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TRANS-BERINGIA COMPARISONS OF MITOCHONDRIAL DNA DIFFERENTIATION IN BIRDS[1]

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Abstract. We compared mitochondrial DNA (mtDNA) restriction fragment profiles from samples of 13 bird species that occur on both sides of Beringia. All but two species, Lapland Longspur (*Calcarius lapponicus*) and Green-winged Teal (*Anas crecca*), exhibited evidence of genetic differentiation, albeit at varying degrees. Several species exhibited mtDNA differentiation consistent with species-level distinctness: Marbled Murrelet (*Brachyramphus marmoratus*), Three-toed Woodpecker (*Picoides tridactylus*), Whimbrel (*Numenius phaeopus*), Mew Gull (*Larus canus*), Black-billed Magpie (*Pica pica*), American Pipit (*Anthus rubescens*), and Rosy Finch (*Leucosticte arctoa*). Other species exhibited levels of mtDNA differentiation intermediate between populations and species: Barn Swallow (*Hirundo rustica*), Common Tern (*Sterna hirundo*), Common Snipe (*Gallinago gallinago*), and Pelagic Cormorant (*Phalacrocorax pelagicus*). Because of small sample sizes, we do not recommend formal taxonomic changes, although our data could be combined with other data to raise several taxa to species level. Our data do not indicate a consistent level of mtDNA differentiation between putatively conspecific populations on different sides of Beringia, suggesting different times of colonization or cessation of gene exchange. Most comparisons of birds within continents exhibit less mtDNA differentiation than our trans-Beringia comparisons, suggesting limited gene flow between continents.

Key words: Geographic variation; mitochondrial DNA; genetic differentiation; taxonomy; Siberia; North America; evolution.

INTRODUCTION

Analyses of mitochondrial DNA (mtDNA) differentiation within avian species have provided information on levels of genetic variation, historical patterns of population fragmentation, hybridization, and population structure (Ball and Avise 1992; Bermingham et al. 1992; Degnan and Moritz 1992; Moore et al. 1991; Zink and Dittmann 1993a, 1993b; Zink 1994). These mtDNA analyses compared populations from the same continent. Although large geographic distances often separated populations compared for mtDNA variation (Ball et al. 1988; Ball and Avise 1992; Zink and Dittmann 1993a, 1993b), the potential exists for long distance dispersal to impede geographic differentiation (Edwards 1993). In this study, we compared populations of 13 species sampled on opposite sides of Beringia. Although some species migrate between the continents, our comparisons are some of the first to test for inter-continental differences. Our Siberian samples came from four general regions in northeastern Russia, Cherskiy and Anadyr in the arctic, the region around Magadan on and near the Okhotsky Sea, and the southern third of the Kamchatka Peninsula; the North American samples came from a variety of geographic sites (Appendix 1). Our goal was not an assessment of the effects of Beringia per se; rather, we estimated the level of mtDNA distinctiveness for 13 species that are distributed across Beringia on different continental land masses. Our data thus provide another perspective on the growing body of information on the geography of mtDNA variation within bird species.

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TABLE 1. Composite haplotypes for comparisons with Old World and New World specimens. Letters indicate fragment profiles for the following restriction endonucleases: *Ava* I, *Ava* II, *Bam*H I, *Ban* I, *Ban* II, *Bgl* I, *Bgl* II, *Eco*R I, *Hinc* II, *Hin*d III, *Ncl* I, and *Stu* I. A "." indicates the "A" pattern. RUS = Russia, and USA = United States.

Haplotype	Location	*n*	Composite pattern	Average *p*-within	Average *p*-between
			Phalacrocorax pelagicus	0.0016	0.0076
1	RUS	1	A A A A A A A A A A A A		
2	RUS	1	. . . . B . . . –		
3	RUS	1	. . B . . . . B . . . –		
4	USA	3	. . . B . B . . . . B B		
			Anas crecca	0.023[1]	NC[2]
1	RUS	1	A A A A A A A A A A A A		
2	RUS, USA	1, 3	B B B B . B B . B B B B		
3	RUS	1	C . . . . B C . .		
			Gallinago gallinago	0.0021	0.006
1	RUS	2	A A A A A A A A A A A A		
2	RUS	1	. . . . B		
3	USA	1	. . . . B C		
4	USA	1	. . . . B		
			Numenius phaeopus	0.0037	0.047
1	RUS	2	A A A A A A A A A A A A		
2	RUS	1	. B		
3	USA	2	. C B B B . B . . . B B		
4	USA	1	. C B B B . B . . . B C		
			Larus canus	0	0.020
1	RUS	3	A A A A A A A A A A A A		
2	USA	1	B B B B B B B . . . B .		
			Sterna hirundo	0.0055	0.0075
1	RUS	2	A A A A A A A A A A A –		
2	RUS	1	. B . . B . . B . . B –		
3	RUS	1	. C . . B . . . . . B –		
4	USA	1	. B . . B . B . . B B B		
5	USA	1	. . . . B . B . . . B .		
6	USA	2	. D . . B . B . . . B .		
			Brachyramphus marmoratus	0.0045	0.060
1	RUS	1	A A A A A A A A A A A A		
2	RUS	2	. . . . . B . . . . B .		
3	USA	1	B B . B B C . . B . C B		
4	USA	1	B C . B B C . . B . C C		
5	USA	1	B D . B B C . . B . C C		
			Picoides tridactylus	0.0	0.055
1	RUS	5	A A A A A A A A A A A A		
2	USA	4	B B B B B B B . B B B B		
			Hirundo rustica	0.0056	0.015
1	RUS	1	A A A A A A A A A A A A		
2	RUS	1	. . . . B		
3	USA	1	. B B . C . . . B . B .		
4	USA	1	. B B . D . . . B . B .		
			Pica pica	0.0034	0.039
1	RUS	2	A A A A A A A A A A A A		
2	RUS	1	. . B		
3	USA	1	. B B B B . B B B B B B		
4	USA	2	. B B B B . B B B B B C		
			Anthus spinoletta	0.0017	0.029
1	RUS	3	A A A A A A A A A A A A		

TABLE 1. Continued.

Haplotype	Location	*n*	Composite pattern	Average *p*-within	Average *p*-between
2	RUS	1	. . . . B .		
3	RUS	1	. . . . B		
4	USA	2	. B . B B B B C . B . B		
			Calcarius lapponicus	0.0042	0.0044
1	RUS	1	A A A A A A A A A A A A		
2	RUS	2	. B B . . . . . B . B .		
3	USA	1	. C . . . . . . B . C .		
4	USA	2	. C B . . . . . B . C .		
5	USA	1	. B . . . . . . B . C .		
6	RUS	1	. B B . . . . . B . C .		
			Leucosticte arctoa	0.0019	0.0190
1	RUS	2	A A A A A A A A A A A A		
2	RUS	1	B		
3	RUS	1	. . . . B .		
4	RUS	1	. . . . . B		
5	USA	1	C B . . B C B B . . C B		

[1] Averaged across all 3 haplotypes.
[2] Not computed; see text.

METHODS

We surveyed mtDNA restriction fragment length polymorphisms from 13 species (Table 1). We first purified mtDNA from frozen tissues following standard protocols (Lansman et al. 1991, Dowling et al. 1990). Each individuals' mtDNA was digested with 12 restriction endonucleases, end-labeled with ^{35}S, and electrophoresed through 0.8–1.2% agarose gels. Autoradiography revealed fragment profiles for each restriction endonuclease, and different profiles were given a different letter. The 12 letters for each individual constitute its composite haplotype. We scored the presence and absence of each restriction fragment, and used the method of Nei and Li (1979) to estimate the percentage nucleotide divergence (p). Although the pattern of restriction sites is preferred for estimating phylogenetic relationships, for estimating p we have found that restriction fragments and sites yield close correspondence (Avise 1994). Also, most haplotypes were closely related (i.e., separated by one or a few restriction sites) which further eliminates biases in using restriction fragments (Dowling et al. 1990). We used the matrix of p-values to construct a UPGMA phenogram that portrays the pattern of genetic similarity among the haplotypes; however, our sample sizes are too small to pursue haplotype phylogenies between taxa.

We summarized the degree of morphological differentiation among subspecies in a qualitative manner, based on comparisons of study skins at the Burke Museum, personal observations, and the literature. Because range disjunctions also play a role in interpreting mtDNA patterns, we determined the nature of discontinuities in range between Siberian and North American samples in addition to Beringia itself. For consistency we follow the specific nomenclature of the 1983 edition of the AOU Check-List, but we augment this with other citations for controversial species. Subspecific names are from Vaurie (1959, 1965) and the 1957 edition of the AOU Check-List; the best range maps for Russian subspecies are found in Dement'ev and Gladkov (1966–1970).

RESULTS

Little intraspecific sequence divergence was found within continents (Table 1). Differentiation between continents was observed in both terrestrial and aquatic birds, migratory and nonmigratory species, and those with and without phenotypic differentiation (see below). The degree of population differentiation between haplotypes from North American and Siberian samples ranged from zero (*Calcarius lapponicus*) to 6.0% (*Brachyramphus marmoratus*). For all but *Anas crecca* and *Calcarius lapponicus*, mtDNA comparisons revealed apparently diagnostic differences between continents. At one extreme, the samples of *Picoides tridactylus* differed at 11 of 12 restriction endonucleases. At the other extreme, samples of *Sterna hirundo* differed at only one. In *Anas crecca*, very divergent haplotypes were discovered (e.g., haplotypes 1 and 3 vs. 2), but haplotype 2 was found both in Siberia and North America.

DISCUSSION

TAXONOMIC COMMENTS

Limits of intra- and inter-specific taxa are sometimes difficult to judge with molecular methods. Some pairs of avian species appear to have extremely similar mtDNA fragment profiles ($p = 0.001$), such as *Zonotrichia leucophrys* and *Z. atricapilla* (Zink et al. 1991), whereas some sibling species, such as *Limnodromus griseus* and *L. scolopaceus*, are highly differentiated ($p = 0.082$; Avise and Zink 1988). There is no particular level of differentiation that is equated with a given taxonomic rank (Johnson and Zink 1983); rather, the pattern of variation sets the limits of taxa (Cracraft 1983). Furthermore, mtDNA data represent a single gene tree that is embedded in the organismal phylogeny (Avise 1994). Thus, we do not advocate species status unless "fixed" mtDNA differences are associated with other character differences such as plumage patterns. Of course, well-differentiated taxa for which no fixed molecular differences are apparent are sometimes considered distinct evolutionary entities (Barrowclough and Gutiérrez 1990). In recognizing the limitations of our sampling (both in terms of numbers of individuals and named taxa), we do not recommend any formal taxonomic changes below.

Our *Phalacrocorax pelagicus* sample represented the subspecies *pelagicus* (Russia) and *resplendens* (U.S.), which are morphologically similar (*resplendens* is somewhat smaller; Palmer 1962) and essentially continuously distributed (*pelagicus* is transberingian in its distribution in the north Pacific). *Phalacrocorax p. pelagicus* is found in the Russian Far East and Alaska, whereas *resplendens* is found on the west coast of North America from British Columbia southward. Our *resplendens* specimens came from Puget Sound in Washington. MtDNA revealed 4 of 12 restriction endonucleases as distinct, but the overall level of differentiation, 0.0076, is relatively low in comparison to other species pairs (Avise and Zink 1988). Further study is needed to determine where phylogeographic breaks (Avise et al. 1987) occur and whether they are associated with subtle discontinuities in morphology, which would indicate evolutionary divisions of perhaps species status.

Samples of *Anas crecca* represented two transcontinentally distributed subspecies *crecca* (Eurasia) and *carolinensis* (North America), which differ in nuptial coloration of males. Apart from the beringia water barrier, there are no major range disjunctions. We found three haplotypes, two of which were highly divergent; haplotypes 1 vs. 2 gave a p-value of 0.036. This level of haplotype differentiation is consistent with species level distinctness. However, haplotype 2 was found both in Russia and U.S., implying gene exchange between the continents. This is consistent with wintering birds of the "wrong" race regularly being reported from Europe and from both coasts of North America. As in some other waterfowl, mixing of divergent mtDNA haplotype lineages among populations has occurred (Avise et al. 1990, 1992). Further study is needed to determine species limits in *A. crecca*.

Our samples of *Numenius phaeopus* included the subspecies *variegatus* (Russia) and *hudsonicus* (U.S.), which differ in morphology. *Numenius p. variegatus* is smaller than *hudsonicus* and also differs in coloration. *Numenius p. variegatus* has a whitish rump, whereas that of *hudsonicus* is uniformly dark, contrasting little in appearance with its back; *variegatus* also lacks the buffy background color in its venter that characterizes *hudsonicus*. Their differences in background coloration gives *variegatus* a strikingly whiter or grayer overall appearance. A large hiatus in central Siberia apparently separates the breeding range of *variegatus* in the Far East from nominate *phaeopus* of northern Europe (Dement'ev and Gladkov 1966–1970). The isolation of the Far East form, its morphological distinction, and the striking mtDNA differences that distinguish it from *hudsonicus* of North America ($P = 0.047$) suggest strongly that two species are involved. Comparison of these two forms with the European race would be worthwhile. At least three species may be represented because the nominate race, *phaeopus*, of Europe is equally as distinct morphologically as the two forms we have compared genetically (although the variation between *phaeopus* and eastern Siberian *variegatus* might be clinal; Cramp and Simmons 1983). *Numenius p. hudsonicus* also has two disjunct breeding populations in North America, one in the Hudson Bay region and the other in the northwestern arctic (Godfrey 1986), but the two populations have not been described racially.

Our samples of *Gallinago gallinago* include the transcontinental subspecies *delicata* (North America) and *gallinago* (Eurasia); there are no major range disjunctions on either continent. Despite being rather similar morphologically, these two forms are sometimes considered different species (Sibley and Monroe 1990). They differ primarily in number of rectrices (14 in *gallinago,* 16 in *delicata*) and width of the outer rectrices. Our data revealed a single mtDNA restriction site difference, and a very low *p*-value between U.S. and Russian haplotypes ($P = 0.006$). Further sampling is required to discern whether there is a discrete mtDNA boundary that would correspond geographically to the break in morphology.

Our *Larus canus* sample represented the subspecies *kamtschatschensis* (Russia) and *brachyrhynchus* (U.S.), which are separated only by the Bering Sea. *Larus c. kamtschatschensis* is a larger and heavier-billed form than North American *brachyrhynchus,* and slightly darker dorsally, especially in juvenal plumage; tail patterns differ in first basic plumages (Cramp and Simmons 1983). The mtDNA data suggest that two species are represented, a possibility also raised by Sibley and Monroe (1990). Previous molecular studies revealed little differentiation over a large area in a gull species (e.g., Bell 1992). Although gulls tend to wander, there are no North American records of *L. c. kamtschatschensis.* The species-level mtDNA differentiation of $p = 0.02$ was consistent with the morphological differentiation of the east Siberian form.

Our *Sterna hirundo* sample represented the subspecies *longipennis* (Russian Far East) and *hirundo* (U.S.); *hirundo* is also the race found in Europe, and the two subspecies appear to intergrade (Cramp 1985). *Sterna h. longipennis* is slightly larger and darker than *hirundo,* but differs principally during the breeding season in having the bill black, and feet dark brown, red or blackish (for other differences see Cramp 1985). In Eurasia, the transition from *hirundo* to *longipennis* occurs in a broad region of central Siberia where populations exhibit much variation in bill and foot color (Vaurie 1965, Dement'ev and Gladkov 1966–1970). North American populations of Common Terns resemble the red-billed birds of Europe and breed more or less continuously from the Atlantic coast westward to the Rocky Mountains. There is, thus, a very large gap separating the breeding ranges of the two forms we sampled. The mtDNA data suggest very limited differentiation, with only a single fixed restriction site, and *p*-value of 0.0075. Further sampling is required to determine if the black-billed race of the Far East can be characterized by a qualitative break in mtDNA, which would indicate two phylogenetic species. Sibley and Monroe (1990) indicate no species-level controversy.

Brachyramphus marmoratus includes two subspecies, *marmoratus* (U.S.) and *perdix* (Russia). The presumed breeding ranges of these forms (few eggs have been found in western Alaska or in Russia) are separated by a distance of about 500 km at the straits lying between the Commander Islands in Russia and the outer-most group of the Aleutians in the United States (Sealey et al. 1982). There is no overlap in size, *perdix* being considerably larger, with a disproportionately longer and more slender bill, white eye-ring in alternate plumage, and lacking the rich reddish browns in its breeding plumage that characterize *marmoratus.* The mtDNA genomes of the two taxa are highly differentiated ($p = 0.060$), more so than most avian species-level taxa (Avise and Zink 1988); we suggest that they are specifically distinct (as did Ridgway [1919]). Despite at least 10 fall and winter records of *perdix* from inland areas throughout North America (Sealey et al. 1991), philopatry and biogeographic barriers must have been in place for a considerable period.

Our samples of *Picoides tridactylus* included the subspecies *tridactylus* and *albidior* (Russia) and *faciatus* and *dorsalis* (U.S.). Populations are continuously distributed across the northern coniferous forests of Eurasia and North America. Alaskan specimens at the Burke Museum are rather similar in coloration to a series of specimens from the Magadan region. Yet our Asian and North American specimens are unambiguously differentiated genetically, both in number of restriction endonucleases with different patterns (11 of 12) and in *p* (0.055). In other mtDNA surveys of continental variation in woodpeckers, little or no differentiation was found (Ball and Avise 1992, Moore et al. 1991). Hence, we suggest that two species are represented on the two continents, a view that seems previously to have been unrecognized (Sibley and Monroe 1990). On both continents, birds from southern populations (many of which are isolated) are much darker than those in the north (Dement'ev and Gladkov 1966–1970, Vaurie 1965). This within-continent differentiation between northern and southern forms is much more impressive than the more subtle differences between birds from either side of the Bering Sea. Given the sedentary nature of these woodpeckers, more extreme morphological differentiation might be expected across Beringia. Perhaps their morphological similarity is due to similarities in their northern environments; their extreme genetic divergence suggests a long history of isolation.

Our samples of *Hirundo rustica* included the subspecies *saturnata* (Russia) and *erythrogaster* (U.S.); we follow Vaurie's (1959) taxonomy. These two races are similar enough that Dement'ev and Gladkov (1966–1970) consider the northeastern-most populations of Asia (that we sampled) also to be *erythrogaster. Hirundo r. saturnata* is variable in ventral coloration, with individuals varying from almost pure white to russet-ochre in their venters. Our two specimens, taken near Magadan, are almost white ventrally, thus being strikingly different from the American subspecies *erythrogaster,* with its reddish belly. These taxa are separated primarily by the Bering Sea. Our samples differed at 5 of 12 restriction endonucleases (p-value 0.015). *Hirundo r. saturnata* closely resembles the European taxon, *rustica.* In the intervening region, geographic variation in coloration is extreme. For example in the region of Lake Baikal (other Burke Museum specimens), north to Yukutsk on the Lena River, Barn Swallows have uniformly dark, chestnut-colored underparts (Dement'ev and Gladkov 1966–1970). Zones of contact between these very different forms should be examined. We suggest that two or more species exist in *H. rustica.*

Our samples of *Pica pica* included the subspecies *camtschatica* (Russia) and *hudsonia* (U.S.). The isolated race found in Kamchatka (the source of our specimens) and the Anadyr region of Russia is situated in closest geographic proximity to North America. Nonetheless, our Russian and U.S. samples are highly differentiated in mtDNA ($p = 0.039$). Morphologically *camtschatica* is among the most divergent of the eurasian races, having much more extensive white in the primaries and the greenest gloss of all (Vaurie 1959); differences apparently also exist in calls (Goodwin 1976). Our Kamchatkan specimens also differ from North American birds in having shorter tails and heavier bills. North American specimens are more similar morphologically to the European populations. Vaurie (1959) observed that four geographically isolated sets of populations occur in the Old World, one ranging from Europe to central Asia, another in northwest Africa, the one we sampled in northeast Asia, and another in southeast Asia. Thus, there are land barriers in addition to the Bering Sea water barrier. We suggest that multiple species exist in *P. pica,* an opinion consistent with that of Goodwin (1976), but not mentioned by Sibley and Monroe (1990). Given the propensity for individuals of these taxa to wander (Goodwin 1976), one might have predicted little differentiation. Apparently barriers to dispersal were in place for a considerable period, and mtDNA evolution may have proceeded faster than that of plumage.

The specific and subspecific status of *Anthus spinoletta* from Asia and North America are controversial. The Water Pipit complex of Europe and central Asia is often treated as specifically distinct (*Anthus spinoletta*) from the American Pipit of Siberia and North America (*Anthus rubescens*; see AOU 1989). Water and American Pipits reportedly are sympatric without interbreeding in the region of Lake Baikal (see Sibley and Monroe 1990). Ventrally American Pipits are heavily streaked whereas Water Pipits are almost unstreaked; they also differ greatly in vocalizations (Alstrom and Mild 1987). What is striking about our sample is that, although the Bering Sea appears to represent a major barrier to gene flow between Asia and North America, it has not resulted in the development of any significant trans-Beringian morphological differentiation. Vaurie (1954) reports being unable to separate breeding season specimens of American ("Water") Pipits from the Commander Islands and from the mouth of the Lena River from breeding specimens taken in North America. Our own comparisons of Russian and American specimens at the Burke Museum corroborate his findings. Yet, eight of 12 restriction endonucleases separated the Russian and U.S. samples, with a p-value of 0.029. If morphological or other genetic differences between these populations are found, we think they should be treated as different species. *Anthus rubescens* winters in southern regions of both continents, suggesting that east Asian and North American populations were isolated long enough to have differentiated in migratory habits (Dement'ev and Gladkov 1966–1970). Several other trans-Beringian colonists make biannual migrations across the Bering Sea to winter only in one continent or the other, despite breeding in both.

Our sample of *Calcarius lapponicus* represented different subspecies (*alascenis* in U.S. and *lapponicus* in Russia). Although there is little morphological differentiation between them, most of our Russian male specimens are more heavily marked with black than North American breeding specimens from Alaska. A phenogram of haplotypes (not shown) did not reveal separation into two continental groups (and would not even if "rooted"). MtDNA data reveal as much differentiation between haplotypes from the same continent as between haplotypes from different continents. Either the two taxa were recently isolated, such that mtDNA lineages are paraphyletic with respect to subspecies boundaries (Avise 1994), or there is current gene exchange. The absence of mtDNA differentiation does not disprove the existence of subspecies, as morphological change is thought to evolve faster than mtDNA monophyly in some birds (Zink and Dittmann 1993a), but not others (e.g., *Picoides tridactylus, Pica pica*; this study).

Species limits in the genus *Leucosticte* are controversial (AOU 1983); recently, the AOU (1993) elevated the three main North American taxa to species level, rather than as subspecies of *L. arctoa.* Our single U.S. specimen is referable to *L. tephrocotis littoralis,* and our Siberian specimens to *L. arctoa pustulata.* These taxa are morphologically differentiated, and the range is fragmented by land barriers in addition to the Bering Sea itself. The North American specimen differed at eight of 12 restriction fragment profiles from the Russian ones, a p-value of 0.019, a level commensurate with several avian species (Zink et al. 1991). It seems likely that two species are represented in our comparison, which is consistent with the opinion of Sibley and Monroe (1990).

General comments. Our study provides insight into the general nature of mtDNA differentiation within species-level taxa distributed on two continents. Rather than study one species intensively, we compared multiple species on continents. Relatively small samples of individuals suffice for estimating degree of mtDNA differentiation. For example, if one were to draw at random two or three Song Sparrow (*Melospiza melodia*) haplotypes from each of two geographically distant populations, which are not genetically differentiated, it is very unlikely that they would suggest geographic differentiation (Zink and Dittmann 1993a). Although our present study requires amplification with more data, several inferences about inter-continental genetic differentiation can be drawn.

Trans-Beringia comparisons of 13 species indicated a variety of degrees of differentiation. Some "species," such as *Picoides tridactylus, Brachyramphus marmoratus, Anthus spinoletta, Pica pica, Larus canus,* and *Numenius phaeopus* are highly differentiated relative to other avian species (Avise and Zink 1988). These six taxa have clearly had relatively long independent histories on either side of Beringia. At the other extreme, some species appear to have been separated relatively recently (*Gallinago gallinago, Phalacrocorax pelagicus, Sterna hirundo*). Only *Calcarius lapponicus* and *Anas crecca* appear to have current gene exchange across Beringia, as evidenced by the occurrence of the same haplotypes on both continents. Thus, unlike many studies of North American birds (e.g., Ball et al. 1988; Zink and Dittmann 1993a, 1993b; Ball and Avise 1992) the majority of trans-Beringian comparisons exhibited intraspecific isolation, at least to some degree. The variation in degree of mtDNA differentiation could be attributed to different dispersal rates, rates of evolution, or historical factors. Unfortunately, reliable estimates of dispersal distances are unavailable, which prevents determining if genetically differentiated species are relatively more sedentary. Without outgroup comparisons, it is not possible to determine if rates of mtDNA differentiation vary across the species compared (Avise 1994).

Our comparisons suggest that the avifauna of each continent consists of species with a variety of past histories, some with long periods of isolation, others relatively recently isolated, and still others currently in contact. This suggests a history of community membership that is at odds with the principal assumption of vicariance biogeography, which presumes that ancestral biotas were stable and widespread, allowing taxa to differentiate in concert (Neigel and Avise 1986, Avise 1992). Many paleoecologists (e.g., Bennett 1990, Pielou 1991) suggest that communities undergo marked changes in species membership over relatively short geological time periods. Our study suggests that species colonized North America and Siberia at different times, judging from the varying degrees of genetic differentiation, resulting in a mosaic of different histories being represented within a single extant community.

If each species-pair was placed in a phylogenetic context, it might be possible to determine the direction of invasions of each continental region. For example, *Hirundo rustica* has different close relatives on both continents; thus, we might ask whether this swallow differentiated in Asia and later invaded North America or vice versa. Assuming that the Siberian and North American populations of *H. rustica* are sister taxa, this resolves into the question of where the closest relative of this sister pair resides. If the nearest phylogenetic relative of this sister pair is an Old World swallow, one might reasonably infer an invasion of the New World from Asia. Such analyses could reveal general rules about the nature of faunal exchange between Asia and North America.

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APPENDIX 1. Specimen localities and dates of collection. Locality is given as country, state, region, county, nearest town or landmark. RUS = Russia, AK = Alaska, LA = Louisiana, WA = Washington, NM = New Mexico, BC = British Columbia (Canada). Museum numbers are preceded by a "B" for Burke Museum or "L" for Louisiana State University. In cases, the catalogue number is for a collector's field number. Magadan Oblast = Magadanskaya Oblast'. Kamchatka = Kamchatskaya Oblast'.

Museum no.	Species	Haplotype	Locality and date
B44193-95	*Phalacrocorax pelagicus*	1–3	RUS, Magadan Oblast, Magadan (29 June 1992)
Bcsw4709-11		4	WA, Jefferson County, Port Townsend (1 Nov. 1992)
B44496	*Anas crecca*	1	RUS, Magadan Oblast, Magadan (5 July 1992)
B43947		2	RUS, Chukotka Republic, Anadyr (11 July 1992)
Bsar6336-38		2	WA, Island County (13 Apr. 1993)
Bsvd104		3	RUS, Magadan Oblast, Stekol'nyy (7 Sept. 1992)
B44496	*Gallinago gallinago*	1	RUS, Yakutia Republic, Cherskiy (9 July 1992)
B44082		2	RUS, Kamchatka, Koryaki (29 July 1992)
B44047		1	RUS, Kamchatka, Koryaki (23 July 1992)
Bsvd231		3	WA, Grant County, Moses Lake, (28 March 1992)
Bsvd232		4	WA, Grant County, Moses Lake (28 March 1993)
B44620-21	*Numenius phaeopus*	1	RUS, Kamchatka, Oktyabr'skiy (25 July 1992)
B44619		2	RUS, Kamchatka, Oktyabr'skiy (25 July 1992)
L154195		3	LA, Cameron Parish, 7 mi. W Old Mouth Mermentau River (9 Apr. 1993)
L130487		4	LA, Cameron Parish, 1 mi. E mouth Calcasieu Pass (4 May 1986)
L122854		3	LA, Cameron Parish, 1 mi. E mouth Calcasieu Pass (5 Apr. 1985)
B44336-38	*Larus canus*	1	RUS, Kamchatka, Oktyabr'skiy (25 July 1992)
Bcsw4707		2	WA, Jefferson County, Port Townsend (1 Nov. 1992)
B44062, 65	*Sterna hirundo*	1	RUS, Kamchatka, Koryaki (23 July 1992)
B44063		2	RUS, Kamchatka, Koryaki (23 July 1992)
B44064		3	RUS, Kamchatka, Koryaki (23 July 1992)
L154201		4	LA, Cameron Parish, 5 mi. W Old Mouth Mermentau River (20 May 1993)
L131003		5	LA, Cameron Parish, 3 mi. W Old Mouth Mermentau River (4 May 1986)
L130522, 130524		6	LA, Cameron Parish, 3 mi. W Old Mouth Mermentau River (4 May 1986)
B44435	*Brachyramphus marmoratus*	1	RUS, Magadan Oblast, Magadan (28 June 1992)
B44433-34		2	RUS, Magadan Oblast, Magadan (28 June 1992)
Bbks410		3	AK, Prince William Sound (19 July 1991)
Bbks408		4	AK, Prince William Sound (20 July 1991)
Bbks413		5	AK, Prince William Sound (15 July 1991)
B44422	*Picoides tridactylus*	1	RUS, Magadan Oblast, Magadan (26 June 1992)
B44310		1	RUS, Kamchatka, Koryaki (22 July 1992)
B50382		2	AK, Haines (12 June 1988)
B50383		2	AK, Haines (12 June 1988)
B50360		2	BC, Bella Coola, Stupendous Mt. (18 June 1988)

APPENDIX 1. Continued.

Museum no.	Species	Haplotype	Locality and date
L135371		2	NM, Taos County, Carson National Forest, S Palo Flechado Pass (19 June 1987)
Bsvd144, 145		1	RUS, Magadan Oblast, Stekol'nyy (15 Sept. 1992)
B44441	*Hirundo rustica*	1	RUS, Magadan Oblast, Magadan (29 June 1992)
B43854		2	RUS, Magadan Oblast, Magadan (29 June 1992)
L154213		3	LA, Cameron Parish, 4.5 mi. W old mouth Mermentau River (9 Apr. 1993)
L154214		4	LA, Cameron Parish, ca 5 mi. E Cameron (9 Apr. 1993)
B44581, 85	*Pica pica*	1	RUS, Kamchatka, Sokhoch (24 July 1992)
B44584		2	RUS, Kamchatka, Sokhoch (24 July 1992)
Bcsw4761		3	WA, Grant County, Moses Lake (27 March 1993)
Bsar6319		4	WA, Grant County, Moses Lake (27 March 1993)
BSAR6298		4	WA, Grant County, about 2 mi. S, 4 mi E Mattawa (6 Sept. 1992)
B44461	*Anthus spinoletta*	1	RUS, Magadan Oblast, above Ola River headwaters (3 July 1992)
B44462		2	RUS, Magadan Oblast, above Ola River headwaters (3 July 1992)
B44079		3	RUS, Kamchatka, Milkovo (28 July 1992)
B44075		1	RUS, Kamchatka, Milkovo (28 July 1992)
B44206		1	RUS, Magadan Oblast, above Ola River headwaters (3 July 1992)
Bcsw4228-29		4	WA, Whatcom County, 12 mi. N, 6 mi. E Mt. Baker summit (17 July 1990)
B44229	*Calcarius lapponicus*	1	RUS, Yakutia Republic, Cherskiy (8 July 1992)
B44315		2	RUS, Kamchatka, Oktyabr'skiy (24 July 1992)
B44079		6	RUS, Chukotka Republic, Anadyr (9 July 1992)
L135120		3	LA, Cameron Parish, East Jetty at mouth of Calcasieu Pass (25 Oct. 1987)
L152665, 152666		4	LA, Acadia: 4 mi. S. Crowley on Parish Road (25 Dec. 1990)
L152664		5	LA, Acadia: 4 mi. S. Crowley on Parish Road (25 Dec. 1990)
B44623	*Leucosticte arctoa*	1	RUS, Kamchatka, Milkovo (28 July 1992)
B44624		2	RUS, Kamchatka, Milkovo (28 July 1992)
B44622		3	RUS, Kamchatka, Milkovo (28 July 1992)
B44366		4	RUS, Kamchatka, Milkovo (28 July 1992)
B44077		1	RUS, Kamchatka, Milkovo (28 July 1992)
Bsar5901		5	WA, Whatcom County, Mt. Baker (17 July 1990)