

BREEDING-SEASON SYMPATRY FACILITATES GENETIC EXCHANGE AMONG ALLOPATRIC WINTERING POPULATIONS OF NORTHERN PINTAILS IN JAPAN AND CALIFORNIA

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Abstract. The global redistribution of pathogens, such as highly pathogenic avian influenza, has renewed interest in the connectivity of continental populations of birds. Populations of the Northern Pintail (*Anas acuta*) wintering in Japan and California are considered separate from a management perspective. We used data from band recoveries and population genetics to assess the degree of biological independence of these wintering populations. Distributions of recoveries in Russia of Northern Pintails originally banded during winter in North America overlapped with distributions of Northern Pintails banded during winter in Japan. Thus these allopatric wintering populations are partially sympatric during the breeding season. The primary areas of overlap were along the Chukotka and Kamchatka peninsulas in Russia. Furthermore, band recoveries demonstrated dispersal of individuals between wintering populations both from North America to Japan and vice versa. Genetic analyses of samples from both wintering populations showed little evidence of population differentiation. The combination of banding and genetic markers demonstrates that these two continental populations are linked by low levels of dispersal as well as likely interbreeding in eastern Russia. Although the levels of dispersal are inconsequential for population dynamics, the combination of dispersal and interbreeding represents a viable pathway for exchange of genes, diseases, and/or parasites.

Key words: *Anas acuta*, avian influenza, banding, genetic, population dynamics, Russia.

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Resumen. La redistribución global de patógenos, como la altamente patógena gripe aviar, ha renovado el interés en la conectividad de las poblaciones continentales de aves. Las poblaciones de *Anas acuta* que invernan en Japón y California son consideradas como distintas desde un punto de vista de manejo. Empleamos datos de recaptura de aves anilladas y de genética poblacional para determinar el grado de independencia biológica de estas poblaciones invernales. La distribución de las recapturas sucedidas en Rusia de individuos de *A. acuta* que fueron anillados originalmente durante el invierno en América del Norte se superpuso con las distribuciones de individuos que fueron anillados durante el invierno en Japón. Por ende, estas poblaciones invernales alopátricas son parcialmente simpátricas durante la estación reproductiva. Las áreas primarias de superposición se ubicaron a lo largo de las penínsulas de Chukotka y Kamchatka en Rusia. Más aún, la recuperación de anillos demostró la dispersión de individuos entre las poblaciones invernales tanto de América del Norte como de Japón y viceversa. Los análisis genéticos de las muestras de ambas poblaciones invernales mostraron poca evidencia de diferenciación poblacional. La combinación de anillado y marcadores genéticos demuestra que estas dos poblaciones continentales están vinculadas por bajos niveles de dispersión y por un probable entrecruzamiento en el este de Rusia. Aunque los niveles de dispersión no tienen efectos sobre la dinámica de las poblaciones, la combinación de la dispersión y del entrecruzamiento representa una vía viable de intercambio de genes, enfermedades y parásitos.

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INTRODUCTION

Recent intercontinental expansion of zoonotic diseases, such as avian influenza, from Asia to Europe (Olsen et al. 2006) has increased interest in understanding movements and contact between populations of birds (Winker et al. 2007). For example, nearly half of avian influenza viruses isolated from Northern Pintails (*Anas acuta*) in Alaska contained at least one RNA segment more closely related to a group of Asian lineages (Koehler et al. 2008), implying intercontinental contact. Pintails banded in North America have, on rare occasions, been recovered in Japan, suggesting some dispersal between these wintering populations (Nicolai et al. 2005). Accordingly, pintails wintering in Japan and North America may not represent independent populations.

Interpretation of various measures of population dynamics in the context of management requires a clear understanding of population structure. Ultimately, populations are defined by four processes: birth, death, immigration, and emigration. Because birth is a primary driver of population dynamics, populations are frequently defined in terms of breeding distributions. While this definition greatly simplifies understanding of population dynamics, it may have little utility for management. The problem occurs when birds from multiple breeding areas winter sympatrically, or, conversely, when birds from several wintering areas breed sympatrically. In many waterfowl species defined breeding populations may not represent manageable populations because certain management actions (e.g., hunting) are applied primarily away from breeding areas during fall migration and winter. Furthermore, migratory ducks typically pair in winter or early in spring migration, so wintering populations may be more clearly defined genetically than breeding populations (Robertson and Cooke 1999).

Genetic linkages among wintering populations can be maintained in several ways (Webster and Marra 2005). Birds may disperse from one wintering population to another; this process can be described via the immigration and emigration components of population dynamics. Alternatively, recruitment to a wintering population may be a result not only of offspring produced by that population but of offspring from a different wintering population as well (i.e., juvenile immigrants). Finally, genetic linkages among distinct wintering populations can happen via interbreeding when breeding distributions overlap. While pairs of ducks typically form well before the birds arrive at their breeding areas, breeding-season sympatry creates the potential for mate switching and/or extra-pair copulations (Austin and Miller 1995). Such interbreeding would facilitate genetic exchange among allopatric wintering populations without actual dispersal of individuals in the classic immigration/emigration context.

We tested the degree of isolation between wintering populations of the Northern Pintail in Japan and California. We combined distributional data on the recovery of pintails

banded in both wintering areas to assess the degree of sympatry during the breeding season and the evidence for bidirectional dispersal between wintering areas. We examined the diversity of nuclear and mitochondrial (mt) DNA of pintails wintering in Japan and California to investigate whether intercontinental movements should be considered seasonal migratory movements or dispersal that leads to gene flow. A lack of population differentiation and evidence of gene flow would suggest that pintails wintering in Japan and North America represent a potential source of intercontinental transfer of pathogens (Winker et al. 2007).

METHODS

BAND-RECOVERY DATA

We used data from the U.S. Geological Survey's Bird Banding Laboratory and the Yamashina Institute for Ornithology (2002) to examine the summer distribution of recovered pintails that winter in Japan and North America and to determine these populations' degree of breeding sympatry. We restricted our queries of the North American data to pintails banded from November to March from 1951 to 2005 and recovered in Russia from 1951 to 2006, and we summarized these data with permission of all active permit holders. We did not consider birds banded in Alaska during summer because the wintering area of these birds was unknown. Similarly, we evaluated records of birds banded in Japan during the same months from 1966 to 2006 and recovered in Russia from April to September from 1966 to 2007. We used a kernel home-range analysis (Hooge et al. 2001) in ArcView to estimate the 95% utilization area for band recoveries from each wintering population. We used ArcGIS to calculate the proportional overlap between these distributions. As an assessment of dispersal, we also queried both data bases for pintails banded anywhere in North America (including Alaska) and recovered in eastern Asia (i.e., Japan, China, and Korea) during winter and for birds banded in Japan and recovered in North America. For these analyses we did not restrict the dates or locations of banding.

DNA-SAMPLE COLLECTION AND LABORATORY METHODS

We collected DNA samples from wintering pintails (males, females, adults, and juveniles) in Japan and California to infer levels of genetic connectivity. In Japan, we collected feather samples from 90 birds captured live in February 2007 in Miyagi Prefecture, Honshu (38° 42.939' N, 141° 4.766' E). In California, we collected tissue samples from 158 pintails shot by hunters throughout the Central Valley, the pintail's main wintering region in western North America. California samples were collected in the Sacramento Valley ($n = 79$; Butte, Glenn, and Colusa counties) and the northern San Joaquin Valley ($n = 67$; Merced and Fresno counties) from October 2006 to

January 2007 and in the southern San Joaquin Valley ($n = 12$; Kings County) from September to November 2005. A subset of samples from each area was used for nuclear genotyping and mtDNA sequencing.

We obtained nuclear microsatellite genotypes from 220 samples (75 from Japan and 145 from California) by using primers in the polymerase chain reaction (PCR) for the following ten loci: Aph μ 1, Aph μ 7, and Aph μ 9 (Maak et al. 2003), Bca μ 10, Bca μ 11, and Hhi μ 5 (Buchholz et al. 1998), and Sfi μ 4, Sfi μ 5, Sfi μ 7, and Sfi μ 8 (Libants et al., unpubl. data; GenBank U63685, U63686, U63688, and AF180449). Amplification of these ten loci by PCR used reagent cocktails identical to those described by Pearce et al. (2005). All loci except Bca μ 11 and Sfi μ 7 were amplified with the same temperature profile (94 °C for 2 min followed by 40 cycles of 94 °C for 15 sec, 50 °C for 15 sec, and 72 °C for 30 sec) with an MJ Research PTC-200 thermal cycler. Bca μ 11 and Sfi μ 7 were amplified with an annealing temperature of 54 °C. We visualized PCR products on 6% polyacrylamide gels by using a LI-COR 4200 DNA sequencer (LI-COR, Inc.). We scored genotypes according to allele size on the basis of an initial comparison to a M13 DNA sequence ladder and then to samples established as size standards that we ran on each subsequent gel.

We amplified and sequenced a 425-base-pair fragment of the control region (domain I) of mtDNA from 113 samples (60 from Japan and 53 from California) by using PCR primers C1 (L78) and H542 (Sorenson and Fleischer 1996). We amplified samples by PCR and visualized them on 5.5% polyacrylamide gels according to methods described by Pearce et al. (2004). We compared sequences to a homologous mtDNA region for the Northern Pintail on GenBank (accession AY112939, Donne-Gousse et al. 2002) and to other closely related waterfowl to ensure similarity because mtDNA primers can amplify nuclear pseudogenes (Sorenson and Quinn 1998). We aligned sequences with AlignIR version 2.0 (LI-COR, Inc.) and identified unique haplotypes with FaBox (Villesen 2007). For all sequences, we identified the type and position of each variable site (transition, transversion, or indel) and used this information in population-genetic analyses. All mtDNA sequences have been deposited in GenBank (accession GQ222072–GQ222184).

GENETIC DIVERSITY AND DIFFERENTIATION

For each microsatellite locus, we calculated allele frequencies, allelic richness (see Kalinowski 2004), observed (H_O), and expected (H_E) heterozygosity with the program ARLEQUIN version 3.0.1 (Excoffier et al. 2005). We also used ARLEQUIN to conduct exact probability tests for deviations from Hardy–Weinberg equilibrium in each sampling area by following the method of Guo and Thompson (1992). We used the program GENEPOP (Raymond and Rousset 1995) to test genotypic linkage disequilibrium for each pair of loci in each sampling area. For mtDNA sequence data, we used ARLEQUIN

to estimate mtDNA-haplotype diversity (h ; Nei 1987) as an index of genetic diversity. We displayed the relationship of all mtDNA haplotypes graphically by constructing a network diagram with the program Network, version 4.2 (Bandelt et al. 1999).

We used ARLEQUIN to generate estimates of inter-population variance in frequencies of nuclear alleles (F_{ST}) and mtDNA haplotypes (Φ_{ST}) to examine patterns of genetic differentiation within and between sampling areas. For mtDNA sequence data, we generated F -statistic analogs by using the Tamura and Nei (1993) model of nucleotide evolution as identified by the program MODELTEST (Posada and Crandall 1998). To examine differentiation between the areas further, we used the Bayesian clustering method of Pritchard et al. (2000) in the program STRUCTURE, version 2.2. We excluded population information from the analysis and assessed the likelihood that the entire data set was composed of individuals from K populations, each of which may be characterized by a unique set of alleles. We then estimated the posterior probability of each possible number of populations in the data between 1 and 6. Results are based on 30 000 Markov-chain Monte Carlo iterations following a burn-in period of 30 000 iterations.

We used the isolation with migration (IM) program (Nielsen and Wakeley 2001) to determine if differences between wintering areas in patterns of mtDNA variation were the result of recent divergence and isolation, gene flow, or both. The IM program uses a Markov-chain Monte Carlo approach to estimate the effective population size of the two wintering groups (θ_{Japan} and $\theta_{\text{California}}$) and migration (dispersal that results in gene flow) rates (m) between groups. For initial runs, we assigned wide, flat priors that were assumed to be uninformative for each parameter. Then, for final runs, we restricted the range of parameter values around the peaks. Estimates of θ_{Japan} and m did not converge well (i.e., tails of posterior distributions did not approach zero) even after the program was run multiple times with different maximum priors for these parameters. We implemented Metropolis coupling by using 10 chains with 10 chain-swap attempts per step, a geometric heating scheme ($g_1 = 0.95$, $g_2 = 0.80$), and a burn-in period of 10^6 steps, recording results every hour (see Hey and Nielsen 2004). We ran IM three times under identical conditions but with different random seeds to assess congruence among runs. Because all three runs gave similar results, we report the peak and 95% intervals of the highest posterior distribution (HPD) of all parameters on the basis of the longest run (21×10^6 steps, 784 hr, lowest effective sample size = 158). We estimated the effective number of female migrants per generation (m) between Japan and California with $M = \theta m/2$, where θ is the effective population size of the total population ($\theta_{\text{Japan}} + \theta_{\text{California}}$) and m is the migration rate scaled to the neutral mutation rate per generation (see Hey and Nielsen 2004). Given our failure to detect differentiation, we constrained the

migration rate as a single, symmetrical parameter with equal levels of dispersal in both directions.

RESULTS

BANDING DATA

A total of 130 pintails banded in North America and recovered in Russia met our criteria. The 90%-kernel use area for the birds banded in North America covered 1.007×10^6 km² (Figure 1). There were 905 Russian recoveries of pintails banded in Japan that met our criteria. The estimated area of use for the population marked in Japan encompassed 1.742×10^6 km², and 45% (i.e., 0.781×10^6 km²) of this area overlapped that used by birds banded in North America. The distribution in Russia of pintails banded in North America included all of the Chukotka Peninsula, most of the Kamchatka Peninsula, and localized areas near Magadan, Chaun Bay, and the Kolyma lowlands (Figure 1). With the exception of the Chukotka Peninsula, the corresponding breeding distribution of birds wintering in Japan included all of these areas and extended farther west to include

the Kolyma River delta as well as areas along the west side of the Sea of Okhotsk and Sakhalin Island (Figure 1).

Twenty-seven of the pintails banded in North America (all months), primarily during fall migration in Alaska, were subsequently recovered while wintering in eastern Asia (25 in Japan, 1 each in China and South Korea). Six of these recoveries were of hatch-year birds banded on Adak Island in September 1979 (Figure 1). Given that pintails do not breed on Adak, the continent from which these birds originated is unknown. The remainder of the birds banded in North America and recovered in Asia were banded on the Alaska mainland, in Canada, or in the contiguous 48 states. These individuals likely spent the winter of banding in North America and dispersed to Asia in a subsequent winter. Forty pintails banded during winter in Japan have been recovered and reported in North America (Canada, the U.S., and Mexico).

GENETIC DIVERSITY AND DIFFERENTIATION

We genotyped a total of 220 samples for 10 nuclear loci. We detected significant deviations from Hardy–Weinberg

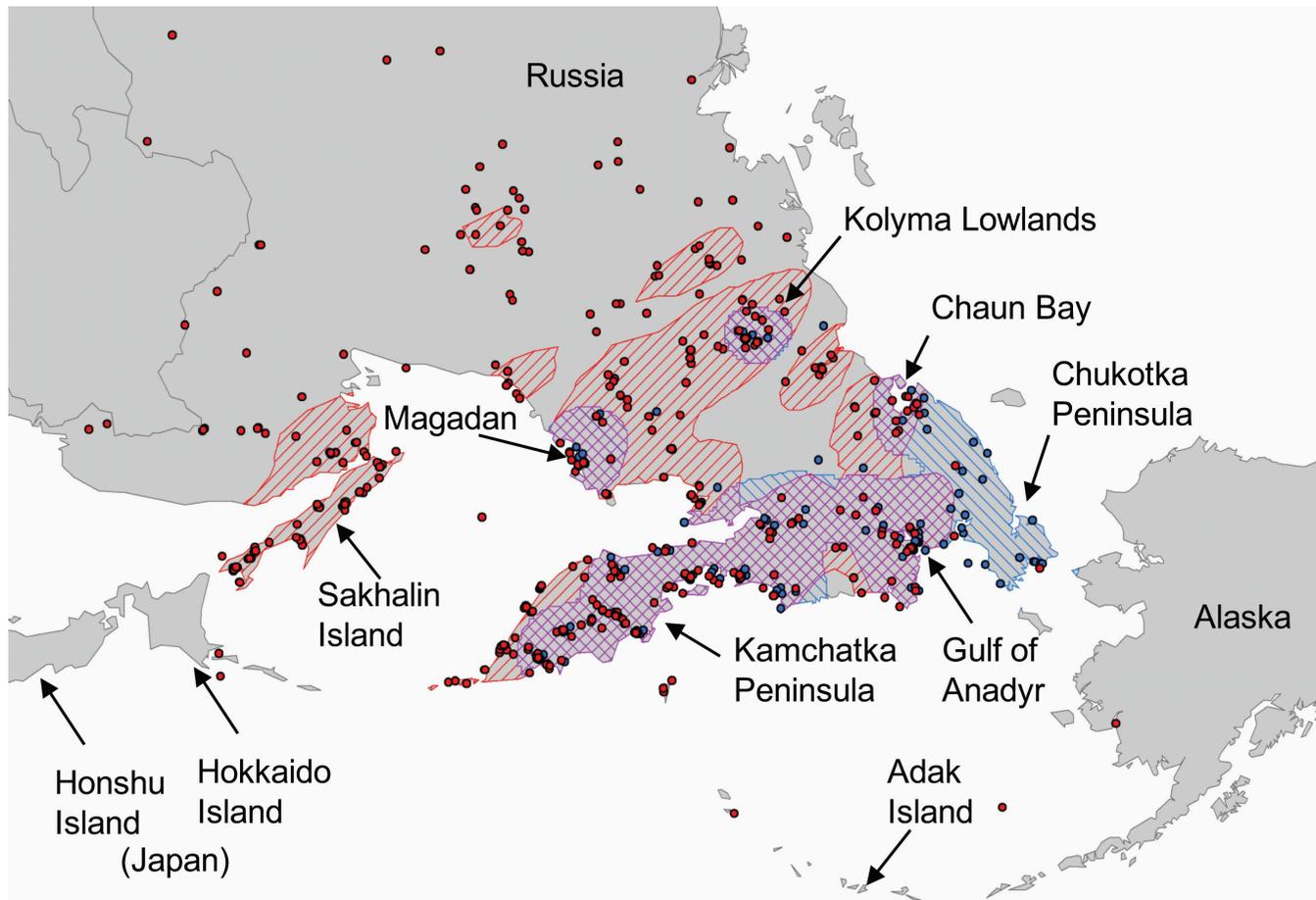


FIGURE 1. Breeding-season recovery locations of Northern Pintails banded during winter (November–March) in Japan (red dots) or North America (blue dots) and recovered in Russia. Hatched areas represent the 90%-kernel home ranges for the Japanese (red) and North American (blue) populations. Cross-hatched areas show where the two distributions overlap.

TABLE 1. Summary statistics for mtDNA sequences and eight nuclear microsatellite loci of the Northern Pintail by sampling area, including number of samples, n (and number of mtDNA haplotypes per site), allelic richness (A) averaged across nuclear loci, mtDNA haplotype diversity (h), and average expected (H_E) and observed (H_O) heterozygosities across nuclear loci.

	Sampling area	
	Japan	California
Mitochondrial		
n	53 (26)	60 (23)
h	0.861	0.854
Nuclear		
$n(A)$	75 (10.5)	145 (11.2)
H_E/H_O	0.71/0.70	0.72/0.72

proportions ($P < 0.05$) in 8 of the 20 area-by-locus combinations. Deviation was noted for Bca μ 11 and Sfi μ 8 in both sampling areas, so we dropped these two loci from further analysis. Average allelic richness for the remaining eight loci ranged from 4.4 (Hhi μ 5) to 26.1 (Aph μ 7) alleles, but standardized allelic richness was similar in both areas (Table 1). For the remaining eight nuclear loci, overall estimates of differentiation were low and not significant ($F_{ST} = 0.002$, $P = 0.95$). Results from program STRUCTURE were similar to those via F -statistics, with K ($\log L = -4843.0$) equaling a single population. Thus, on the basis of nuclear microsatellite data, both sets of analyses (F -statistics and Bayesian assignment) suggested no differentiation between pintails from California and Japan.

We sequenced 425 base pairs of the mtDNA control region from 113 pintails (Table 1). Forty-three unique mtDNA haplotypes defined by 33 variable sites (30 transitions and 3 transversions) were identified among the 113 samples. No insertions or deletions were observed. The reference sequence of Donne-Gousse et al. (2002) from GenBank (AY112939) was identical to our haplotype 1 (GenBank GQ222072), the most common haplotype among our samples from Japan (36%) and California (32%). Six haplotypes (1, 5, 6, 12, 17, and 24), representing 64% of all sequences, were shared by the two sampling areas. A haplotype network involved numerous nodes and single branches with no clear phylogeographic clustering of haplotypes by sampling area (Figure 2). For mtDNA, the level of differentiation was low and not significant ($\Phi_{ST} = 0.002$, $P = 0.44$).

Parameter estimates from the IM program formed unimodal posterior distributions, though the tails of distributions for θ_{Japan} (effective size of Japan sample) and m (migration rate) did not approach zero, indicating that there was no support for a hypothesis of no gene flow between populations. Setting wider priors did not change the locations of peaks in

the posterior distributions. The estimate of θ_{Japan} peaked at 69.7 (lower 95% HPD: 60.7–1,463.2), double that of the estimate for $\theta_{\text{California}}$, which peaked at 34.5 (95% HPD: 21.5–845.5). The peak estimate for the bidirectional dispersal rate (m) between Japan and California was large ($m = 4.7$), and the 95% HPD did not overlap zero (1.5–49.9), suggesting the hypothesis of no gene flow can be rejected. Converting these values of m , we estimated the effective number of bidirectional dispersers per generation between Japan and California wintering areas to be 244.8, although the error around this estimate is large (95% HPD: 78–2599).

DISCUSSION

Our analyses demonstrate that populations of pintails wintering in Japan and California are not genetically isolated. Band recoveries demonstrate that some individuals disperse to wintering areas in both directions (this study, Nicholi et al. 2005). Although such movements appear to be relatively rare, they may partially explain the lack of genetic differentiation between wintering populations. The breeding-season sympatry we document would also facilitate genetic exchange in the absence of dispersal. Thus, the observed genetic exchange likely results from the combination of dispersal and interbreeding between these wintering populations.

While the overall distribution of recoveries of pintails banded in North America overlaps substantially with recoveries of birds marked in Japan, the proportion of the North American population that crosses over the Bering Sea in a given year is unknown (Henny 1973, Udvardy and Engilis 2001). Udvardy and Engilis (2001) speculated that there is a “sizable” movement from wintering areas in California to breeding areas in Siberia. Miller et al. (2005) documented that four pintails marked with satellite transmitters in California crossed over into Russia. After the failure rate of transmitters is accounted for, these four birds represent approximately 5% of the total sample of pintails with transmitters that were still functioning during the breeding season (Miller et al. 2005). Given that >1 000 000 Northern Pintails winter in the Central Valley of California, the data of Miller et al. (2005) suggest that perhaps as many as 50 000 pintails may cross the Bering Strait in a given year. Although this extrapolation is based on a small sample, Miller et al. (2005) marked only females, whereas males may be more inclined to undertake longer migrations (Derksen and Eldridge 1980). Furthermore, the attachment of radio transmitters may have limited the migratory ability of some marked individuals (Ward and Flint 1995). Accordingly, we conclude that it is common for California-wintering pintails to cross into Russia each summer (Henny 1973, Udvardy and Engilis 2001).

If the probabilities of band recovery and reporting in each area are similar, the likelihood of regular intercontinental movement between the two wintering populations appears to be different. Birds marked in North America were recovered

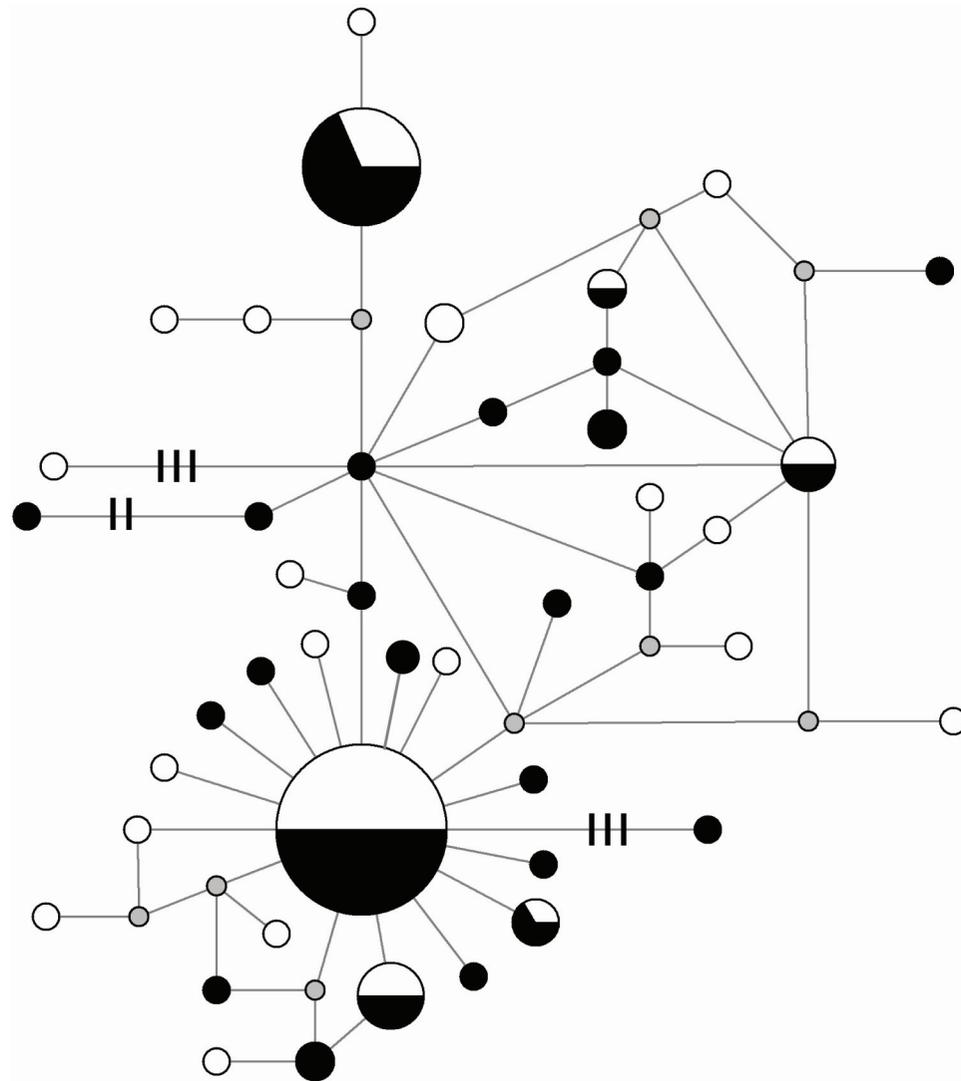


FIGURE 2. MtDNA haplotype network for 113 samples (43 haplotypes) of the Northern Pintail from Japan (white circles) and California (black circles). The most common haplotype (1), represented by the largest circle, was present in an equal number ($n = 19$) of birds in Japan and California. A single-site substitution links each circle except where bars are present; these denote haplotypes differing by multiple substitutions. Circles are proportional to the observed number of each haplotype. Small gray dots are inferred haplotypes. These data demonstrate that mtDNA haplotypes do not sort according to the two wintering populations from which they were sampled.

regularly in Russia, but birds marked in Japan were rarely encountered in Alaska during the breeding season. Therefore, breeding-season sympatry results primarily from birds in the North American population crossing into Asia during summer rather than the reverse. This difference in migratory behavior may persist from historic differences in breeding distributions in the Beringian unglaciated refugium during the Laurentide glacial maximum (see Miller et al. 2005). These movements, and subsequent interbreeding and dispersal into Asia, may help explain the larger effective population size (θ_{Japan}) suggested by the IM analysis. Other indices for mtDNA and nuclear loci, however, do not suggest greater genetic diversity within Asia (Table 1). Pintails wintering in Japan may

originate from a larger breeding distribution than those wintering in California.

Rates of both band recovery and genetic dispersal suggest that overall levels of intercontinental dispersal are low. Thus, dispersal by individuals can explain a portion of the genetic exchange between wintering populations. Breeding-season sympatry likely further contributes to genetic exchange. If females of North American origin interbreed with males of Asian origin (or vice versa), the resulting offspring would appear as dispersers from a genetic perspective but would be considered normal recruits in a standard population-dynamics context. Cronin et al. (1996) concluded that there is no genetic differentiation within pintails breeding across North America,

and our data expand this conclusion to include birds wintering in Japan and breeding in eastern Russia. Such genetic exchange certainly indicates “biological contact” among largely segregated wintering populations. Koehler et al. (2008) demonstrated that viruses isolated from pintails in Alaska and wild birds in Japan show evidence of genetic exchange, and our results demonstrate the potential pathways for this viral exchange. Given that direct dispersal is apparently rare, we suspect that the majority of contact between these populations occurs during the breeding season in eastern Russia. Accordingly, population genetics may be useful for assessing potential contact among apparently allopatric populations and provide insight into the relative risk of transfer of diseases, such as avian influenza.

For practical management, populations wintering in Japan and California are considered distinct. Our band-recovery data indicate that levels of dispersal are not sufficient to influence population dynamics. Accordingly, management focused on one wintering population should have negligible effects on the other wintering population. Genetic data, however, suggest that these disparate wintering populations originate from a single breeding population: the allopatric wintering populations on two continents are somewhat sympatric during the breeding season. While the proportion of overlap is relatively large for the Japanese population, it is very small (<5%) for the North American population (Austin and Miller 1995, Miller 2005). Thus even a proportionally small overlap in breeding distributions results in genetic exchange sufficient to preclude differentiation. Given that these wintering populations share and exchange genes, it follows that they should also be expected to share and exchange diseases and parasites (Jahangir et al. 2009).

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