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RESEARCH ARTICLE

Comparative population structure of cavity-nesting sea ducks

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ABSTRACT

A growing collection of mtDNA genetic information from waterfowl species across North America suggests that larger-bodied cavity-nesting species exhibit greater levels of population differentiation than smaller-bodied congeners. Although little is known about nest-cavity availability for these species, one hypothesis to explain differences in population structure is reduced dispersal tendency of larger-bodied cavity-nesting species due to limited abundance of large cavities. To investigate this hypothesis, we examined population structure of three cavity-nesting waterfowl species distributed across much of North America: Barrow's Goldeneye (*Bucephala islandica*), Common Goldeneye (*B. clangula*), and Bufflehead (*B. albeola*). We compared patterns of population structure using both variation in mtDNA control-region sequences and band-recovery data for the same species and geographic regions. Results were highly congruent between data types, showing structured population patterns for Barrow's and Common Goldeneye but not for Bufflehead. Consistent with our prediction, the smallest cavity-nesting species, the Bufflehead, exhibited the lowest level of population differentiation due to increased dispersal and gene flow. Results provide evidence for discrete Old and New World populations of Common Goldeneye and for differentiation of regional groups of both goldeneye species in Alaska, the Pacific Northwest, and the eastern coast of North America. Results presented here will aid management objectives that require an understanding of population delineation and migratory connectivity between breeding and wintering areas. Comparative studies such as this one highlight factors that may drive patterns of genetic diversity and population trends.

Keywords: band-recovery, Barrow's Goldeneye, *Bucephala,* Bufflehead, cavity-nesting, Common Goldeneye, migratory connectivity, mitochondrial DNA, mtDNA, population genetics

Estructura poblacional comparada de patos marinos que anidan en cavidades

RESUMEN

Una colección creciente de información genética del ADN mitocondrial (ADNmt) de especies de aves acuáticas a través de Norteamérica sugiere que entre las especies que anidan en cavidades, aquellas de tamaño grande exhiben mayores niveles de diferenciación poblacional que sus congéneres de tamaño más pequeño. Aunque se conoce poco sobre la disponibilidad de cavidades para que estas especies aniden, una hipótesis para explicar las diferencias en la estructura poblacional es la tendencia a la dispersión reducida de especies de tamaño más grande que anidan en cavidades debido a la abundancia limitada de cavidades grandes. Para evaluar esta hipótesis, examinamos la estructura poblacional de tres especies de patos anidantes en cavidades que se distribuyen a través de Norteamérica: *Bucephala islandica, B. clangula*, y *B. albeola*. Comparamos los patrones de estructura poblacional usando la variación en secuencias de la Región Control del ADNmt y los datos de recuperación de anillos para las mismas especies y regiones geográficas. Los resultados fueron áltamente congruentes entre tipos de datos, demostrando patrones de poblaciones estructuradas en *B. islandica* y *B. clangula*, pero no en *B. albeola*. De acuerdo con nuestras predicciones, la especie anidante de cavidades de menor tamaño, *B. albeola,* exhibió el menor nivel de diferenciación poblacional debido a su mayor dispersión y flujo genético. Los resultados proveen evidencia de la existencia de poblaciones discretas del Viejo y del Nuevo Mundo en *B. clangula*, y de diferenciación de grupos regionales de *B. islándica* y *B. clangula* en Alaska, el Pacífico noroccidental y la costa este de Norteamérica. Los resultados aquí presentados serán de ayuda para el manejo de poblaciones que requiera de un entendimiento de la delimitación poblacional y la conectividad migratoria entre

sitios de reproducción y sitios de invernada. Los estudios comparativos como este resaltan los factores que podrían generar patrones de diversidad genética y tendencias poblacionales.

Palabras clave: Bucephala islandica, recuperación de anillos, *Bucephala albeola*, *Bucephala clangula*, anidantes en cavidades, conectividad migratoria, ADN mitocondrial, genética de poblaciones

INTRODUCTION

Comparative population genetic approaches to the examination of multiple and widespread species are useful in determining whether each taxon has been similarly influenced by historical isolating mechanisms (Avise 2000). Two main conclusions can be made from recent comparative population genetic studies of avian species. First, sympatric taxa distributed across similar regions exhibit a range of phylogeographic patterns (Zink et al. 2001, Qu et al. 2010, Humphries and Winker 2011). Second, levels of population genetic structure are not correlated with taxonomic similarity (i.e. closely related taxa do not share similar phylogeographic patterns, genetic diversity values, and levels of gene flow between populations; Gómez-Díaz et al. 2006, Friesen et al. 2007). Thus, comparisons among species can aid in the identification of isolating barriers (Klicka et al. 2011) and their demographic impacts on populations (Hewitt 2000, Hansson et al. 2008). Additionally, genetic information can be used to infer aspects of species biology, such as flexibility of natural- and life-history traits, and thus the response to past and future changes in climate (Qu et al. 2010).

Sea ducks (tribe Mergini) are a group of 18 extant waterfowl species distributed across a variety of habitats, largely in the Northern Hemisphere, the Brazilian Merganser (*Mergus octosetaceus*) being the exception (Johnsgard 1965). Of these 18 species, 7 are either obligate or semi-obligate cavity-nesting species, all 7 of which are secondary cavity-nesters, which means that they rely on naturally occurring cavities from tree decay or breakage or on excavator species that bore holes into trees. High levels of nest-site fidelity, a possible indicator of population structure, are well documented in nest-box studies of cavity-nesting sea ducks (Gauthier 1990, 1993, Eadie et al. 1995, 2000). However, patterns of fidelity may be driven by variables other than cavity availability, such as competition, food requirements, brood habitat, and body size (Boyd et al. 2009). For example, despite high levels of breeding-site fidelity, Pearce et al. (2008) found little evidence of population genetic structure in the Hooded Merganser (*Lophodytes cucullatus*), which likely are not limited by nest-cavity availability (Denton et al. 2012). By contrast, another cavity-nesting sea duck, the Common Merganser (*M. merganser*), exhibits a high degree of population genetic structure across North America (Figure 1). These findings led Pearce et al. (2009a) to hypothesize that population structure among cavity-nesting ducks could be influenced by body size and cavity competition. Among cavity-nesting species of waterfowl, the Common Merganser has the largest body size, requiring larger cavities that may be rare in some forested landscapes (Vaillancourt et al. 2009). As a result, the Common Merganser may exhibit greater fidelity and population structure than smaller-bodied congeners (e.g., the Hooded Merganser). Thus, there may be a positive relationship between body size and level of population structure among cavity-nesting waterfowl due to a greater abundance of smaller cavities and rarity of large cavities.

We further explored the hypothesis that relative body size may influence population structure in cavity-nesting sea ducks by examining three additional species: Barrow's Goldeneye (*Bucephala islandica*), Common Goldeneye (*B. clangula*), and Bufflehead (*B. albeola*). Our prediction was that small-bodied cavity-nesting birds would show lower levels of population structuring because of their ability to use a wider variety of cavities for nesting (i.e. both small- and large-diameter trees), whereas large-bodied birds would be restricted to nesting in relatively large-diameter trees with cavities. To test this, we determined the extent of population overlap, in terms of geographic overlap and gene flow, using leg-band recovery information and mitochondrial DNA (mtDNA) sequence data collected across broad geographic regions (Alaska, western and eastern North America, Iceland, and Denmark). Although nuclear DNA (e.g., microsatellite loci) often are incorporated into population genetic studies for a more contemporary perspective on gene flow, levels of differentiation among waterfowl species for these molecular markers typically are very low (Figure 1) because of male-mediated dispersal (Peters et al. 2012, Kraus et al. 2013). Therefore, instead of nuclear DNA, we incorporated analyses of band-recovery data for an independent perspective on the structure of migratory flyways and populations (Guillemain et al. 2005, Flint et al. 2009). Because of the relative ease of capturing Common Goldeneye, Barrow's Goldeneye, and Bufflehead in artificial nest boxes and by other methods, thousands of individuals of these species have been banded across North America and Europe.

METHODS

Band Recovery Mapping

We used band recoveries to delineate wintering areas used by birds of each species captured in different breeding areas and to determine the extent of overlap between

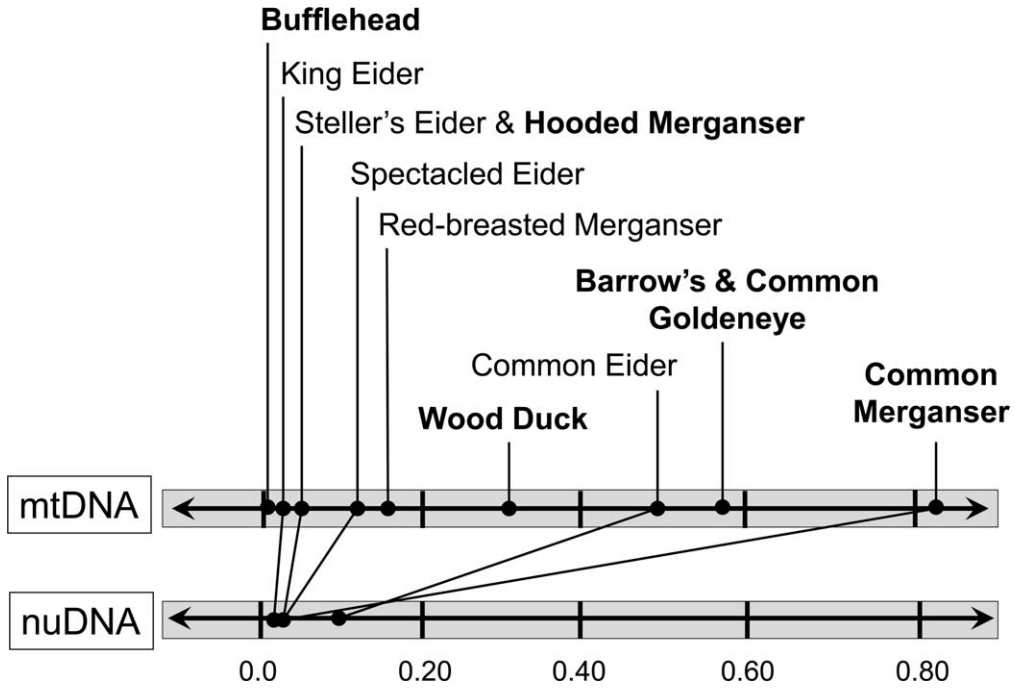

FIGURE 1. Estimates of genetic differentiation for 11 waterfowl species, as measured by F_{ST} from large, geographic-scale studies in North America. Cavity-nesting species are shown in bold. For five species, both mitochondrial DNA (mtDNA) and nuclear DNA (nuDNA) results are shown to illustrate the lower levels of population differentiation observed with nuDNA markers in waterfowl species. From left to right, species names represent results from Bufflehead (*Bucephala albeola*; this study), King Eider (*Somateria spectabilis*; Pearce et al. 2004), Steller's Eider (*Polysticta stelleri*; Pearce et al. 2005), Hooded Merganser (*Lophodytes cucullatus*; Pearce et al. 2008), Spectacled Eider (*S. fischeri*; Scribner et al. 2001), Red-breasted Merganser (*Mergus serrator*; Pearce et al. 2009a), Wood Duck (*Aix sponsa*; Peters et al. 2005), Common Eider (*S. mollissima*; Sonsthagen et al. 2011), Barrow's Goldeneye (*B. islandica*; this study), Common Goldeneye (*B. clangula*; this study), and Common Merganser (*M. merganser*; Pearce et al. 2009a, 2009b). Studies with $F_{ST} > 0.2$ represent cases of significant population structuring (category II from Avise 2000). For mtDNA, values are based on control-region sequences, except for King Eider and Steller's Eider, which are from cytochrome *b*.

winter distributions as an indicator of potential gene flow. Because pair-bond formation in waterfowl likely occurs on nonbreeding areas (Rodway 2007), overlap or use of multiple wintering areas by a breeding population may influence dispersal and, thus, gene flow among populations (Robertson and Cooke 1999). Therefore, we plotted band recoveries for each of the three *Bucephala* species within North America, focusing on broad regional scales that resembled our DNA sampling scheme (below). All band-recovery data were provided by the U.S. Geological Survey Bird Banding Laboratory (BBL; downloaded July 2011). In some cases, recoveries were grouped by geographic area for analysis (see Table 1). We used only band-recovery data from normal, wild birds that were shot, retrieved, and reported (i.e. no "found dead" or "injured" types of recoveries). The final dataset contained a total of 1,827 band recoveries from across North America (Table 1). We plotted locations of leg-band recoveries made in winter (November–March) for ducks banded during summer (May–August). Because we were interested in the degree of population overlap between genetic and band-recovery data, we did not map recovery data separately for each age, sex, and recovery type (i.e. direct vs. indirect). Similarly, genetic data were not analyzed separately by age, sex, or resident–migrant status. This allowed us to maximize the detection of population overlap in both genetic and band-recovery datasets.

We used a kernel home-range analysis (Hooge et al. 2001) in ArcView to estimate the 95% utilization area for band recoveries from each regional group. Our use of winter band recoveries excludes northward molt migration or postbreeding dispersal that may take place after banding and before recovery during winter. Long-distance and northward molt and postbreeding migrations are common in waterfowl (Salomonsen 1968, Hohman et al. 1992) and may substantially broaden the geographic distribution of certain breeding populations. However, band recoveries from molt-migration areas do not appear in the BBL database, likely because these migrations occur in late summer and well before the start of the sport hunting season (i.e. when most waterfowl bands are recovered).

TABLE 1. Summary of DNA and band-recovery data from 1934 to 2009 used to examine population structure in Barrow's Goldeneye, Common Goldeneye, and Bufflehead within and outside North America (also see Figure 2). Numbers represent sample sizes of DNA from each location and numbers of band-recovery reports from birds banded in the same areas. Additional sampling and mtDNA haplotype information is presented in Table 2 in the Appendix.

	Sampling and banding location					
	Alaska–Yukon	Western North America	Central North America	Eastern North America	Outside North America	Total
Barrow's Goldeneye						
DNA	27	28[b]	–	38[e]	22 (Iceland)	115
Band recoveries	86[a]	376	–	–	–	462
Common Goldeneye						
DNA	30	22	–	24[e]	22 (Denmark)	98
Band recoveries	12[a]	–	726[c]	144[f]	–	882
Bufflehead						
DNA	20	36	10[d]	32[e]	–	98
Band recoveries	22[a]	240	221[c]	–	–	483

[a] Includes birds banded in the Yukon Territory for Barrow's Goldeneye ($n = 37$), Common Goldeneye ($n = 8$), and Bufflehead ($n = 5$).
[b] Includes DNA samples from Idaho ($n = 7$).
[c] Includes Common Goldeneye banded in Alberta ($n = 113$), Saskatchewan ($n = 39$), and Minnesota ($n = 574$) and Bufflehead banded in Alberta ($n = 166$) and Saskatchewan ($n = 55$).
[d] Includes DNA samples from Minnesota ($n = 5$) and Wisconsin ($n = 4$). These samples were merged into the Eastern North America group for analysis.
[e] Includes Barrow's Goldeneye samples from Quebec ($n = 38$), Common Goldeneye samples from Ontario ($n = 24$) and Bufflehead samples from Ontario ($n = 1$), New Jersey ($n = 11$), Maryland ($n = 4$), North Carolina ($n = 5$), Virginia ($n = 8$), Delaware ($n = 1$), and Pennsylvania ($n = 3$).
[f] Includes Common Goldeneye banded in Maine ($n = 49$), Ontario ($n = 68$), New Brunswick ($n = 9$), and Quebec ($n = 18$).

DNA Sample Collection and Analysis

We obtained a total of 311 DNA samples from across North America and Europe (Table 1; Figure 2; Table 2 in the Appendix) for Barrow's Goldeneye ($n = 115$), Common Goldeneye ($n = 98$), and Bufflehead ($n = 98$) through captures of breeding birds, collection of nest-box material, tissues from scientific collections in summer, and tissues from birds harvested by sport hunters during fall and winter. Because few breeding samples were available for all species and geographic areas, winter samples (collected between October 1 and January 31) were obtained from tissues of male and female birds collected by hunters in North America (for all three species) and Denmark (Common Goldeneye only) (Table 1). For Bufflehead, only 5 breeding samples were available from the Yukon Territory. The remaining 93 samples were collected during winter. Because of these sampling constraints, we limited our molecular computations to broad regional differences in mtDNA nucleotide diversity.

We extracted DNA from all samples using methods described in Pearce et al. (2008). We amplified and sequenced an approximately 400-base-pair fragment of the control region (domain I) of mtDNA by using primers MMCRL F and MMCRL R, which were designed for the Common Merganser in Europe (Hefti-Gautschi et al. 2009) and following methods described by Pearce et al. (2009a). We aligned all sequences with the program AlignIR version 2.0 (LI-COR, Lincoln, Nebraska) and organized multiple sequences into unique haplotypes using FaBox (Villesen 2007). The final sequence length used in analyses was 400 bases in Barrow's Goldeneye, 442 bases in Common Goldeneye, and 462 bases in Bufflehead. To assess levels of genetic differentiation among breeding locations, we calculated overall and population pairwise levels of F_{ST} from haplotype frequencies using Nei's average distance in the program Arlequin version 3.5 (Excoffier and Lischer 2010). We examined the homogeneity of mtDNA haplotype distributions within and among populations using an analysis of molecular variance (AMOVA) in Arlequin and inferred haplotype diversity for each species and sampling region using haplotype networks. All mtDNA haplotypes have been accessioned in GenBank (KF954779–KF954851).

RESULTS

Band Recoveries

There were 462 winter recoveries of Barrow's Goldeneye banded during the summer between 1948 and 2009 (Table 1), and the greatest percentage (51%) of recoveries of these bands occurred in November. Barrow's Goldeneye recoveries were banded as a mix of ages (48% juveniles, 52% adult) and sexes (28% male, 31% female, 41% unknown). A map of 95% kernel home ranges of all band recoveries

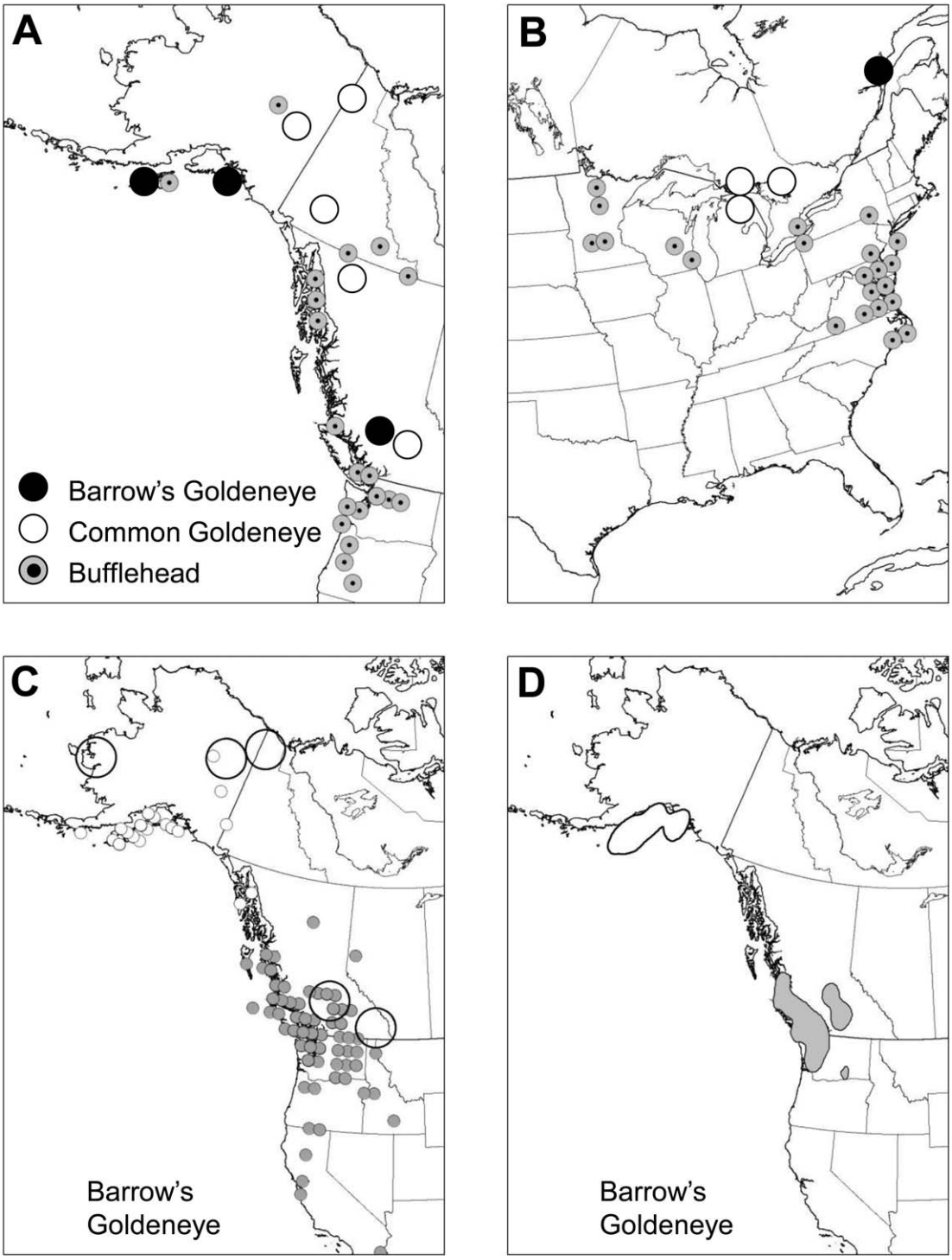

FIGURE 2. Location of DNA sample locations for Barrow's Goldeneye, Common Goldeneye, and Bufflehead in (**A**) Alaska–Yukon and western North America and (**B**) eastern North America. Additional Barrow's and Common Goldeneye samples were obtained from Iceland and Denmark, respectively (not shown). (**C**) Distribution of Barrow's Goldeneye summer banding locations (large open circles) and winter band recoveries, colored by banding area: Alaska–Yukon (white) and western North America (gray). Circles of both banding and recovery locations may represent more than one event. (**D**) 95% kernel home ranges for recoveries of birds banded in Alaska–Yukon (white polygon) and western North America (gray polygon).

showed no overlap between birds banded in Alaska and British Columbia (Figure 2D), but some individual recovery locations were within 450 km of each other in southeast Alaska and coastal British Columbia. Most Alaska recoveries were concentrated around Kodiak Island and the northern portion of the Gulf of Alaska, whereas recoveries of banded birds banded in British Columbia were distributed near the original banding sites and in western Washington.

There were 882 winter recoveries of Common Goldeneye banded during summer between 1940 and 2010 (Table 1; Figure 3A, 3B), with the greatest percentage (57%) of recoveries occurring in November. Most birds (73%) were banded as juveniles, and sexes were approximately equal (50% male, 47% female, 3% unknown). The lack of band-recovery data from birds marked in British Columbia prohibited comparison with those banded in Alaska. Consequently, it is unknown whether these two breeding populations winter in different geographic areas. A map of the 95% kernel home ranges of band recoveries of Common Goldeneye marked in Alaska showed no overlap with other recovery distributions (Figure 3C). However, some Common Goldeneye recoveries occurred within 350 km of each other (in southeast Alaska and coastal British Columbia), and 2 Common Goldeneye banded in Alaska were recovered well outside the Alaska kernel home range (1 in southwestern Manitoba and 1 in southern California). Birds banded in Alberta and Saskatchewan had similar recovery distributions (Figure 3C), with most bands (87%) encountered west of Saskatchewan banding areas (–102.4° longitude). Recoveries from nearly all eastern banding areas (Maine, Quebec, and New Brunswick) were distributed within the region of banding (Figure 3A, 3D). A portion of the 95% kernel home range for Alberta overlapped that of Ontario banding areas in the Great Lakes and Chesapeake Bay regions (Figure 3C, 3D). Recoveries of Common Goldeneye banded in Minnesota and Ontario were predominantly distributed in the eastern United States and Canada (Figure 3D). Only 9% of Minnesota bands were recovered west of –96.0° longitude, the position of the westernmost banding location. Home ranges for Minnesota- and Ontario-banded Common Goldeneye also overlapped in the Great Lakes and Chesapeake Bay regions (Figure 3D).

There were 483 winter recoveries of Bufflehead banded during the summers of 1934–2009 (Table 1), and these occurred primarily (41%) in November. No summer banding data were available from the Atlantic Coast of North America. At the time of banding, birds were mostly (70%) adult and sexes were evenly distributed (42% male, 43% female, 15% unknown). Similar to those of Barrow's Goldeneye, winter recoveries of Bufflehead banded in British Columbia were distributed along the western North American coast. However, birds banded in Alaska also may winter within the geographic distribution of those banded in British Columbia (Figure 4A, 4C). The broad spatial distribution of band recoveries for Bufflehead across North America (Figure 4B) resulted in 95% kernel home ranges that include a greater amount of offshore ocean areas (Figure 4C, 4D), which is likely an overestimation of coastal distribution.

MtDNA Diversity and Population Genetic Stucture

A similar number of mtDNA haplotypes were observed in Barrow's Goldeneye ($n = 17$) and Common Goldeneye ($n = 16$) samples collected in North America and Iceland. Bufflehead exhibited a larger number of haplotypes ($n = 28$). An additional 12 Common Goldeneye haplotypes were observed in Danish samples. Haplotype diversity was variable across sampling regions for all species but was remarkably similar among North American and Icelandic samples of Barrow's and Common Goldeneye (Figure 5A, 5B). Each region had one or a few common haplotypes, with a few additional rarer haplotypes differentiated from the common lineage by a single nucleotide substitution. Samples of Barrow's Goldeneye from Iceland were all identical in haplotype. Winter samples of Common Goldeneye from Denmark exhibited much higher haplotype diversity (Figure 5B), as did Bufflehead samples (Figure 5C).

North American samples of Barrow's Goldeneye clustered into three groups of haplotypes (Figure 5A) that correspond closely to the geographic region of sampling (Alaska, British Columbia and Idaho, and Quebec). Overall genetic differentiation among sampling areas was high ($F_{ST} = 0.576$, $P < 0.001$), and all pairwise tests (not shown) were similarly high (F_{ST} range: 0.313–0.921), with the greatest value between the British Columbia and Iceland samples. The AMOVA revealed that 57.6% of the total genetic variation was distributed among populations.

North American Common Goldeneye samples clustered into three groups of haplotypes (Figure 5B) corresponding to the geographic region of sample collection (Alaska and Yukon, British Columbia, and Ontario). Denmark was a separate group and differed by 12 bases from North American samples. The only evidence of haplotype sharing among sampling regions occurred between Ontario and the Yukon Territory (haplotype 3). All three Ontario samples with this haplotype were from immature birds collected in June and July, and the Yukon samples were from adult birds sampled in April. The overall difference among sampling areas was relatively high ($F_{ST} = 0.825$, $P < 0.001$), and all pairwise F_{ST} statistics (not shown) were high and significant among North American comparisons (F_{ST} range: 0.398–0.664) and between North American and Danish sampling areas (F_{ST} range: 0.844–0.913). In the AMOVA, 82.6% of the total genetic variation was distributed among populations. The proportion of the total genetic variation explained by differences among

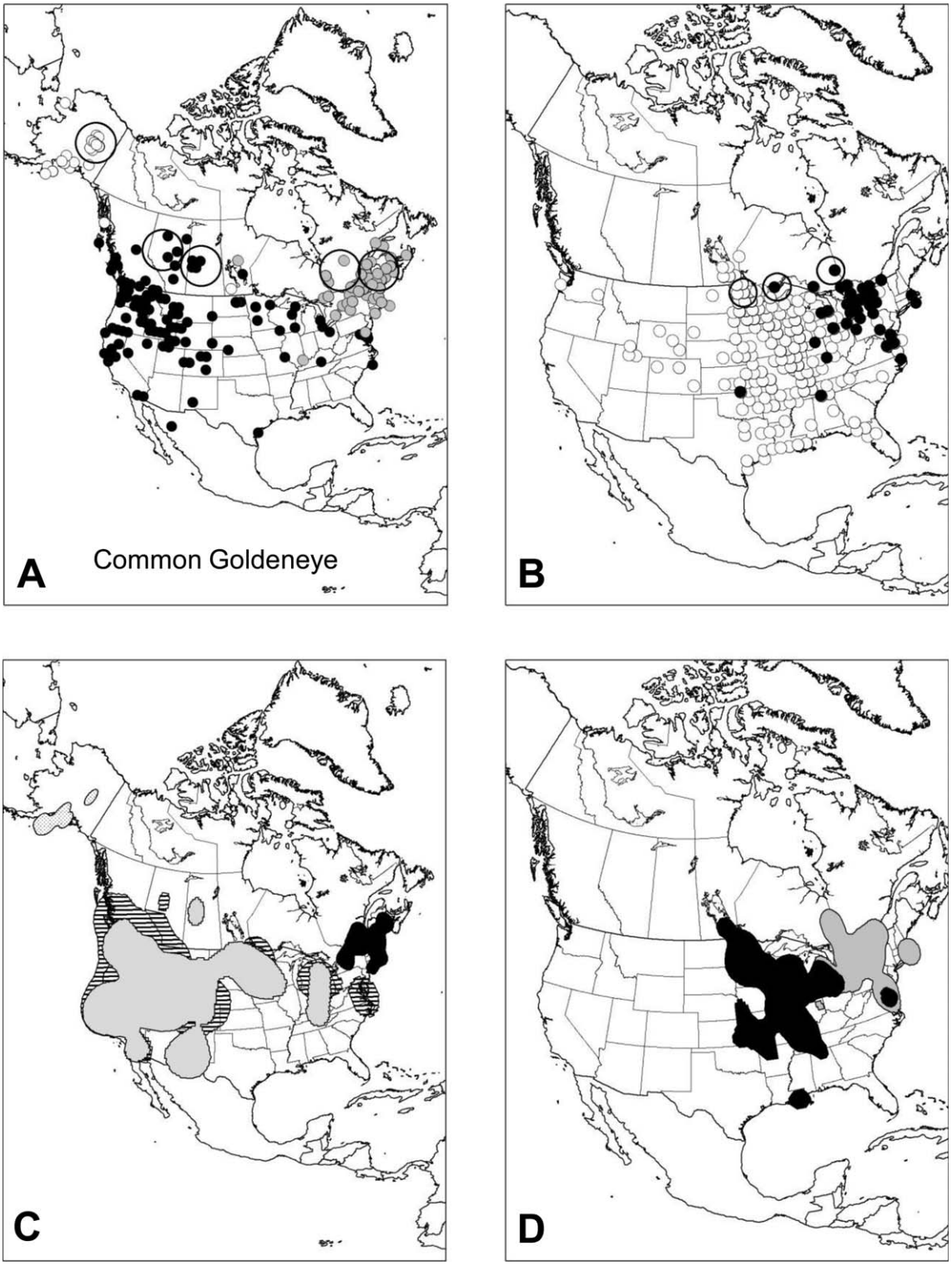

FIGURE 3. (**A**) Distribution of Common Goldeneye summer banding locations (large open circles) and winter band recoveries colored by banding area: Alaska (white), Alberta and Saskatchewan (black), and eastern North America (gray). (**B**) Distribution of Common Goldeneye summer banding locations (large open circles) and winter band recoveries by banding area: Minnesota (white) and Ontario (black). Circles of both banding and recovery locations may represent more than one event. (**C**) 95% kernel home ranges for winter band recoveries of birds banded in Alaska (stippled polygon), Alberta (horizontal striping), Saskatchewan (gray), and eastern North America (black). (**D**) 95% kernel home ranges for winter band recoveries of birds banded in Minnesota (black polygon) and Ontario (gray).

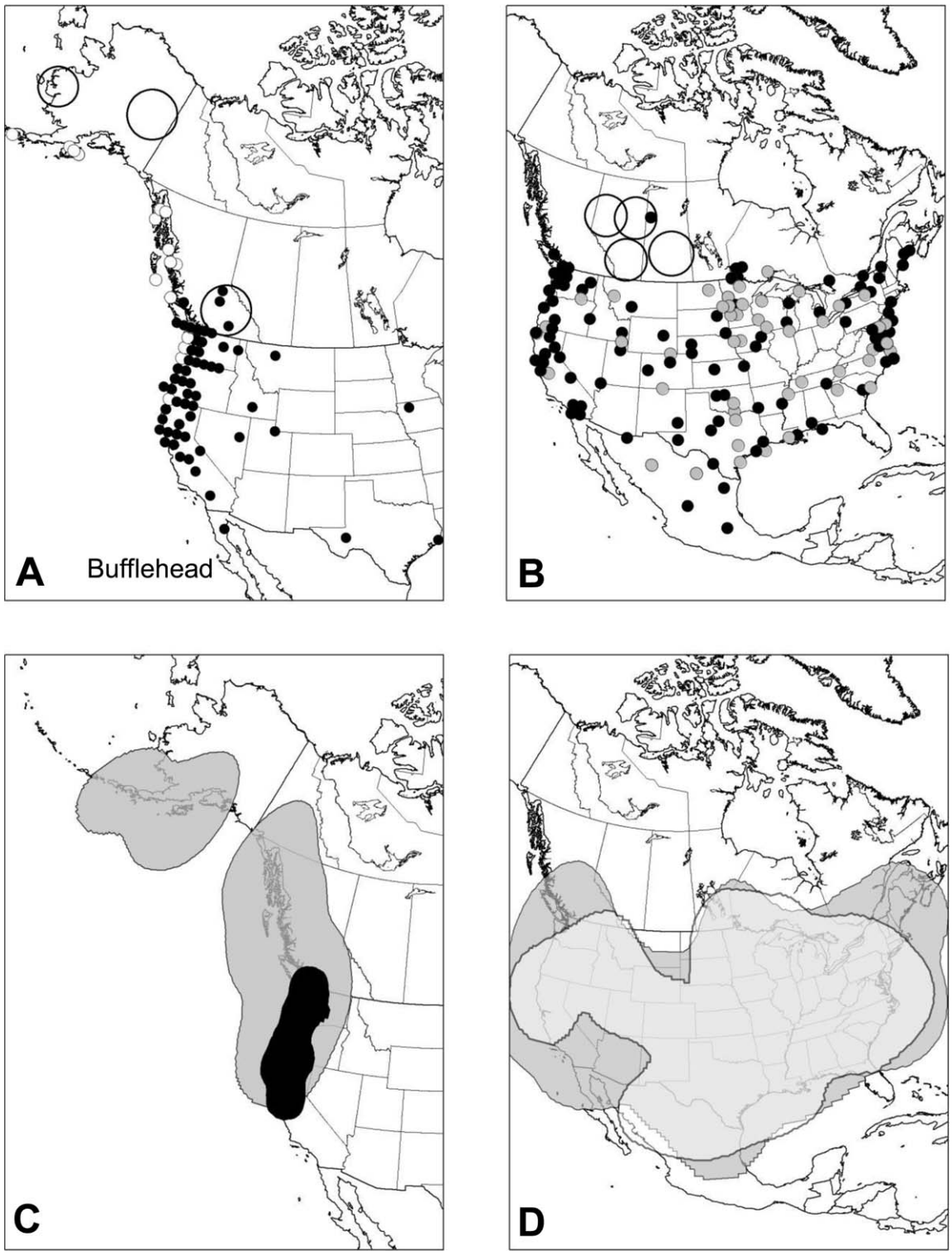

FIGURE 4. (**A**) Distribution of Bufflehead summer banding locations (large open circles) and winter band recoveries, colored by banding area: Alaska (white) and western North America (black). Map does not show one band recovery in Maine (from British Columbia) and one in Kamchatka, Russia (from Alaska). (**B**) Distribution of Bufflehead summer banding locations (large open circles) and winter band recoveries, colored by banding area in central North America: Alberta (black) and Saskatchewan (gray). Circles of both banding and recovery locations may represent more than one event. (**C**) 95% kernel home ranges for winter band recoveries of birds banded in Alaska (gray) and western North America (black). (**D**) 95% kernel home ranges for winter recoveries of birds banded in central North America: Alberta (dark gray polygon) and Saskatchewan (light gray).

populations was 52.8% when the Danish samples were excluded from the analysis.

For Bufflehead, there were two common haplotypes (1 and 2; Figure 5C) found in all North American sampling areas. Singleton haplotypes also were observed in each of the three broad sampling regions. The overall genetic difference among sampling areas was low ($F_{ST} = –0.007$, $P = 0.731$), and all pairwise comparisons yielded similarly low and nonsignificant F_{ST} values, including between Alaska and Eastern North America ($F_{ST} = –0.001$, $P = 0.324$). Thus, Bufflehead (the smallest species) exhibited the lowest level of mtDNA population differentiation (Figure 1).

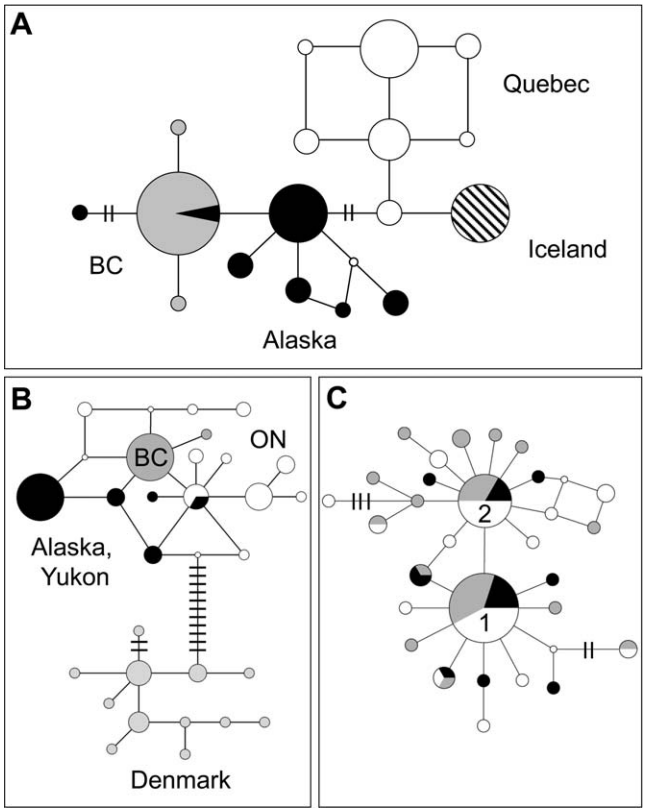

FIGURE 5. MtDNA haplotype networks for (**A**) Barrow's Goldeneye (black for Alaska, gray for British Columbia, white for Quebec, and diagonal for Iceland), (**B**) Common Goldeneye (black for Alaska–Yukon, gray for British Columbia, white for Ontario, light gray for Denmark), and (**C**) Bufflehead (black for Alaska–Yukon and Northwest Territories, gray for western North America, and white for eastern North America; see text). A single site substitution links each circle except where bars are present, which denote multiple substitutions between haplotypes. Circles are drawn proportionally to the observed number of each haplotype. The smallest open circles in each network represent inferred haplotypes that were not sampled. Numbers within larger circles correspond to the haplotype number.

DISCUSSION

Consistent with our prediction, the smallest cavity-nesting species, the Bufflehead, exhibited the lowest level of population differentiation, whereas Barrow's and Common Goldeneye displayed intermediate levels of population genetic structure compared with those of the Common Merganser (Figure 1). Although correlative, our results link species-specific genetic differentiation to nest-cavity requirements that may be driven by differences in body size. While others have suggested that site availability may be limiting for cavity-nesting species (Vaillancourt et al. 2009), our data suggest that such limitation has, over time, had a greater influence on larger-bodied species. As such, our results suggest that it may be useful to examine the status and trends of nest cavities suitable for larger-bodied species of sea ducks (Denton et al. 2012). Additionally, data presented here aid in the identification of populations for monitoring by delineating regional groups and revealing patterns of migratory connectivity between breeding and wintering areas.

None of the study species displayed levels of differentiation observed in the Common Merganser (Hefti-Gautschi et al. 2009, Pearce et al. 2009a, 2009b), the largest cavity-nesting sea duck. Thus, there may be a cost of breeding dispersal to large-bodied species (Common Merganser and both goldeneye) in terms of locating suitable cavities in unfamiliar habitats before the initiation of the nesting period. By contrast, smaller-bodied cavity-nesting waterfowl such as the Bufflehead and Hooded Merganser may exhibit more inconsistent patterns of natal and breeding fidelity because smaller cavities may be more abundant and dispersal may be a mechanism to limit intraspecific aggression observed among cavity-nesting waterfowl (Savard 1982, Boyd et al. 2009). Other natural history attributes are likely involved in patterns of population structure among cavity-nesting waterfowl, but smaller body size may facilitate dispersal. Other observations corroborate our conclusions of higher dispersal and gene flow in Bufflehead than in their larger-bodied congeners. Corrigan et al. (2011) found a consistently lower artificial-cavity occupancy rate for Bufflehead in comparison to Common Goldeneye, suggesting that natural cavities were not limited for Bufflehead on the study areas examined. Evans et al. (2002) found that the average volume of natural nest cavities for Bufflehead was less than half that of natural cavities used by Barrow's Goldeneye and that natural cavities used by Bufflehead were located in smaller trees with smaller entrance openings. The ability to nest in smaller and, likely, younger trees would facilitate dispersal and colonization. Accordingly, we observed a star-like mtDNA haplotype network for Bufflehead (Figure 5C), which is a common pattern in species that show evidence of population expansion or high rates of dispersal (Avise 2000).

We found general agreement between two independent data sources (mtDNA variation and band-recovery information) regarding the continental-scale spatial patterns of population subdivision for Bufflehead, Barrow's Goldeneye, and Common Goldeneye. This comparison is more informative than comparing mtDNA with nuclear DNA because it provides direct quantification of migratory connectivity between breeding and wintering areas, and of winter distribution overlap among different breeding populations. Nuclear DNA is often used as an independent assessment of patterns of population differentiation and evolutionary history inferred from mtDNA. However, such comparative assessments (using nuclear and mtDNA) in waterfowl often are of limited value because male gene flow homogenizes allelic frequencies at nuclear loci (Peters et al. 2012). Indeed, past studies observed comparatively low levels of population differentiation at nuclear loci (Figure 1). However, broader-scale examinations have found the comparison between mtDNA and nuclear DNA more informative (Peters et al. 2007). Differences in nuclear DNA for waterfowl species often equal those of mtDNA when compared across distances where male dispersal is rare, such as between continental landmasses (Peters et al. 2012). Thus, smaller-scale studies of population differentiation might examine other, nongenetic datasets with which to compare mtDNA variation, such as radiotelemetry and band-recovery data, particularly for species in which the patterns of dispersal vary between the sexes.

The mtDNA haplotype networks for Barrow's and Common Goldeneye suggest either limited gene flow or incomplete lineage sorting between populations in Alaska and the Pacific Northwest. Although the kernel home-range analysis suggests separate wintering distributions for both goldeneye species banded in Alaska and the Pacific Northwest, individual recovery locations within southeastern Alaska are geographically close enough to allow population interchange (Figures 2C, 3A). There was very limited band-recovery information for Barrow's Goldeneye from the eastern portion of North America (4 band recoveries), and these were not included in our analysis. However, satellite telemetry data from Barrow's Goldeneye show that eastern populations remain in that region for late summer wing molt and for winter (Robert et al. 2002, Savard and Robert 2013). Thus, interchange between eastern and western North American populations of Barrow's Goldeneye is likely nonexistent or extremely rare. Bufflehead banded in Alaska winter both within the state and across the Pacific Northwest, but those banded in British Columbia remain in that area during the winter. Bufflehead, unlike goldeneye species, show limited population connectivity between breeding and wintering areas across North America. Similarly, genetic data from Bufflehead show a pattern of no differentiation, with two common haplotypes found across all sampling locations.

The mtDNA information from our study provides evidence that Barrow's and Common Goldeneye populations are genetically distinct across North America, but differences are shallow, with only one or two base-pair substitutions separating haplotypes. Similarly, only a single nucleotide substitution differentiates Barrow's Goldeneye in Iceland from those in North America. By contrast, Pearce et al. (2009a) observed a greater divergence among Common Merganser mtDNA haplotypes from Alaska, British Columbia, and the western and eastern coasts of North America. Thus, mtDNA patterns within Barrow's and Common Goldeneye studied here suggest either recent colonization and limited haplotype diversification or reduction of historical variation through population bottlenecks or selection. By contrast, Common Goldeneye from Europe exhibit a greater level of divergence from North American samples, with 11 nucleotide substitutions between haplotype groups. Similarly, Pearce et al. (2009a) observed Old World populations of Common Merganser to be highly differentiated from New World samples (19 nucleotide substitutions).

We are aware that use of predominantly winter samples for Bufflehead may mask patterns of breeding-ground population genetic structure if wintering areas were composed of multiple breeding areas. However, we would then expect band-recovery data from Bufflehead to show patterns of differentiation between the west and east coasts of North America. Instead, band-recovery data provided no evidence of connectivity between particular breeding and wintering areas of Bufflehead. There also is no evidence of Alaska-specific mtDNA haplotypes (Figure 5C). The two common haplotypes in the network are star-shaped, evidence of recent population expansion. Another issue with our sampling scheme was that most samples from both goldeneye species from British Columbia and Iceland originated from single locales. If natal-site fidelity were high, this would contribute to low mtDNA diversity in one sampling area if females were related. However, nonbreeding goldeneye samples did not have substantially greater mtDNA diversity than breeding samples and haplotype diversity in other regions, such as Quebec. Samples from Iceland were representative of a small (~2,000 individuals) resident population, and all were collected in the Mỳvatn area, the primary breeding area of Barrow's Goldeneye in Iceland. Therefore, we do not believe that our sampling scheme led to spurious conclusions.

North American populations of goldeneye and Bufflehead have been increasing since 1957 (based on the annual Waterfowl Breeding Population and Habitat Survey conducted by the U.S. Fish and Wildlife Service and Canadian Wildlife Service; Smith 1995, Flint 2012).

However, because Common and Barrow's Goldeneye cannot be reliably differentiated in this survey, counts of both species are aggregated into one general "goldeneye" category, thus precluding the estimation of species-specific population trends. Consequently, it may be advantageous to use ancillary data (e.g., mtDNA and band recoveries) for assessing population delineation, migratory connectivity, and gene flow among sea duck populations, as has been done in other waterfowl (Guillemain et al. 2005, Flint et al. 2009).

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APPENDIX

TABLE 2. List of number, bird status, and haplotype observed in each geographic region of sampling for Barrow's Goldeneye, Common Goldeneye, and Bufflehead.

Population assignment	State/Province	Site name	Bird status	*n*	Haplotype number(s)
Barrow's Goldeneye					
Alaska	Alaska	Prince William Sound	Nonbreeding	13	1, 2, 4
	Alaska	Portage Valley	Breeding	2	5, 6
	Alaska	Kodiak Island	Nonbreeding	6	1, 7
	Alaska	Kodiak Island	Breeding	3	1, 3
	Alaska	Seward	Spring migrant	3	1, 4, 7
Western North America	British Columbia	Riske Creek	Likely breeding	21	6, 16, 17
	Idaho	NA	Likely breeding	7	6
Eastern North America	Quebec	Tadoussac	Breeding	38	9, 10, 11, 12, 13, 14, 15
Outside North America	Iceland	Mỳvatn	Breeding	22	8
Common Goldeneye					
Alaska–Yukon	Fairbanks	Chena River	Breeding	22	4, 5
	Yukon Territory	NA	Breeding	8	1, 2, 3
Western North America	British Columbia	100 Mile House	Breeding	22	6, 7
Eastern North America	Ontario	Wanapitei Lake	Breeding	6	3, 10, 11, 16
	Ontario	Ranger Lake	Breeding	16	3, 8, 10, 11, 12, 13, 14, 15
	Ontario	Sault Saint Marie	Breeding	2	3, 9
Outside North America	Denmark	Grund Fjord	Wintering	3	18, 24, 25
	Denmark	Randers Fjord	Wintering	5	17, 19, 20, 21
	Denmark	Aarup	Wintering	14	19, 20, 21, 22, 23, 26, 27, 28
Bufflehead					
Alaska–Yukon	Alaska	Fairbanks	Wintering	3	1, 5, 6
		Kodiak	Wintering	2	2, 4
		Southeast	Wintering	10	1, 2, 3
	Yukon Territory	Morley R., Laird R., Frances R.	Likely breeding	5	8, 9, 10
Western North America	British Columbia	Alert Bay, Crofton, Semiahmoo Bay	Wintering	16	1, 2, 8, 11–14
	Washington	Multiple counties	Wintering	9	1, 2, 4
	Oregon	Multiple counties	Wintering	11	1, 2, 14–20
Central North America	Minnesota	Multiple counties	Wintering	5	1, 2, 21
	Wisconsin	Multiple counties	Wintering	4	1, 2, 11, 22
Eastern North America	Ontario	Windemere Basin	Wintering	1	1
	New Jersey	Ocean County	Wintering	11	1, 2, 4, 12, 23, 24
	Maryland	Multiple counties	Wintering	4	1, 2, 22, 25
	North Carolina	Multiple counties	Wintering	5	1, 2, 26
	Virginia	Multiple counties	Wintering	8	1, 2, 28, 29
	Delaware	Kent County	Wintering	1	1
	Pennsylvania	Multiple counties	Wintering	3	2, 27