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PHYLOGEOGRAPHY OF THE MALLARD (*ANAS PLATYRHYNCHOS*): HYBRIDIZATION, DISPERSAL, AND LINEAGE SORTING CONTRIBUTE TO COMPLEX GEOGRAPHIC STRUCTURE

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Abstract.—Population genetic variation in Mallards (*Anas platyrhynchos*; $n = 152$) from Western Russia, North Asia, the Aleutian Islands, and mainland Alaska was investigated using 667 base pairs of the 5′-end of the mitochondrial DNA (mtDNA) control region. DNA sequencing revealed two clades that correspond to Avise et al.'s (1990) group A and B mtDNA haplotypes. Group A haplotypes (80.3%) were widespread in all localities from Western Russia to Alaska. Group B haplotypes (19.7%), by contrast, were found primarily in mainland Alaska, where they occurred at high frequency (77.4%), but they also occurred at low frequencies (declining east to west) in the Aleutian Islands (11.8%) and the Primorye region of North Asia (4.4%). Group B haplotypes were not observed in Western Russia or elsewhere in North Asia outside Primorye. Consequently, Mallards exhibited substantial genetic structure between Old World and New World ($\Phi_{ST} = 0.4112–0.4956$) but possessed little genetic structure within the Old World continental area ($\Phi_{ST} = 0.0018$). Nonetheless, when only group A haplotypes were included in the analysis, Mallards from the Aleutian Islands differed (albeit with low levels of divergence) from each of the other three sampled regions in the Old World and New World ($\Phi_{ST} = 0.0728–0.1461$, $P < 0.05$). Mallards inhabit the Aleutian Islands year-round, so these insular populations may be isolated from Asian and North American populations that occur in the Aleutian Islands only during migration. Overall weak phylogeographic structure and low genetic differentiation within Asia, and between Asia and North America when only group A haplotypes were evaluated, is probably explained by large long-term population sizes and significant intra-continental dispersal. The coexistence and nonrandom distribution of two divergent mtDNA haplotype lineages in Alaska, the Aleutian Islands, and the Primorye region of North Asia, but not in Western Russia or elsewhere in North Asia, is consistent with historical and contemporary hybridization and incomplete sorting of A and B mtDNA haplotype lineages in Mallards and closely related species inhabiting the Old World and New World. *Received 22 August 2004, accepted 1 March 2005.*

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Филогеография кряквы (*Anas platyrhynchos*): сложная географическая структура как результат сортировки линий мтДНК, гибридизации и расселения

Резюме.—Исследован полиморфизм нуклеотидных последовательностей 5′-фрагмента контрольного региона митохондриальной ДНК кряквы (*Anas platyrhynchos*; $n = 152$) из западной России, Северной Азии, Алеутских островов и Аляски. На основании данных секвенирования мтДНК выявлены две группы гаплотипов, которые соответствуют A и B группам гаплотипов Эйвиса с соавт. (Avise et al. 1990). Гаплотипы A группы (80.3%) обнаружены во всех выборках. B гаплотипы (19.7%) встречаются с самой высокой частотой на Аляске (77.4%), и с меньшей частотой на Алеутских островах (11.8%) и в Приморском крае (4.4%). Гаплотипы B группы отсутствуют в выборках из западной России и Северной Азии (за исключением Приморья). Показано, что популяции кряквы Евразии и Северной Америки значительно дифференцированы ($\Phi_{ST} = 0.4112–0.4956$), в то же время на территории Евразии генетическая подразделенность кряквы практически отсутствует ($\Phi_{ST} = 0.0018$). При использовании в анализе только A группы гаплотипов выявлена дифференциация алеутской популяции (хоть и незначительная) от популяций западной России, Северной Азии и Аляски ($\Phi_{ST} = 0.0728–0.1461$, $P < 0.05$). Изоляция алеутской популяции может быть обусловлена тем, что значительная часть популяции является местной и практически не покидает острова в течение года, тогда как кряквы из Азии и Северной Америки залетают на Алеутские острова только во время миграций. Слабая филогеографическая структура и низкая генетическая дифференциация кряквы в Азии, и между Азией и Северной Америкой (в случае анализа только A группы гаплотипов) наиболее вероятно объясняется большой численностью популяций и значительной натальной дисперсией кряквы. Одновременное присутствие и неслучайное распределение двух дивергентных групп гаплотипов мтДНК в выборках из Аляски, Алеутских островов и Приморского края согласуется с исторической и современной гибридизацией и незавершенной сортировкой линий гаплотипов мтДНК кряквы и близкородственных ей видов, населяющих Евразию и Северную Америку.

PHYLOGEOGRAPHIC PATTERNS OF birds (Aves) have been studied at various geographic scales. However, relatively few Holarctic waterfowl (Anatidae) species have been studied (Cronin et al. 1996, Lanctot et al. 1999, Scribner et al. 2001, Kulikova et al. 2004, Pearce et al. 2004). Waterfowl are an important migratory component of the Holarctic avifauna, and their phylogeography and population genetics at high latitudes can provide insight into how these climatologically variable regions have affected avian lineages. Waterfowl also represent an unusual exception to the male-biased philopatry and female-biased dispersal that is the prevalent pattern in other birds (Rohwer and Anderson 1988, Anderson et al. 1992). Pair formation in most Holarctic migratory ducks occurs on the wintering grounds (McKinney 1992, Oring and Sayler 1992), where considerable mixing of birds from different nesting areas can occur; yet mated pairs frequently return to the female's natal or prior nesting area, such that most gene flow in Northern Hemisphere waterfowl is thought to be male-mediated. Maternally inherited mitochondrial DNA (mtDNA) is thus an excellent tool for phylogeographic studies of waterfowl, though it likely underestimates nuclear gene flow for most species.

The Mallard (*Anas platyrhynchos*) is the most numerous and well-known waterfowl species with a Holarctic distribution and thus serves as

a model for waterfowl studies in the Holarctic. The Mallard's breeding range in the Palearctic extends from the British Isles and North Africa, through Europe and Russia, to the Pacific coast from the Kamchatka Peninsula to northern Japan and northeastern China (Shevareva 1968, Johnsgard 1978, Drilling et al. 2002). In the Nearctic, the species primarily breeds in the western and central parts of North America. Most Mallards are migratory, and spring and fall flights can exceed many thousands of kilometers. However, many populations in temperate Western Europe and North America are also resident where open water is available year-round.

Mallards are also noteworthy because they have hybridized extensively with other closely related species worldwide. After being introduced into Australia and New Zealand, Mallards hybridized with the Grey Duck (*A. superciliosa*; Braithwaite and Miller 1975, Gillespie 1985). Eastward expansion of Mallards into American Black Duck (*A. rubripes*) habitat in North America has resulted in an increase in the frequency of ducks showing hybrid Mallard × American Black Duck plumage characteristics and a decline in American Black Duck numbers (Brodsky and Weatherhead 1984, D'Eon et al. 1994). In addition, the endemic Hawaiian Duck (*A. wyvilliana*) has hybridized with Mallards on the island of Oahu (Browne et al. 1993). Hybrids between Mallard and Mottled Duck (*A. fulvigula*) in North America (Mazourek and Gray 1994) and Mallard and Eastern Spot-billed Duck (*A. zonorhyncha*) in the Russian Far East have also been documented (Zhuravlev et al. 2002).

The population genetic structure of Mallards has not been studied adequately, particularly for Eurasian populations. Seasonal migrations and potential for high rates of gene flow without simple geographic directionality suggest that Mallard populations may show very little geographic structure. On the other hand, Shevareva (1968) identified nine Mallard populations in the territory of the former Soviet Union using banding records. In addition to providing insight into how strong seasonality, concordant seasonal migration, and historical processes have affected Holarctic avian lineages, knowledge of Mallard population structure and distribution is necessary to develop measures for management, because the Mallard is the most popular game duck in Eurasia and North America.

We investigated Mallard mtDNA genetic differentiation in Western Russia, North Asia, the Aleutian Islands, and mainland Alaska. Our objectives were to (1) reconstruct the phylogenetic relationships of Mallard mtDNA haplotypes sampled broadly throughout the Holarctic, (2) test whether haplotype frequencies differ between the Old World and New World (and between these continents and the Aleutian Islands), and (3) further evaluate evidence of interspecific hybridization and incomplete lineage sorting of Mallard mtDNA haplotypes in different geographic regions.

Methods

We collected 152 Mallards from Western Russia (Arkhangel'skaya, Astrakhan'skaya; n = 13), North Asia (Kazakhstan, Mongolia, Primorye, Khabarovsk, Magadan; n = 91), the Aleutian Islands (n = 17), and mainland Alaska (n = 31). We recorded specific collecting localities and museum catalogue numbers for vouchered specimens and combined specimens into general localities and regional samples (Table 1). DNA was extracted from liver and muscle tissues using a DNeasy Tissue Kit (Qiagen, Valencia, California). We amplified the 5′ end of the mtDNA control region: positions 79–773 in the chicken (*Gallus gallus*) mitochondrial genome (Desjardins and Morais 1990). Control region primers included L78 (Sorenson and Fleischer 1996) and H774 (Sorenson et al. 1999). Polymerase chain reactions (PCR) were done in a DNA Engine DYAD thermal cycler (MJ Research, Waltham, Massachusetts) using 50 μL reactions containing template DNA, 2.5 μL of each primer (10 mM), 5 μL of 10 mM dNTPs, 5 μL of 25 mM $MgCl_2$, 5 μL of 10× PCR buffer, and 0.25 μL Taq DNA Polymerase. Thermal cycling was as follows: 7 min preheat at 94°C, followed by 45 cycles of 20 s at 94°C, 20 s at 52°C, 1 min at 72°C, and a final extension of 7 min at 72°C. The PCR products were electrophoresed in agarose, excised from the gel, and purified using QIAquick Gel Extraction Kits (Qiagen). Both strands were cycle-sequenced using BigDye Terminator Cycle Sequencing Kits diluted four-fold, followed by electrophoresis on an ABI 3100 automated DNA sequencer (Applied Biosystems, Foster City, California).

TABLE 1. Specimens and sources of genetic material included in the present study.

Catalogue (field–prep) number [a]	Sex	Haplotype [b]	Locality and date
		Western Russia	
Arkhangel'skaya Oblast'			
BellMNH (BRB 428)	M	A-8	Kargopol'skiy Rayon; 56 km S, 23 km W Kargopol; Medvedevo Village; 60°59'56"N, 38°33'22"E; 26 May 2002
BellMNH (BRB 444)	M	A-3	Kargopol'skiy Rayon; 56 km S, 23 km W Kargopol; Medvedevo Village; 60°59'56"N, 38°33'22"E; 29 May 2002
BellMNH (BRB 445)	M	A-80	Kargopol'skiy Rayon; 56 km S, 23 km W Kargopol; Medvedevo Village; 60°59'56"N, 38°33'22"E; 29 May 2002
BellMNH (IUK 672)	M	A-84	Kargopol'skiy Rayon; 56 km S, 23 km W Kargopol; Medvedevo Village; 60°59'56"N, 38°33'22"E; 2 June 2002
BellMNH (IUK 673)	M	A-18	Kargopol'skiy Rayon; 56 km S, 23 km W Kargopol; Medvedevo Village; 60°59'56"N, 38°33'22"E; 2 June 2002
BellMNH (SVD 2723)	M	A-7	Kargopol'skiy Rayon; 56 km S, 23 km W Kargopol; Medvedevo Village; 60°59'56"N, 38°33'22"E; May 2002
BellMNH (SVD 2724)	M	A-7	Kargopol'skiy Rayon; 56 km S, 23 km W Kargopol; Medvedevo Village; 60°59'56"N, 38°33'22"E; May 2002
BellMNH (SVD 2725)	M	A-72	Kargopol'skiy Rayon; 56 km S, 23 km W Kargopol; Medvedevo Village; 60°59'56"N, 38°33'22"E; May 2002
BellMNH (SVD 2726)	M	A-81	Kargopol'skiy Rayon; 56 km S, 23 km W Kargopol; Medvedevo Village; 60°59'56"N, 38°33'22"E; May 2002
BellMNH (SVD 2738)	M	A-83	Kargopol'skiy Rayon; 56 km S, 23 km W Kargopol; Medvedevo Village; 60°59'56"N, 38°33'22"E; 2 June 2002
Astrakhanskaya Oblast'			
UWBM 56702 (CSW 5555)	M	A-7	Astrakhan', 15 km S, 22 km W; 46°13'N, 47°46'E; 2 June 1996
UWBM 56923 (SVD 1153)	M	A-85	Astrakhan', 15 km S, 22 km W; 46°13' N, 47°46'E; 4 June 1996
UWBM 56924 (SVD 1154)	F	A-3	Astrakhan', 15 km S, 22 km W; 46°13'N, 47°46'E; 4 June 1996
		North Asia	
Kazakhstan			
UWBM 46390 (DAB 231)	M	A-80	Almaty Oblysy; Akkol', 10 km S, 45 km W; 44°53.6' N, 75° 07.3' E; 394 m; 17 May 1993
UWBM 46391 (DAB 232)	F	A-86	Almaty Oblysy; Akkol', 10 km S, 45 km W; 44°53.6'N, 75°07.3'E; 394 m; 17 May 1993
UWBM 46274 (CDS 4837)	F	A-79	Almaty Oblysy; Alma-Ata, 35 km N, 25 km W; Sorbulak Köl; 43° 38.9'N, 76°33' E; 21 May 1993

TABLE 1. Continued.

Catalogue (field–prep) number [a]	Sex	Haplo-type [b]	Locality and date
Mongolia			
UWBM 69923 (CSW 5899)	–	A-82	Dornod Aymag; Nömrögiyn Gol; 47°00′N, 119°22′E; 2,800 ft; 27 May 1998
Khabarovskiy Kray			
UAM 9118	–	A-17	Khabarovskiy Kray, Russia; 70 km ENE Khabarovsk; 48°40′N, 136°00′E; 26 April 1999
UWBM 46882 (BKS 932)	F	A-32	Khabarovskiy Kray, Russia; Ozero Evoron; 51°23′N, 136°33′E; near Goryun River; 17 June 1993
UWBM 47068 (CSW 4828)	F	A-25	Khabarovskiy Kray, Russia; Nizhnetambovskoye, 18 km S, 35 km W; delta of Goryun River; 50°45′N, 137°43′E; 15 June 1993
UWBM 47160 (SAR 6383)	M	A-78	Khabarovskiy Kray, Russia; Nizhnetambovskoye, 18 km S, 35 km W; delta of Goryun River; 50°45′N, 137°43′E; 15 June 1993
Magadanskaya Oblast′			
UWBM 44374 (JMB 1220)	M	A-76	Magadanskaya Oblast′, Russia; Balagannoye, near Tauy River; 59°38′N, 149°07′E; 3 August 1992
		Aleutian Islands, Alaska	
Near Islands			
UAM 20084 (CLP 382)	–	A-75	Attu Island; 12 September 1999
UAM 11613 (DAR 120)	F	A-75	Attu Island; 8 October 2000
UAM 14537 (UAMX 2184)	F	A-75	Attu Island; 17 October 2000
UAM 14532 (ABJ 121)	M	A-7	Attu Island, Henderson Pt.; 7 May 2001
UAM 14531 (DAR 216)	F	A-29	Attu Island; 18 May 2001
UAM 15021 (UAMX 1738)	–	A-75	Attu Island; 1 June 2001
UAM 13528 (UAMX 1739)	–	A-75	Attu Island; 1 June 2001
UAM 13955 (UAMX 1741)	–	A-75	Attu Island; 1 June 2001
UAM 11327 (DDG 1775)	M	A-75	Shemya Island; 27 May 2000
UAM 11328 (DDG 1776)	F	A-73	Shemya Island; 27 May 2000
UAM 18960 (DDG 1777)	M	A-74	Shemya Island; 28 May 2000
UAM 18961 (DDG 1782)	M	A-77	Shemya Island; 3 June 2000
UAM 15060 (DDG 1787)	M	A-73	Shemya Island, 52°43′ N, 174°07′ E; 5 June 2000
UAM 13480 (DDG 1882)	M	A-73	Shemya Island; 3 June 2001
UAM 14195 (DDG 1883)	M	B-71	Shemya Island; 3 June 2001
Andreanof Islands			
UAM 13042 (DAR 146)	–	B-51	Adak Island; 28 May 1997
UAM 18087 (JMM 161)	M	A-52	Adak Island; 23 December 2000
		Mainland Alaska	
Alaska Peninsula			
UAM 14530 (KGM 383)	M	B-62	Izembek National Wildlife Refuge, Grant Point Road; 55°15′56″ N, 162°52′10″W; 27 August 2001
UAM 17850 (KGM 384)	F	B-62	Izembek National Wildlife Refuge, Grant Point Road; 55°15′56″ N, 162°52′10″ W; 27 August 2001
UAM 18485 (KGM 385)	F	B-62	Izembek National Wildlife Refuge, Grant Point Road; 55°15′56″N, 162°52′10″ W; 27 August 2001
UAM 14534 (KGM 391)	M	A-52	Cold Bay, near Airport; 55°13′45″N, 162°44′04″W; 27 August 2001

TABLE 1. Continued.

Catalogue (field–prep) number [a]	Sex	Haplo-type [b]	Locality and date
UAM 17851 (KGM 392)	M	B-63	Izembek National Wildlife Refuge, Izembek Lagoon, near Grant Point; 28 August 2001
UAM 14535 (KGM 414)	F	A-87	Izembek National Wildlife Refuge, Grant Point Road; 55°15′55″N, 162°52′10″W; 30 August 2001
Kodiak Archipelago			
UAM 17792 (UAMX 2929)	F	A-7	Kodiak Island; 12 April 2001
FWS (RHM104/P158961)	F	B-64	Kodiak Island; 2001
FWS (RHM239/P158928)	M	B-66	Kodiak Island; 2001
UAM 17849 (UAMX 2930)	M	A-7	Kodiak Island; 13 April 2001
Yukon Delta			
FWS Band No. 947-72811	M	B-52	Yukon Delta National Wildlife Refuge; Kgun Lake; 8 August 2000
South-central Alaska			
FWS (RHM202/P164298)	F	B-68	Kenai Borough; 2001
FWS (RHM253/P164293)	F	B-70	Kenai Borough; 2001
FWS (RHM207/P164652)	M	B-69	Sustina Falls; 2001
Interior Alaska			
UAM 20076 (UAMX 808)	F	B-53	Fairbanks International Airport; 21 April 1999
UAM 20077 (UAMX 809)	F	A-7	Fairbanks International Airport; 2 April 1999
UAM 20078 (UAMX 810)	M	OWM-D	Fairbanks International Airport; 2 April 1999
UAM 20079 (UAMX 811)	M	B-55	Fairbanks International Airport; 9 May 1999
UAM 20080 (UAMX 812)	F	B-59	Fairbanks International Airport; 29 April 1999
UAM 11917 (KSW 3037)	M	B-56	Fairbanks; 26 May 1999
UAM 11918 (KSW 3038)	M	B-21	Fairbanks; 22 May 1999
UAM 11925 (KSW 3045)	–	B-35B	Fairbanks; 29 May 1999
UAM 11926 (KSW 3046)	M	B-58	Fairbanks; 25 May 1999
UAM 11944 (KSW 3064)	M	B-60	Fairbanks; 16 May 1999
UAM 14061 (UAMX 1620)	M	B-57	Fairbanks, South Cushman Street; 8 May 2001
UAM 20027 (UAMX 2535)	M	B-41	Fairbanks; Goldstream Valley; Ballaine Road; 21 May 2002
UAM 20026 (UAMX 2538)	M	B-54	Fairbanks; South Cushman Street; 23 May 2002
UAM 11193 (KGM 007)	M	A-7	Chena River Flood Control Project; 19 May 2000
UAM 20083 (KGM 618)	M	B-61	Yukon River; 65°53′N, 149°43′W; 12 June 2002
Southeast Alaska			
FWS (RHM179/P164775)	F	B-67	Juneau; 2001
FWS (RHM147/A151761)	M	B-65	Prince of Wales Island; 2001

[a] Catalogue (field–prep) numbers for specimens at the University of Alaska Museum (UAM), Bell Museum of Natural History (BellMNH), University of Washington Burke Museum (UWBM), and U.S. Fish and Wildlife Service (FWS) Wing Bee.

[b] Haplotype numbers correspond to the numbers listed in GenBank for the present study and by McCracken et al. (2001) and Kulikova et al. (2004). Collecting data for specimens (n = 82) from Primorye, Russia, are reported in Kulikova et al. (2004).

Sequences from opposite mtDNA strands were reconciled and verified for accuracy using SEQUENCHER 3.1 (Gene Codes, Ann Arbor, Michigan). Sequences are archived in GenBank (accession numbers AY506868–AY506870, AY506873–AY506901, AY506904–AY506908, AY506910–AY506917, AY506919–AY506944, AY506974–AY506984 [Kulikova et al. 2004], AY928831–AY928900 [present study]).

We used PAUP* 4.0b10 (Swofford 1998) and unweighted parsimony to estimate the phylogenetic relationships of each unique Mallard

haplotype. Tree searches were performed in two steps: 500 random-addition replicates, each limited to 100 trees, followed by a single search, with no limit, using all minimum-length trees from the first round as starting trees. Searches were heuristic, with tree-bisection-reconnection (TBR) branch-swapping and gaps coded as a fifth character state. Two divergent mtDNA clades were observed, and all trees were rooted at the midpoint. We used the software TCS (Clement et al. 2000) to illustrate unrooted haplotype networks for each clade. Ambiguities in the haplotype network were resolved using the criteria suggested by Crandall and Templeton (1993).

Haplotype diversity (H) and nucleotide diversity (π) were calculated using ARLEQUIN, version 2.0 (Schneider et al. 2000). Analysis of molecular variance (AMOVA; Excoffier et al. 1992), pairwise mismatch distributions, and Rogers' (1995) model of sudden population expansion for species and haplotype lineages were also calculated using ARLEQUIN, version 2.0. Pairwise Φ_{ST} values and P-values were calculated (1) among all populations including all haplotypes and (2) among all populations excluding group B haplotypes. Bonferroni correction factors ($\alpha = 0.05$; Sokal and Rohlf 1981) were used for those tests. We used a 4×2 G-test of independence (Sokal and Rohlf 1981) to test the null hypothesis that group A and B haplotypes (Avise et al. 1990) were distributed randomly in the four regions.

We used coalescent analysis as implemented in FLUCTUATE, version 1.3 (Kuhner et al. 1998) to estimate the neutral parameter theta ($\theta = N_e\mu$, where N_e is the effective female population size and μ is the mutation rate) and the growth rate parameter (g) from posterior distributions of mtDNA gene trees. Transition–transversion ratios for the A and B clades were set to 29.35 and 17.55, respectively, using values obtained from MODELTEST, version 3.06 (Posada and Crandall 1998), and Markov-chain Monte Carlo analyses were repeated with different numbers of short and long chains until parameter estimates stabilized. Final parameter estimates were obtained with 10 short chains of 1,000 steps and three long chains of 15,000 steps, with posterior sampling increments every 20 generations. We used hierarchical likelihood ratio tests to compare the model with g set to zero (i.e. a stable population) and allowed to vary. Significance was determined using the chi-square distribution with one degree of freedom.

Results

Mitochondrial DNA Control Region Sequence Variation

We identified 103 unique haplotypes comprising 666–667 nucleotides among 152 control region sequences. Of the 667 control-region nucleotide positions, 87 (13.0%) were variable, and 60 (9.0%) were parsimony informative. All but four variable positions occurred within the first 351 positions of the 5′ end of the control region; the other substitutions occurred at positions 372, 521, 639, and 661. Transitions occurred at 82 positions, and transversions occurred at six positions. Two positions possessed both transitions and transversions. Three one-base deletions were present in single individuals at positions 165, 206, and 210. A fourth indel was present at position 211. A gap at that position was observed in Mallards from North Asia (7), the Aleutian Islands (2), and Alaska (24), but not in Mallards from Western Russia. That indel generally discriminates the two divergent haplotype groups identified in previous studies (Avise et al. 1990, McCracken et al. 2001, Kulikova et al. 2004, M. D. Sorenson and R. J. Harrigan unpubl. data). In our data set, however, three Primorye Mallards with group A haplotypes in addition to all group B haplotypes had a gap at position 211 instead of thymine or cytosine. Average nucleotide base composition was 33.3% C, 25.9% T, 25.3% A, and 15.5% G and similar to that of other birds (Baker and Marshall 1997). No evidence of coamplified nuclear mtDNA (Sorenson and Fleischer 1996, Sorenson and Quinn 1998) was observed in our data.

Seventy-nine haplotypes were observed only in a single individual, 22 were shared by 2–4 individuals, and two were shared by 7 and 16 individuals, respectively. Mean number of nucleotide differences between haplotypes was 9.0 ± 1.5 (mean ± SD) and varied from 1 to 24. Mean nucleotide (π) and haplotype (H) diversity were 0.0120 ± 0.0062 and 0.9847 ± 0.0050, respectively (Table 2). The highest nucleotide diversity was found in Alaska, whereas the lowest occurred in Western Russia. Haplotype diversity was lowest in the Aleutian Islands (H = 0.8235 ± 0.0840).

PHYLOGENETIC RELATIONSHIPS AMONG HAPLOTYPES

Unweighted parsimony analysis of 103 unique Mallard haplotypes produced hundreds of thousands of most parsimonious trees (length = 177, consistency index (CI) = 0.53, rescaled consistency index (RC) = 0.44). The strict consensus tree included two divergent haplotype groups separated by 9–24 substitutions, corresponding to Avise et al.'s (1990) group A and B haplotypes and the type 1 and 2 haplotypes identified by Johnson and Sorenson (1999). Correspondence among group A and B and type 1 and 2 haplotypes was based on comparison with data previously reported by McCracken et al. (2001) and Kulikova et al. (2004). Haplotype relationships for one arbitrarily chosen most-parsimonious tree rooted on the midpoint and unrooted haplotype networks are illustrated in Figures 1–3.

The mean number of nucleotide differences between group A and B haplotypes was 11.2 ± 2.9 (mean ± SD), whereas the mean number of differences among haplotypes within each clade was 4.3 ± 0.7 and 5.6 ± 0.9, respectively. Group A haplotypes included 80.3% of sampled Mallards (n = 122; Table 2), including representatives from each of the four localities in Asia and North America and 73.8% (n = 76) of the unique haplotypes. Group B haplotypes occurred in the remaining 19.7% of Mallards (n = 30) and were found in three of the four localities (North Asia, Aleutian Islands, Alaska), though they were notably absent from Western Russia. Moreover, 81.5% (n = 22) of the 27 group B haplotypes occurred exclusively in mainland Alaska. In the Aleutian Islands, only two B haplotypes were found. The other three group B haplotypes formed a separate clade within the B lineage and all occurred in individuals from Primorye (Figs. 1, 3).

The most common group A haplotype (A7) was found in all four populations, ranging from Western Russia to Alaska. Five additional group A haplotypes were shared by individuals from two or more populations. In most cases, those haplotypes differed from each other by no more than 2–3 substitutions. In the group B clade, ~50% of haplotypes differed by 2–5 substitutions. The central haplotype was B35, but the most common haplotype was B62 (Fig. 3). Most group B haplotypes were singletons. Two group B haplotypes (B51, B71) occurred in two Mallards from the Aleutian Islands, and three group B haplotypes (SB6, SB7, SB9) occurred in four Mallards from the Primorye region. All other group B haplotypes occurred exclusively in mainland Alaska.

Demographic analysis of mtDNA data showed signs of exponential population growth. The observed distributions of the pairwise nucleotide differences among group A and B haplotypes did not differ from the distribution expected under Rogers' (1995) model of sudden population expansion (P-values > 0.07; Fig. 4). Tajima's (1989) D also differed from zero for both the group A and B haplotype clades (D_A = –2.14, P < 0.005; D_B = –1.47, P < 0.06). Group A and B haplotype clades both possessed star-like topologies, suggestive of rapid population expansion (Figs. 2 and 3). Coalescent analyses provided further evidence of population expansions. The null hypothesis of zero population growth was rejected, and growth rate parameters were positive for both clades (group A haplotypes: θ = 1.00, 95% confidence index (CI) = 0.99–1.02, g = 1,007.75, 95% CI = 959.83–1,055.67, $\chi^2 > 9.00$, df = 1, $P < 0.01$; group B haplotypes: θ = 0.54, 95% CI = 0.47–0.61, g = 659.72, 95% CI = 622.66–696.78; $\chi^2 > 9.00$, df = 1, $P < 0.01$).

POPULATION DIFFERENTIATION

Overall, 36.3% of observed genetic variation was partitioned among populations. Within clade

TABLE 2. Numbers of Mallard individuals and haplotypes sampled, frequencies of group A and B haplotypes, haplotype diversity (H), and nucleotide diversity (π) for each locality.

Locality	Number of individuals	Number of haplotypes	Group A haplotypes (%)	Group B haplotypes (%)	H (mean ± SD)	π (mean ± SD)
Western Russia	13	10	100	0	0.9583 ± 0.0363	0.0052 ± 0.0031
North Asia	91	67	95.6	4.4	0.9872 ± 0.0054	0.0083 ± 0.0045
Aleutian Islands	17	9	88.2	11.8	0.8235 ± 0.0840	0.0084 ± 0.0048
Alaska	31	26	22.6	77.4	0.9806 ± 0.0162	0.0130 ± 0.0069

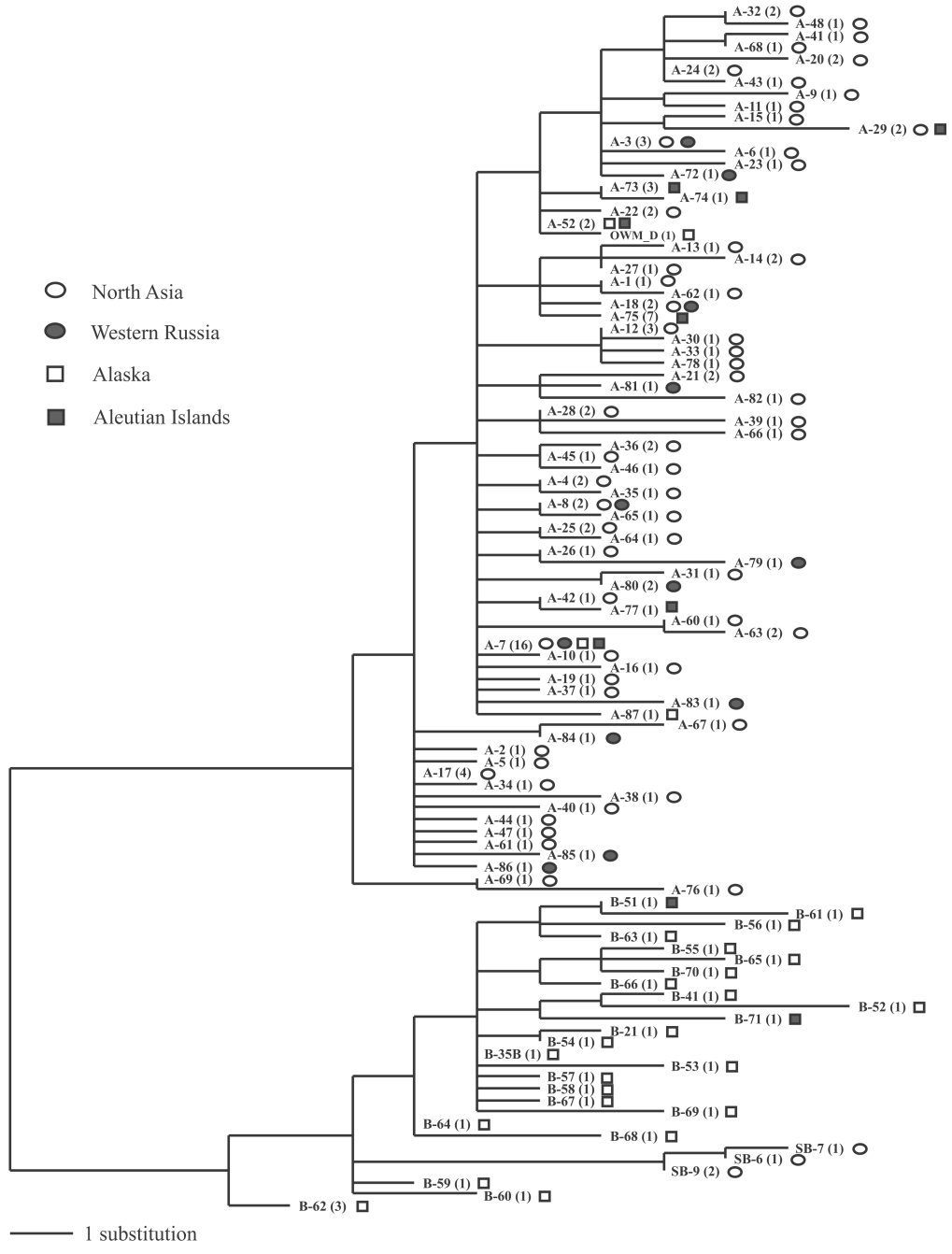

FIG. 1. One of hundreds of thousands of most parsimonious trees illustrating group A and B mtDNA control region haplotypes found in Mallards from Western Russia, North Asia, the Aleutian Islands, and mainland Alaska (length = 177, CI = 0.53, RC = 0.44). Group A and B haplotype numbers for individuals sampled from the Russian Far East and North America correspond to haplotype numbers listed in GenBank by McCracken et al. (2001) and Kulikova et al. (2004), whereas the other haplotype numbers are new to this study. Numbers in parentheses indicate the numbers of individuals that possessed each haplotype.

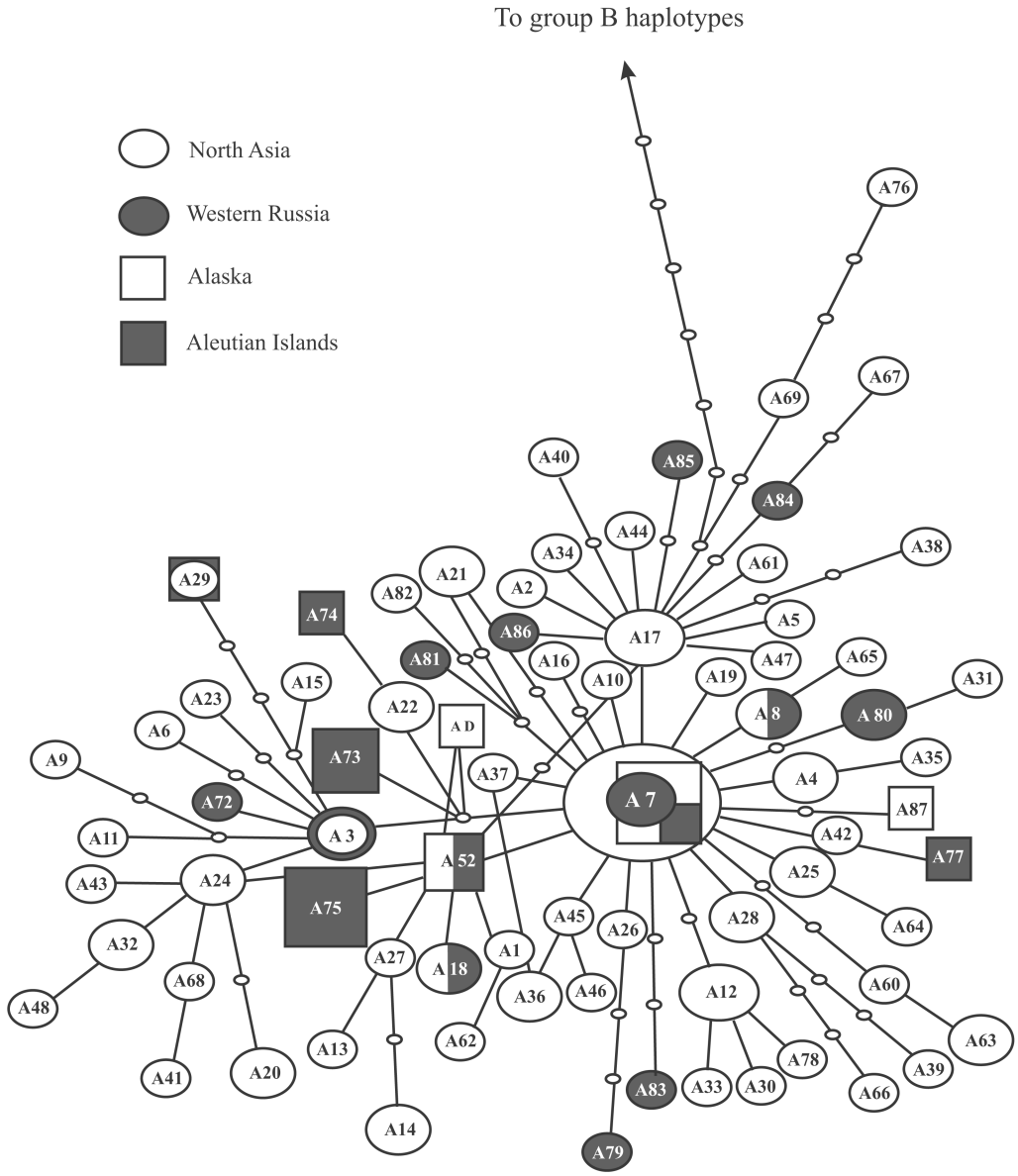

FIG. 2. Unrooted network illustrating the phylogenetic relationships of group A mtDNA control region haplotypes of Mallards. Haplotype numbers correspond to numbers in Figure 1, and the size of each ellipse is proportional to the number of individuals with each haplotype. Small ellipses indicate intermediate ancestral haplotypes that were not sampled.

A, 3.6% of the variation was accounted for by variation among populations, and 44.0% by variation among populations in the B clade. Thus, variation was concentrated primarily within populations, but much more so in clade A than in clade B.

Western Russia differed from the other regions in its lack of group B haplotypes. By contrast, Alaska had the highest frequency of B haplotypes (22 of 27). In North Asia and the Aleutian Islands, B haplotypes occurred infrequently. Group A and B haplotypes were not distributed randomly among the four different sampling regions ($G_{adj} = 36.24$, $P < 0.0001$).

Pairwise Φ_{ST} values calculated for all

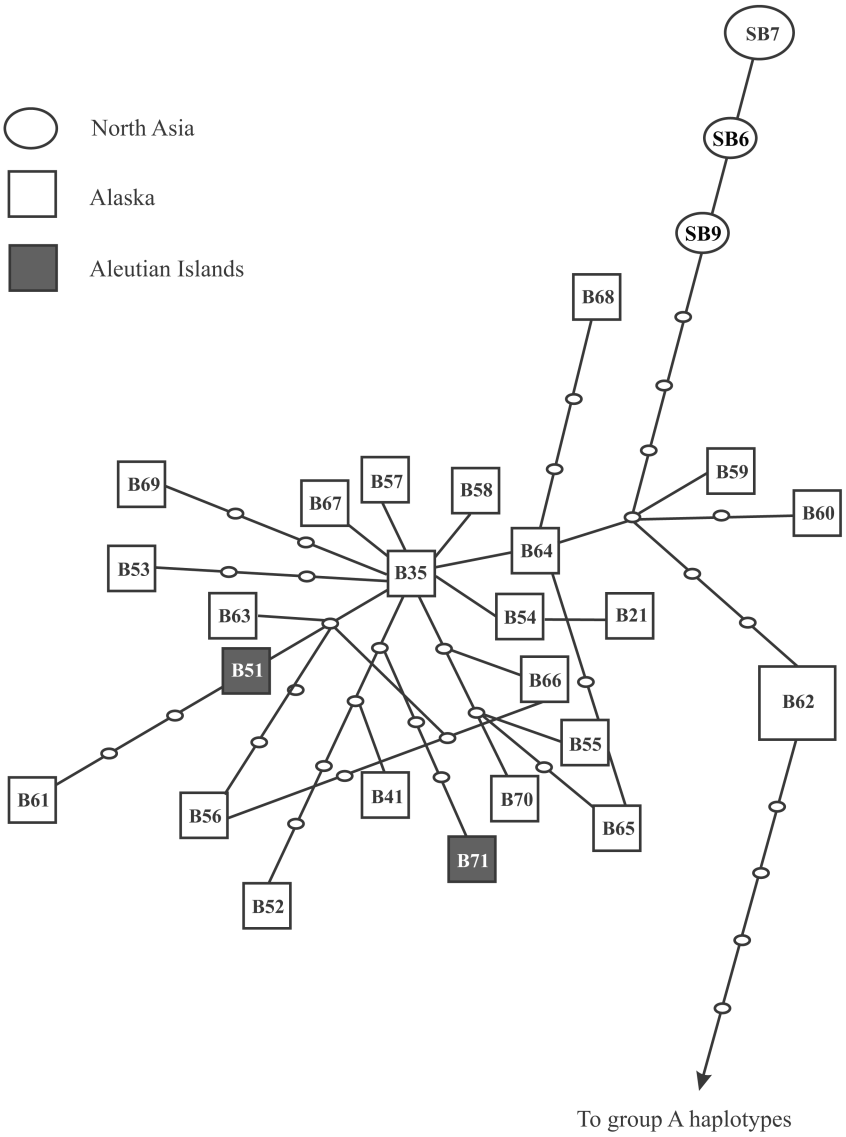

FIG. 3. Unrooted network illustrating the phylogenetic relationships of group B mtDNA control region haplotypes of Mallards. Haplotype numbers correspond to numbers in Figure 1, and the size of each ellipse is proportional to the number of individuals with each haplotype. Small ellipses indicate intermediate ancestral haplotypes that were not sampled.

haplotypes ranged from 0.0018 (North Asia vs. Western Russia) to 0.4956 (Western Russia vs. Alaska), with the highest values observed in pairwise comparisons that included mainland Alaska ($\Phi_{ST} > 0.4112$; Table 3). All other pairwise Φ_{ST} values were relatively low, indicating low levels of genetic divergence among Asian populations. The Φ_{ST} values for group A haplotypes varied from 0.0015 (Alaska vs. Western Russia) to 0.1461 (Aleutian Islands vs. Alaska; Table 3). In this series of pairwise comparisons, only the Aleutian Islands differed from other localities, but not for the Aleutian Islands vs. Alaska with a Bonferroni-corrected $\alpha = 0.0083$ for six pairwise comparisons ($\Phi_{ST} = 0.0728–0.1461$; Table 3).

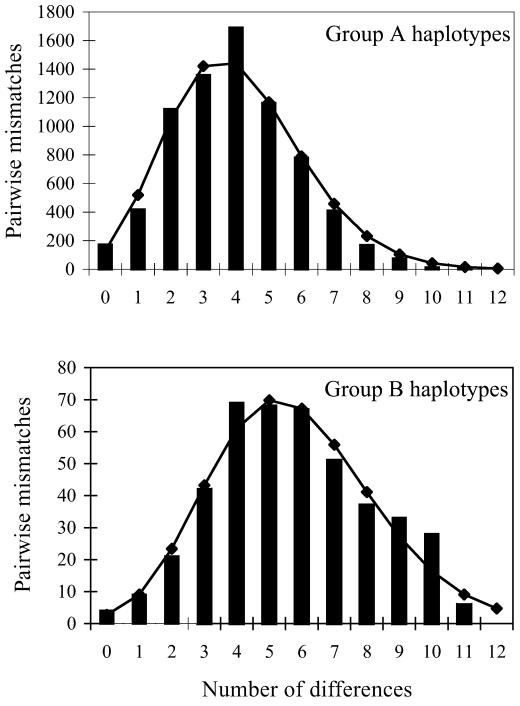

FIG. 4. Pairwise mismatch distributions for group A and B mtDNA control region haplotypes of Mallards. Numbers of pairwise mismatches expected from Rogers' (1995) model of sudden population expansion are illustrated by the black lines.

DISCUSSION

PHYLOGEOGRAPHIC STRUCTURE

The mtDNA phylogeny included two divergent haplotype groups that correspond to Avise et al.'s (1990) group A and B and the type 1 and 2 haplotypes identified by Johnson and Sorenson (1999). Group A haplotypes were most common and were found in Western Russia, North Asia, the Aleutian Islands, and mainland Alaska (Fig. 5). By contrast, most group B haplotypes occurred only in Alaska or the Aleutian Islands, though three group B haplotypes occurred in the Primorye region of the Russian Far East. Those three haplotypes, however, formed a separate subclade nested within the group B clade, differing by at least five mutation steps from all other group B haplotypes (Kulikova et al. 2004).

The paraphyly of Mallard mtDNA is well documented. Mallard mtDNA haplotypes are paraphyletic with respect to the Hawaiian Duck, American Black Duck, Mexican Duck, Mottled Duck, and Eastern Spot-billed Duck (Avise et al. 1990, McCracken et al. 2001, Rhymer 2001, Kulikova et al. 2004). Group A and B mtDNA haplotypes were previously found in North American and Asian Mallards, whereas only group B haplotypes occurred in the above-mentioned monochromatic relatives of the Mallard from North America and the Hawaiian Islands. Eastern Spot-billed Duck, which is sympatric and hybridizes with Mallards in the Russian Far East and northeastern China, had both types of haplotypes, but B haplotypes in that species (hereafter "group SB") were different from North American B haplotypes found in American Black Duck, Mottled Duck, and Mexican Duck (Kulikova et al. 2004).

The distribution of group A and B haplotypes in Eurasian and North American Mallards can be explained by at least two hypotheses. The "Asian invasion" hypothesis, first articulated by Palmer (1976), albeit not in genetic terms, implies "out of Asia" colonization and subsequent introgressive hybridization between the Mallard and its close relatives as the cause of mtDNA paraphyly (Johnson and Sorenson 1999, McCracken et al. 2001, Kulikova et al. 2004). In the context of the mtDNA analyzed here, that corresponds to Mallards bearing group A

TABLE 3. Pairwise Φ_{ST} values (*P*-values in parentheses)[a] between localities for group A and B haplotypes combined (below diagonal) and for group A haplotypes alone (above diagonal) in Mallards.

Locality	1	2	3	4
1 Western Russia	–	0.0035 (0.3131)	**0.1100 (0.0040)**	0.0015 (0.4175)
2 North Asia	0.0018 (0.3193)	–	**0.0728 (0.0001)**	0.0149 (0.6585)
3 Aleutian Islands	**0.0750 (0.0069)**	0.0478 (0.0169)	–	0.1461 (0.0433)
4 Alaska	**0.4956 (0.0001)**	**0.4930 (0.0001)**	**0.4112 (0.0001)**	–

[a] Pairwise Φ_{ST} and *P*-values given in bold type are significant after Bonferroni corrections for six pairwise comparisons.

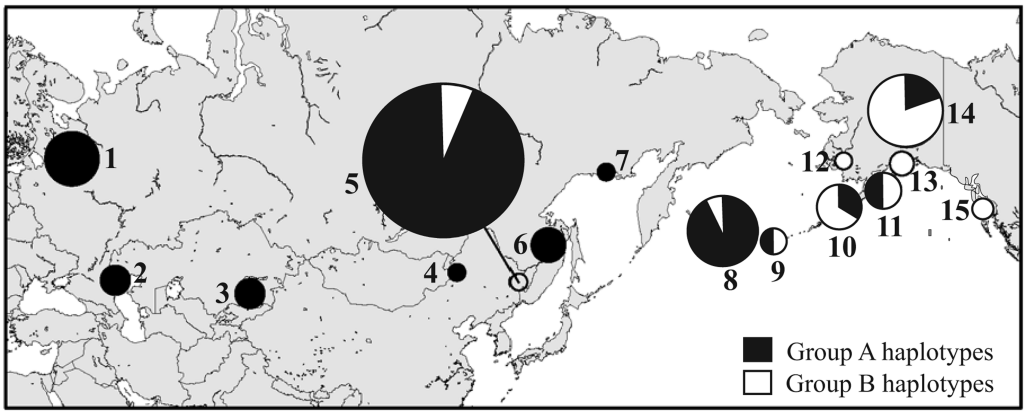

FIG. 5. Localities where Mallards were collected for this study and the frequencies of group A (black) and B (white) mtDNA control region haplotypes at each locality: (1) Astrakhanskaya Oblast', Russia; (2) Arkhangel'skaya Oblast', Russia; (3) Kazakhstan; (4) Mongolia; (5) Primorye, Russia; (6) Khabarovsk Kray, Russia; (7) Magadanskaya Oblast', Russia; (8) Near Islands, Aleutian Islands, Alaska; (9) Andreanof Islands, Aleutian Islands, Alaska; (10) Alaska Peninsula; (11) Kodiak Island, Alaska; (12) Yukon Delta, Alaska; (13) south-central Alaska; (14) interior Alaska; (15) southeast Alaska. The size of each circle is proportional to the number of individuals sampled, and the pie diagrams show the proportions of individuals with group A and B haplotypes.

haplotypes colonizing and introgressing with closely related species characterized by group B haplotypes. The conspicuous absence of group B haplotypes from Western Russia is consistent with hybridization as the source of group A and B haplotype mixing in sampled populations. In Western Russia and Europe, the Mallard distribution does not overlap with any other closely related species. The same is true of Mallards breeding in North Asia, though those populations probably hybridize with Eastern Spot-billed Ducks where they co-occur in the Russian Far East (e.g. Primorye), Korea, northern Japan, and northeastern China (Kulikova et al. 2004). The three group B haplotypes we identified in Mallards from Primorye (SB6, SB7, SB9) are group SB Eastern Spot-billed Duck haplotypes (Kulikova et al. 2004), and their presence in the Mallard gene pool supports hybridization as the source of shared group A and B haplotypes in Mallards and Eastern Spot-billed Ducks from Primorye.

The hybridization hypothesis does not account as easily for the distribution of haplotypes in North America. In Alaska, 77% of Mallards have B haplotypes, and those individuals probably do not occur in proximity to American Black Ducks, Mottled Ducks, or Mexican Ducks during the annual cycle (the nearest North American species from which Alaskan Mallards could acquire group B haplotypes). If hybridization is responsible for the high frequency of group B haplotypes in North America, B haplotypes should occur at increased frequencies in Mallards from eastern North America and the Gulf Coast, where the Mallard's range overlaps those of American Black Ducks and Mottled Ducks. Group B haplotypes, however, are present at high frequencies throughout North America (M. D. Sorenson and R. J. Harrigan unpubl. data).

An alternative hypothesis, proposed by Avise et al. (1990; see also Ankney et al. 1986, Omland 1997) involves incomplete sorting of mtDNA lineages from a polymorphic ancestral gene pool. Species composing the Mallard complex probably diverged recently in terms of effective population sizes, such that the probability is high that reciprocal monophyly has not yet been achieved for multiple loci (and, in the context of the present study, for mtDNA in particular). If, as Omland (1997) proposed, a Holarctic Mallard gave rise to several monochromatic species by peripheral isolation and peripatric speciation, it is unlikely that group B haplotypes would drift to fixation in all four monochromatic species (Black Duck, Mottled Duck, Mexican Duck, Hawaiian Duck), assuming that

both A and B haplotypes were present in the ancestral Mallard population in North America. Thus, it is likely that group A haplotypes were historically restricted to Mallards in Eurasia, whereas the North American species diverged from an ancestral Mallard population with only B haplotypes. The preponderance of group A haplotypes in Asia and the gradual transition to B haplotypes moving east through the Aleutians and into Alaska suggest that the origin of group A and B haplotypes in the Mallard complex reflects a period of historical isolation between Eurasia and North America. Under that model, group A haplotypes in Mallards should decline in frequency from west to east across North America, but the opposite pattern has been observed (M. D. Sorenson and R. J. Harrigan unpubl. data). A possible explanation for that unexpected result is that game-farm releases of Mallards bearing group A haplotypes and hybridization with wild Mallards and American Black Ducks in eastern North America are responsible for the high frequencies of A haplotypes observed in the region. The fact that distinct group B haplotypes are found in Eastern Spot-billed Duck (group SB occurs at a frequency of 39% in the Primorye region; Kulikova et al. 2004) also complicates the above scenario. If the two spot-bill species diverged by peripatric speciation from Mallards in East Asia, they should have only group A haplotypes. Future sampling of populations throughout southern Asia may help to explain the relatively high frequencies of both A and SB haplotypes in Eastern Spot-billed Ducks. In summary, existing data do not support a single explanation for paraphyly of mtDNA haplotypes in Mallards. Instead, a combination of evolutionary processes, including historical and contemporary range expansion, hybridization, and incomplete lineage sorting have likely shaped the current distribution mtDNA haplotype lineages in Mallards and closely related species inhabiting both Asia and North America.

Population Differentiation

Total among-population variation was low, and most of that variation occurred between the group A and B clades or among populations within the group B clade. The Alaska mainland population had the highest genetic diversity and pairwise Φ_{ST} values compared with other populations, because 77.4% of Alaska Mallards carried group B haplotypes and most other populations lacked or possessed few group B haplotypes. The only other locality that consistently yielded significant Φ_{ST} values was the Aleutian Islands, which had the lowest haplotype diversity and differed from other localities when only the group A haplotypes were considered. The fact that seven Aleutian individuals shared a unique haplotype not recorded elsewhere strongly suggests limited exchange between the Aleutians and other populations. We hypothesize that this is because many Mallards that breed in the Aleutian Islands are resident year-round (D. Gibson pers. obs.) and are thus potentially isolated from other Asian and North American Mallard populations that occur in the Aleutian Islands during migration. This observation emphasizes the importance of wintering area in determining population structure in waterfowl.

The overall lack of genetic structure between Mallards from Western Russia and North Asia (and mainland Alaska when only the group A haplotypes are considered) suggests that Mallards exhibit considerable population connectedness and relatively high gene flow. Also, the widespread occurrence of the most common group A haplotype in all four localities suggests that ancestral haplotypes have been retained on both continents or that significant gene flow across the Bering Sea has occurred. Surprisingly, however, no group B "North American" haplotypes (excluding group SB "Eastern Spot-billed Duck" haplotypes) have been identified in Asia, despite the fact that 77.4% of mainland Alaskan Mallards in our study had group B haplotypes. If gene flow across the Bering Sea is ongoing at present, our finding suggests that the predominant direction of female dispersal across the region has been west-to-east rather than east-to-west.

In conclusion, our results show substantial phylogeographic structure between the Old World and New World but little genetic structure within the Old World continental area. Moreover, the Aleutian Islands population differs from other populations in East Asia and Alaska (when only the group A haplotypes are considered). The geographic distribution of group A and B Mallard haplotypes also suggests that Old World Mallards have acquired group B haplotypes by hybridization with the closely

related Eastern Spot-billed Duck, but in the New World the co-occurrence of these haplotype groups is more consistent with incomplete lineage sorting or recent changes in the geographic distribution of group A haplotypes, or both. Populations that share A and B haplotypes in Eurasia appear to be geographically limited to the southern portion of the Russian Far East. Further analysis involving population samples from the Palearctic and multiple nuclear loci will be required before comprehensive conclusions about the genetic structure of Holarctic populations can be drawn. Nuclear loci will be particularly important, because the nonrecombinant, matrilineally inherited transmission of mtDNA represents only one, sexually biased fraction of the hereditary pathways occurring in a population's genetic history.

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