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Mitochondrial DNA suggests recent origins in two coastal avian subspecies in northwestern North America.

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ABSTRACT

Genetic studies of subspecies endemic to Haida Gwaii (Queen Charlotte Islands), British Columbia and the Alexander Archipelago of southeast Alaska have frequently found genetic corroboration for these phenotypically based taxa. Divergence and speciation are common among island populations of birds, and evidence suggests this region has fostered such divergence during previous glacial maxima. We examined genetic divergence in mitochondrial DNA (mtDNA) of two coastal subspecies endemic to this region: sharp-shinned hawk (*Accipiter striatus perobscurus*) and great blue heron (*Ardea herodias fannini*). Genetic diversity in both species was remarkably low, with both coastal subspecies possessing only the most common haplotype found in continental populations. We found low but significant population divergence between *A. s. perobscurus* and continental populations of sharp-shinned hawks and no significant population divergence in the herons. The refugial history of the region suggests that these subspecies may have arisen relatively recently compared with other regional endemics for which genetic and phenotypic data both show divergence. Alternatively, species-wide selective sweeps of mtDNA prior to divergence may have rendered this genetic marker less useful for tracking that divergence.

INTRODUCTION

The Pleistocene epoch that began about 2.6 million years ago is characterized by dramatic fluctuations in Earth's climate (Berger 1984). Global cooling on a 100,000-year cycle caused a series of glaciations that had a profound effect on the distribution of species (Avise and Walker 1998). Genetic evidence has suggested that isolation during Pleistocene glacial cycles promoted divergence and speciation in habitats fragmented by the advance and retreat of continental ice sheets (Weir and Schluter 2004). Many phylogenetic and population genetic

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studies have focused on Haida Gwaii (Queen Charlotte Islands), British Columbia and the surrounding region due to the number of endemic taxa from the area that have been described for many classes of organisms, including birds (Topp and Winker 2008), plants (Ogilvie 1989), insects (Kavanaugh 1989), and mammals (Fleming and Cook 2002). Many bird species exhibit genetic differentiation consistent with a glacial refugium near Haida Gwaii during the last glacial maximum (e.g., Pruett et al. 2013, Topp and Winker 2008, Withrow et al. 2014).

For this study, we asked two questions: (1) Do genetic data reflect observed patterns of phenotypic divergence in two coastal avian populations in northwestern North America? And (2) do these two coastal populations share a pattern of genetic divergence consistent with the Haida Gwaii region serving as a refugium during the Pleistocene? Specifically, we examined the northwestern coastal subspecies of sharp-shinned hawks (*Accipiter striatus perobscurus*) and great blue herons (*Ardea herodias fannini*). Both of these subspecies are examples of regional endemic populations that have undergone sufficient phenotypic differentiation from the widespread continental populations to be recognized as subspecies (Snyder 1938, Chapman 1901, Dickerman 2004a-c). *A. s. perobscurus* occurs in the breeding season from southeastern Alaska along the adjacent coast of British Columbia to Vancouver Island and winters from Haida Gwaii (HG) to Vancouver Island and south to Santa Barbara, California (Dickerman 2004c). *A. s. perobscurus* is darker (Fig. 1a), with relatively short wings and tails, and relatively long but thin tarsi compared to the continental *A. s. velox* (Dickerman 2004c). *A. h. fannini* is resident in southeastern Alaska and south through HG, with nesting recorded north to Prince William Sound (Dickerman 2004b). This is a range restriction for the subspecies based on the study of Dickerman (2004b). While it is not the range currently envisaged by the Canadian Wildlife Service's management plan for this subspecies (Environment Canada 2016), their decision (COSEWIC 2008) was based on the status quo of AOU (1983) and Payne (1979), neither of which represents the critical revision of the topic that Dickerman (2004b) represents (and the American Ornithologists' Union has not critically evaluated subspecies since 1957). *A. h. fannini* has a distinctively darker gray plumage than mainland subspecies (Fig. 1b), and it also has a significantly shorter exposed culmen and tarsi (Dickerman 2004a, b).

Figure 1. Ventral and dorsal images of adult males of our study species A) *Accipiter striatus*; and B) *Ardea herodias*, with the focal subspecies in each case on the left and the continental form on the right.

METHODS

We sequenced the mitochondrial gene NADH dehydrogenase subunit 2 gene (ND2) of *A. striatus* and *A. herodias* and compared genetic attributes of these two coastal subspecies with their respective continental populations to examine genetic distinctiveness. While mitochondrial sequence variation is not expected to be coupled with genetic differentiation resulting from

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selection of phenotype, it can provide a deeper understanding of the evolutionary history of intraspecific variation (e.g., Topp and Winker 2008).

Tissue samples from 25 *Accipiter striatus* and 36 *Ardea herodias* were obtained from the University of Alaska Museum, the University of Washington Burke Museum, and the Museum of Southwestern Biology (Appendix). Specimens were chosen based on collection localities and selected to maximize geographic coverage of both species' ranges (Fig. 2).

We amplified 987 and 1024 base pairs (bp) of the mitochondrial NADH dehydrogenase subunit 2 gene for *Ardea herodias* and *Accipiter striatus,* respectively. ND2 is a commonly used mitochondrial marker in birds, and it has proven to be informative and approximately neutrally evolving (Zink et al. 2005), enabling us to estimate population parameters with reasonable confidence (Lovette 2004). DNA was extracted from frozen tissues using a DNeasy Tissue Kit following the manufacturer's protocol (Qiagen, Valencia, California, USA).

Amplifications were done using ND2 primers L5215 (Hackett 1996) and H6313 (Johnson and Sorenson 1998). Polymerase chain reaction (PCR) amplification was conducted using 0.8 µL of each primer at 10 mM concentration, 0.5 µL of a 10 mM solution of dNTPs, 0.13 µL of Taq DNA polymerase, 1.6 µL of 25 mM MgCl2, 5 µL of 5X Taq Buffer (Promega, Madison, Wisconsin, USA), 14.5 µL water, and 2 µL of extracted DNA template for a total reaction volume of 25 µL. The PCR thermal regime started with 2 min at 94 C, followed by 39 cycles of 94 C for 30 seconds, 52 C for 1 min, 72 C for 2 min, and with a final elongation step at 72 C for 5 min. The PCR cleanup and sequencing were done at the High-Throughput Genomics Unit (University of Washington, Seattle, Washington, USA), using an ExoSAP cleaning process and cycle sequencing with BigDye chemistry on an ABI 3730XL high-throughput capillary sequencer (Applied Biosystems, Foster City, California, USA). Cycle sequencing amplifications were done using the initial sequencing primers. Sequences were aligned and edited using Sequencher version 4.7 (Gene Codes, Ann Arbor, Michigan, USA).

Median joining networks illustrating haplotype frequencies of mtDNA from *A. herodias* and *A. striatus* were generated using Network version 4.6.1.3. Neutrality of the mtDNA sequences were tested by calculated Fu and Li's D^* and F^* statistics (Fu and Li 1993) and Tajima's D (Tajima 1989) using DnaSP version 5 (Librado & Rozas 2009). R_2 values (Romis-Onsins & Rozas 2002) were generated using DnaSP version 5 to infer changes in population size. To determine whether estimates were significant, we ran coalescent simulations with 50,000 replicates and 95% confidence intervals using a model of constant population size (Librado & Rozas 2009). Simulations were run three times for confirmation. We used Arlequin ver. 3.5.1.2 (Excoffier et al. 1992) to calculate pairwise F_{ST} values between northwestern subspecies and continental subspecies for ND2 sequences with 10100 permutations and to determine whether these estimates differed from zero.

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RESULTS

Accipiter striatus

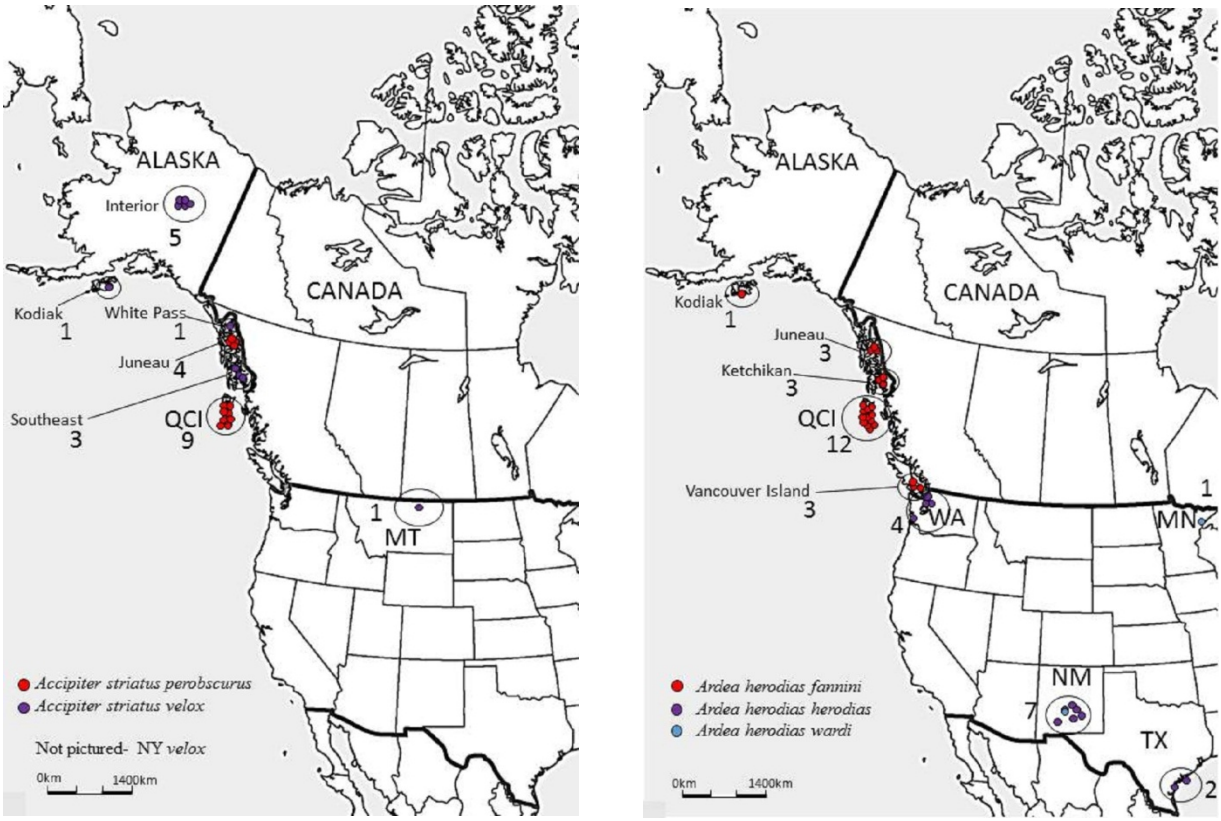
We obtained 1024 bp of ND2 data from 25 *Accipiter striatus* sampled from 8 different locations ranging from the interior of Alaska to New York (Fig. 2). Four of the 1024 sites were variable, and there were five unique haplotypes (Fig. 3). Haplotypes differed by only a single base pair, and all *A. s. perobscurus* shared the most common haplotype found among continental birds (Fig. 3). Two haplotypes represent A-G transitions in the third codon position, and two represent A-G transitions in the second codon position.

Estimates of population expansion and genetic structure were calculated for all specimens. Population expansion was indicated by strongly significant values for R_2 ($P < 0.0001$; Table 1). Fu and Li's F^* and D^* differed significantly from zero ($P < 0.001$). Tajima's D was negative but was not significant ($P > 0.05$; Table 1). Despite low genetic diversity, we found a low but significant level of population structure (average pairwise difference; $P < 0.05$; Table 1).

Ardea herodias

We obtained 987 bp of ND2 data from 36 *Ardea herodias* sampled from 9 different locations ranging from Kodiak Island to the Texas coast (Fig. 2). Two of the 987 sites were variable, resulting in three unique haplotypes. The haplotype network illustrates low divergence among haplotypes and no structure between *A. h. fannini* and *A. h. herodias* & *A. h. wardi* (Fig. 3). Both haplotypes represent C-T transitions in the third codon position.

Estimates of population expansion, and genetic structure were calculated for all specimens. Population expansion was indicated by strongly significant values for R_2 ($P < 0.0001$; Table 1). Fu and Li's F^* and D^* differed significantly from zero ($P < 0.01$). Tajima's D was positive but not significant ($P > 0.05$; Table 1). The two populations did not exhibit significant differentiation as indicated by a low but not significant F_{ST} ($P > 0.05$; Table 1).



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143 **Figure 2**. General sample locations are shown with large circles. Numbers equal sample size
144 within each circle. Dots indicate approximate locations of individuals to show sample density;
145 colors correspond to subspecies.

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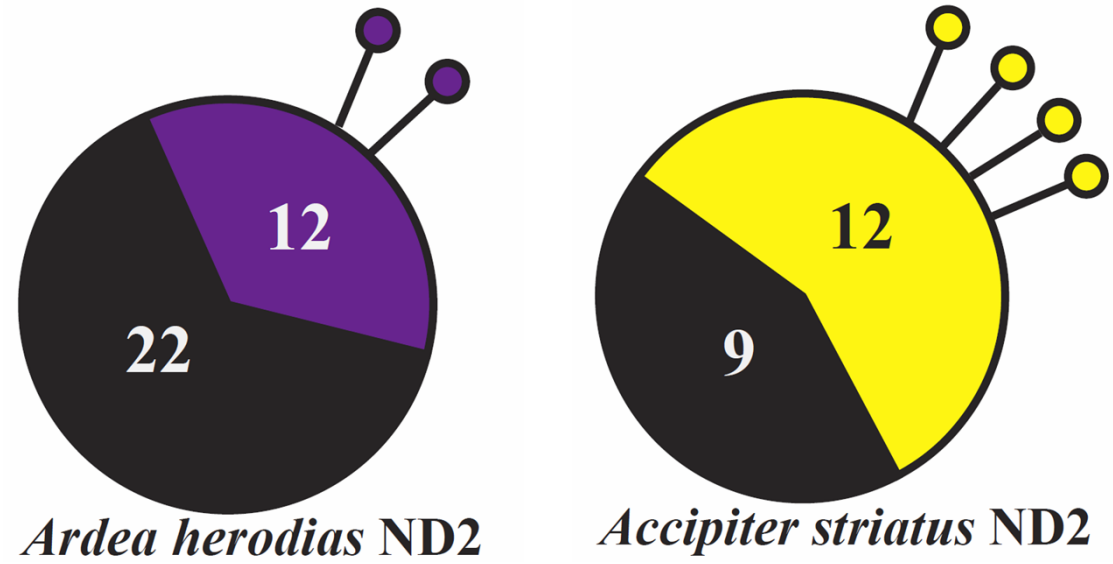

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Figure 3. Haplotype networks showing the ND2 sequences from 25 *Accipiter striatus* and 36 *Ardea herodias*. Colors indicate focal subspecies (black) versus continental populations: black = *A. s. perobscurus* and *A. h. fannini*; yellow= *A. s. velox*; purple = *A. h. herodias* and *A. h. wardi*. Numbers correspond to number of individuals of each haplotype. Except for small circles, which represent one individual each.

DISCUSSION

Genetic Diversity

Patterns of low genetic diversity are expected from isolated ancestral populations that experienced rapid post-glacial expansion, while higher genetic diversity is expected for a refugial population that was isolated in the HG region during the last glacial maximum (Hewitt 1996). Our results revealed remarkably low genetic diversity in both *A. herodias* and *A. striatus* and did not show any unique genetic attributes (i.e., haplotypes) within the coastal subspecies. Pruett et al. (2013) observed similar patterns of low genetic diversity in other Haida Gwaii avian populations, including sooty grouse (*Dendragapus fuliginosus*), red-breasted sapsucker (*Sphyrapicus ruber*), northern saw-whet owl (*Aegolius acadicus*), and Swainson's thrush (*Catharus ustulatus*); in each case, the low diversity was attributed to post-glacial colonization approximately 13,000-19,000 years before present.

Both species exhibited greater genetic diversity in continental populations, which is consistent with expectations of higher genetic diversity in larger populations (Hartl & Clark 1989). Previous research has shown low genetic diversity in *A. striatus* across North America in the ND2 and COI mitochondrial genes (Pearlstine 2004). A comparable study of mitochondrial genetic diversity of *A. herodias* has yet to be conducted.

Population Expansion

Our data support a departure from neutrality in ND2, showing significant values for Fu and Li's $F^*$and D^* in both *A. herodias* and *A. striatus*. This pattern is highlighted by strongly significant R_2 values, suggesting a population expansion in both species. Tajima's D, which is less sensitive to population expansion than Fu and Li's $F^*$and D^* (Romis-Onsins & Rozas 2002), was not significant in either species, but showed negative values for *A. striatus* and positive values for *A. herodias*. This suggests a stronger signal for expansion in *A. striatus*, and possibly a more recent expansion event relative to *A. herodias*. These results are consistent with previous findings indicating a signature of rapid expansion in western populations of *A. striatus* in response to the retreat of glacial ice at the end of the last glacial maximum (LGM; Hull & Girman 2005).

Genetic Divergence

Despite low genetic diversity, *A. s. perobscurus* did exhibit significant differentiation from the continental population. Additional sampling of continental *A. herodias*, if it yielded more haplotypes, might also reveal significant differentiation between these populations.

It is likely that Haida Gwaii was one of several ice-free areas that existed along the northwest coast of North America during the LGM at least 13,000 years before present (Hetherington et al. 2003). This type of biogeographic history suggests two possible explanations for our results. One scenario is that the coastal lineages of *A. herodias* and *A. striatus* have split from continental populations and underwent rapid expansion relatively recently compared with other regional endemics. This would account for the lack of divergence despite morphological distinctiveness from the continental phenotypes. Another possibility is that the common haplotypes observed are positively selected alleles that have reduced the genetic variation in the two species due to a strong selective sweep prior to divergence. Genetic differentiation would consequently be difficult to determine using mtDNA.

In both coastal subspecies we have a mismatch between phenotypic and genetic divergence. Differences between mitochondrial DNA and nuclear genes coding for phenotype could account for this disparity. Additional sampling and sequence data are warranted to further examine population structure and diversity within *A. striatus* and *A. herodias*.

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Table 1. Summary of statistics of populations of *Accipiter striatus* and *Ardea herodias*. N = sample size, π = nucleotide diversity, H = haplotype diversity. D_T = Tajima's D, F^* = Fu and Li's F^*, D^* = Fu and Li's D^*, R_2 = Romis-Onsins & Rozas' R_2 statistic, F_{ST} = average pairwise divergence.[a]

Species	N	π	H	D_T	F^*	D^*	R_2	F_{ST}
Accipter striatus	25	0.0003	0.300	-0.0189	-0.0024***	-0.0157***	0.1622****	0.0228*
Ardea herodias	36	0.0001	0.070	0.0001	-0.0007**	-0.0015**	0.1480****	0.1068

[a] Levels of significance: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; ****$P < 0.0001$.

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300 APPENDIX I

301 Specimens used in this study, with identifiers [University of Alaska Museum (UAM), Burke
302 Museum (UWBM) and University of Southwestern Biology (NK) voucher numbers, and
303 GenBank accession numbers]. Collection localities are also included.

Species	Voucher Number	Collecting Localities	GenBank Accession Number
Ardea herodias fannini (British Columbia Population)	UAM22572, UAM22573, UAM22600, UAM24726, UAM24727, UAM34646, UAM34655, UAM34656, UAM34659, UAM34647, UAM34648, UAM34649, UAM34652,UAM34653, UAM24728	Queen Charlotte Island, Graham Island, Vancouver Island	KX083598, KX083589, KX083587, KX083596, KX083597, KX083603, KX083604, KX083605, KX083606, KX083607, KX083608, KX083609, KX083610, KX083611, KX083595
Ardea h. fannini (Alaska Population)	UAM7767, UAM13500, UAM18947, UAM25904, UAM25905, UAM18137, UAM20826	Juneau, Ketchikan, Kodiak Island	KX083594, KX083590, KX083593, KX083586, KX083585, KX083588, KX083592
Ardea h. herodias (Continental Population)	UAM14169	Minnesota	KX083591
Ardea h. herodias (Washington Population)	UWBM66270, UWBM74070, UWBM77579, UWBM80456	Everett, Bow, Kingston, Hoquiam	KX083599, KX083600, KX083602, KX083601
Ardea h. wardi (New Mexico Population)	MSB20590, MSB20432, NK10321, NK116085, MSB23064, MSB22225, MSB22224	Guadalupe, Sandoval, Bernalillo counties, San Miguel, Sierra counties	KX083617, KX083618, KX083613,KX083614, KX083612,KX083619, KX083620
Ardea h.wardi (Texas Population*)*	MSB18304 , MSB18344	Matagorda, Refugio counties	KX083615, KX083616
Accipiter striatus perobscurus (British Columbia Population)	UAM8083, UAM8998, UAM27278, UAM28334, UAM28335, UAM28336, UAM28337, UAM28338, UAM28339, UAM28340	Queen Charlotte Island, Graham Island	KX083635, KX083631, KX083629, KX083630, KX083621, KX083622, KX083624, KX083625, KX083623,KX083626
Accipiter striatus perobscurus (Alaska Population)	UAM29602, UAM25662, UAM23815, UAM27052	Juneau, Ketchikan	KX083639, KX083640, KX083641, KX083642
Accipiter s. velox (Alaska Population)	UAM26110, UAM29603, , UAM11257, UAM13481, UAM18494, UAM22264, UAM22474, UAM22165, UAM9372	White Pass, Dyea, Kodiak, Fairbanks	KX083627, KX083628, KX083632, KX083633, KX083634, KX083636, KX083637, KX083638, KX083643
Accipiter s. velox (Continental Population)	UAM29639, UAM15081	New York, Montana	KX083645, KX083644

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