clustering analyses indicated a highest likelihood of $K = 1$. When we examined assignment probabilities from our analyses of $K = 2$ with our interaction parameter set at 0 and 0.5, only 6/333 (0.018%) had assignment probabilities to cluster 1 higher than 0.8 and no individuals assigned to cluster 2 with assignment probabilities higher than 0.8. When our interaction parameter was increased to 0.99, 4/333 (0.012%) individuals had assignments probabilities to cluster 1 lower than 0.8 and 3/333 (0.009%) individuals assigned to cluster 2 with assignment probabilities higher than 0.8.

DISCUSSION

Bayesian and frequentist approaches to analyzing population assignments of 333 American white pelicans at ten microsatellite loci revealed a complete lack of genetic structure across their North American range. Despite the potential for genetic structuring based on: (1) the continental divide limiting dispersal between eastern and western individuals; (2) natal/breeding philopatry common among many waterbirds; and (3) the occurrence of resident breeding populations in Texas, we found no evidence for genetic differentiation at any level. Although additional markers, such as mitochondrial (mt)DNA, and an expanded sampling scheme are necessary to fully verify complete panmixia, the results obtained in the present study strongly suggest a complete lack of genetic structure in this widely distributed, colonial waterbird.

A complete lack of genetic differentiation across the range of a species is an uncommon phenomenon. In those few species in which range-wide panmixia has been observed [e.g. rasp coral (*Pocillopora verrucosa* Ellis and Solander, 1796) Ridgway, Hoegh-Guldberg & Ayre, 2001; European plaice (*Pleuronectes platessa* Linnaeus, 1758) Hoarau *et al*., 2002; Dawson's burrowing bee (*Amegilla dawsoni* Rayment, 1951) Beveridge & Simmons, 2006; hooded seal (*Cystophora cristata* Erxleben, 1777) Coltman *et al*., 2007; banded goby (*Caffrogobius caffer* Gunther, 1874) Neethling *et al*., 2008], genetic homogeneity across the species range has been generally attributed to high mobility and dispersal. Although the high mobility of pelicans appears to enable long-distance dispersal, movement capabilities alone may not predict patterns of genetic structuring (Friesen *et al*., 2007).

Many highly mobile species are capable of long-distance movements, yet strong natal philopatry and barriers to dispersal (both apparent and cryptic) often limit gene flow and maintain at least some degree of genetic structuring (Friesen *et al*., 2007). Although historic and contemporary barriers such as land or ice are the best predictors of population genetic structuring in seabirds, many species still exhibit structuring in the absence of physical barriers (Friesen *et al*., 2007), which may be a result of behavioural differences among groups. For example, black-browed albatrosses (*Thalassarche melanophrys* Temminck, 1828) with different foraging grounds differ genetically (Burg & Croxall, 2001) and population-specific non-breeding areas often predict the presence of phylogeographic structure (Friesen *et al*., 2007). Although a small number of seabirds lack genetic differentiation (e.g. grey-headed albatross (*T. chrysostoma* Forster, 1785); Burg & Croxall, 2001), detection of at least some degree of genetic structuring in part of the range appears to be common, regardless of whether apparent barriers to dispersal exist (Friesen *et al*., 2007).

Although the Continental Divide has been the basis for defining separate eastern and western metapopulations in pelicans (Anderson & King, 2005), the data obtained in the present study suggest that, despite what may be an important demographic barrier, gene flow is high enough across the entire range to preclude differentiation. Many terrestrial bird species are genetically differentiated across the North American Continental Divide as a result of historic processes such as occupying eastern and western glacial refugia (Lovette, Clegg & Smith, 2004; Peters, Gretes & Omland, 2005) or contemporary processes, such as the Great Plains and Rocky Mountains acting as major barriers to dispersal. The current classification of pelicans into eastern and western metapopulations separated by the Continental Divide (Anderson & King, 2005) is supported by band return data from 1922–1981, which indicated significant demographic isolation between groups (Anderson & Anderson, 2005). A conservative approach of including only returns of birds > 4 years old revealed that 24/360 (3.7%) of nestlings banded east of 110° longitude were subsequently recovered west of 110° longitude, whereas 31/292 (10.6%) banded in the west were

recovered east of 110° longitude (Anderson & Anderson, 2005). On the basis of the lack of genetic structure observed in the present study, current levels of gene flow across the Continental Divide appear to be high enough to preclude genetic isolation. In addition, although demographically pelicans do appear to fit a metapopulation model, local extinctions and recolonizations may enhance gene flow through frequent 'reshuffling' of alleles, rather than leading to differentiation (Wade & McCauley, 1988). However, the use of additional markers, such as mtDNA, may reveal patterns of differentiation where nuclear markers do not (e.g. Mylecraine *et al*., 2008), and discriminate between contemporary and historic patterns of gene flow and the potential for sex-biased population structure (Prugnolle & de Meeus, 2002).

We predicted that southern populations would exhibit significant genetic differentiation from the northern populations; however, we observed no genetic differentiation of birds nesting in the Padre Island National Seashore, Texas. Breeding pelicans have been recorded in Texas and northern Mexico since at least 1907 (Oberholser & Kincaid, 1974) and have likely been present for centuries (Chapman, 1988), suggesting that recent colonization/expansion is unlikely to account for the lack of genetic structure. One potential explanation for the lack of observed structure is that the southern breeding colonies are composed of both local breeders and migratory birds from elsewhere in the range that remained in the south rather than returning north to their natal region. After fledging, pelicans from northern breeding colonies migrate south to wintering grounds in the southern USA and coastal Mexico (Strait & Sloan, 1975; Knopf & Evans, 2004). In double-crested cormorant (*Phalacrocorax auritus* Lesson, 1831) breeding colonies in central Florida, little genetic differentiation was found between resident birds and migratory populations from the Great Lakes and Atlantic coast that overwinter in central Florida (Green *et al*., 2006). The results of the present study suggest that mixing of resident and migratory pelicans may be occurring in over-wintering areas such as the Laguna Madre of Texas, thereby limiting any genetic differentiation between southern and northern colonies. Overall, the provenance of breeders at the Texas colony remains unknown; future studies employing banding, geolocators, satellite transmitters, and/or biogeochemical markers are needed to better understand the relationship between resident and migratory birds in Texas. Biogeochemical markers (e.g. stable isotopes) may indicate a bird's geographical origin where microsatellites do not; however, because pelicans do not breed until ≥ 3 years of age, samples that can be obtained non-invasively (e.g. feathers) will only provide an estimate of the last moult location and not natal origin. Tissues with longer turnover rates, such as bone, may not only provide an indication of natal origin, but also require the destructive sampling of breeders.

Unlike many other colonial waterbirds, pelicans may not be constrained by philopatry and their capability for long-distance movement likely facilitates frequent long-distance dispersal. High dispersal in American white pelicans, compared to other colonial waterbirds, may be driven by erratic fluctuations in colony size driven by water-level fluctuations (Moreno-Matiella & Anderson, 2005), disease (Rocke *et al*., 2005) or other disturbances that force dispersal and lead to frequent remixing of individuals at breeding colonies. Thus, we suggest that the panmictic genetic structure of pelicans is a result of high dispersal and erratic local colony dynamics leading to movement and genetic exchange. Because it would be unwieldy to manage pelican populations at the true scale of their genetic metapopulation, we suggest that classification of American white pelicans into separate groups based on geography may be practical for distinguishing and managing pelican populations, as long as managers are aware that such groupings will not reflect genetically distinct groups. Thus, rather than management plans aimed at protecting genetically distinct populations, plans should focus instead on regional numbers and demographic patterns, especially at the level of colonies that have significant local ecological and social value.

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