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Phylogenomics reveals ancient and contemporary gene flow contributing to the evolutionary history of sea ducks (Tribe Mergini)

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ABSTRACT

Insight into complex evolutionary histories continues to build through broad comparative phylogenomic and population genomic studies. In particular, there is a need to understand the extent and scale that gene flow contributes to standing genomic diversity and the role introgression has played in evolutionary processes such as hybrid speciation. Here, we investigate the evolutionary history of the Mergini tribe (sea ducks) by coupling multi-species comparisons with phylogenomic analyses of thousands of nuclear ddRAD-seq loci, including Z-sex chromosome and autosomal linked loci, and the mitogenome assayed across all extant sea duck species in North America. All sea duck species are strongly structured across all sampled marker types (pair-wise species $\Phi_{ST} >$ 0.2), with clear genetic assignments of individuals to their respective species, and phylogenetic relationships recapitulate known relationships. Despite strong species integrity, we identify at least 18 putative hybrids; with all but one being late generational backcrosses. Most interesting, we provide the first evidence that an ancestral gene flow event between long-tailed ducks (*Clangula hyemalis*) and true Eiders (*Somateria spp.*) not only moved genetic material into the former species, but likely generated a novel species — the Steller's eider (*Polysticta stelleri*) — via hybrid speciation. Despite generally low contemporary levels of gene flow, we conclude that hybridization has and continues to be an important process that shifts novel genetic variation between species within the tribe Mergini. Finally, we outline methods that permit researchers to contrast genomic patterns of contemporary versus ancestral gene flow when attempting to reconstruct potentially complex evolutionary histories.

1. Introduction

Broad comparative phylogenomic and population genomic studies continue to shed light on the intricacies of speciation (Campbell et al., 2018; Cutter and Payseur, 2013; Ellegren, 2014; Lavretsky et al., 2019; Ottenburghs et al., 2017a), including ancient and contemporary rates of gene flow and their impact on the evolution of species. Once considered a relatively minor player in the speciation process, gene flow is a particularly important evolutionary process across lineages (e.g., plants (Rentsch and Leebens-Mack, 2012; Rieseberg et al., 2003), fish (Keller et al., 2012; Seehausen, 2006; Taylor et al., 2006; Vonlanthen et al., 2012), insects (Consortium, 2012; Fontaine et al., 2015; Kunte et al., 2011), birds (Brelsford et al., 2011; Grant and Grant, 2020; Hermansen et al., 2011; Kleindorfer et al., 2014; Lavretsky et al., 2015b; Lavretsky et al., 2020; Vallender et al., 2007), and mammals (Amaral et al., 2014; Miller et al., 2012; Rutledge et al., 2015)), including humans (Green et al., 2010; Meyer et al., 2012). Even infrequent bouts of gene flow can leave lasting imprints on the genome, ultimately having consequences ranging from species barrier reinforcement (Dobzhansky, 1940; Hoskin et al., 2005; Rundle and Nosil, 2005; Schluter, 2009) to complete species breakdown in which one (i.e., speciation reversal; Kearns et al., 2018; Seehausen, 2006; Webb et al., 2011) or both (i.e., hybrid swarm; Wells et al., 2019) interacting species are lost. Other potential consequences of interspecific interactions include the potential for adaptive introgression (Hedrick, 2013) and the creation of hybrid zones (Barton and Hewitt, 1989). More recently, burgeoning molecular evidence of hybrid speciation in which a population of hybrids co-exist with their parental species and through time speciate into a novel taxon has been seen to increase biodiversity (Jacobsen and Omland, 2011; Mallet, 2007; Mavarez and Linares, 2008; Schumer et al., 2014). Consequently, broad species comparisons have been central to reconstructing evolutionary histories (Lavretsky et al., 2014; Malinsky et al., 2018a).

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The high rates of hybridization and gene flow among avian species complexes (Grant and Grant, 1997b; Ottenburghs, 2019; Ottenburghs et al., 2015; Rheindt and Edwards, 2011) have been attributed to their dispersal ability (Greenwood, 1980), chromosomal stasis (Ellegren, 2010), and relatively low levels of reinforcement (Grant and Grant, 1997b). In addition to postzygotic isolation, which takes several million years to evolve between vertebrate species (Fitzpatrick, 2004; Price and Bouvier, 2002), general genomic conservancy and synteny may make it much longer for bird species (Lijtmaer et al., 2003a). Rather, prezygotic isolation is considered the more important mode of reproductive isolation between bird species (Grant and Grant, 1997a; Price, 2008; Randler, 2006). In fact, although belonging to one of the oldest avian orders (Jarvis et al., 2014; Livezey, 1997), species within Order Anseriformes (i.e., ducks, geese, and swans) show the highest rates of hybridization (Johnsgard, 1960; Lijtmaer et al., 2003b; Livezey, 1986), with 30–40% of species capable of hybridizing (Grant and Grant, 1992) and about 20% producing viable hybrids (Ottenburghs, 2019; Ottenburghs et al., 2015; Scherer and Hilsberg, 1982). Gene flow has therefore clearly played a role in the evolution of many waterfowl species, likely facilitated by a variety of life-history traits (e.g., mixed flock migration, nest and brood parasitism, extra-pair copulation) that naturally increase chances of interspecific interactions (Hartman et al., 2012; Ottenburghs, 2019; Ottenburghs et al., 2017b; Randler, 2005, 2006).

Here, we reconstruct evolutionary relationships to explore the extent to which gene flow has impacted the genomes and evolutionary trajectories within sea ducks, tribe Mergini. Mergini is comprised of 15 described species representing four lineages (Baldassarre, 2014; Kear, 2005). In general, sea ducks are best characterized as being a K-selected species with the following life-history traits: they are relatively long-lived (i.e., maximum longevity 9.1–23 yrs; Mallory, 2015) with delayed maturation (i.e., 2–3 + yrs; Eadie and Savard, 2015), have relatively small clutch sizes (i.e., avg. 3.5–9.5 eggs/nest; Mallory, 2015), and demonstrate seasonal or long-term monogamy (Eadie and Savard, 2015). Moreover, like other waterfowl, sea ducks generally exhibit strong female breeding site fidelity and male-biased dispersal (Anderson et al., 1992). These life-history traits may explain the apparent mito-nuclear discord, in which the lack of population structure seen in nuclear loci contrasts with high levels of structure seen in mitochondrial DNA (Peters et al., 2012). Many sea duck species display occasional to frequent interspecific brood parasitism (e.g. common eider (*Somateria mollissima*) and white-winged scoter (*Melanitta deglandi*)) that is common within cavity nesters (e.g., bufflehead (*Bucephala albeola*), Barrow's goldeneye (*Bucephala islandica*), common goldeneye (*Bucephala clangula*), hooded merganser (*Lophodytes cucullatus*), common merganser (*Mergus merganser*), and red-breasted merganser (*Mergus serrator*); Eadie and Savard, 2015). Sea ducks generally form large monospecific flocks in winter–spring where pair formation occurs (Eadie and Savard, 2015). However, many species winter in the same general area (Silverman et al., 2013), migrate in mixed species flocks (e.g., Anderson et al., 2020; Goudie et al., 2020), and, in some instances, persist in large mixed flocks during winter (White and Veit, 2020). Thus, despite seasonal monogamy, there are frequent opportunities for interspecific interactions that may result in hybridization among sea duck species. Although a total of 13 species pair hybrids have been reported in the wild (Finley and Huot, 2010; Martin and DiLabio, 1994; Ottenburghs, 2019; Ottenburghs et al., 2015; Trefry et al., 2007), phylogenetic studies have largely been conducted with a small number of markers and/or samples or were confined to single species (Iverson et al., 2004; Pearce et al., 2005; Pearce et al., 2004; Peters et al., 2012; Sonsthagen et al., 2011); fewer have specifically attempted to assess hybridization rates (Brown et al., 2020; Sonsthagen et al., 2019); but also see review in Talbot et al. (2015).

Towards reconstructing evolutionary relationships and assessing levels of gene flow, we employ a comparative phylo- and population-genomics approach in which we assay thousands of nuclear loci across several representatives of each extant North American sea duck species, as well as sequences of the entire mitochondrial genome (mitogenome) for a single representative of each species. Despite the assumption that hybridization is generally rare in sea ducks, given the propensity for waterfowl to interbreed and the number of hybrids already documented, we expect to recover evidence for gene flow among sea duck lineages. First, given that pair bonding in ducks often occurs on wintering grounds, we expected to recover hybrids between species that often admix on wintering and spring grounds (e.g., Eadie et al., 2020; Goudie et al., 2020). Additionally, if interspecific brood parasitism increases rates of mis-imprinting that promotes interspecific breeding (Randler, 2005), we expected the majority of contemporary hybrids to involve at least one species that displays high rates of interspecific brood parasitism (i.e., goldeneye species, bufflehead, and hooded mergansers; Eadie and Savard, 2015).

2. Material and methods

2.1. Sampling, bioinformatics, & data processing of ddRAD-seq

A total of 363 sea duck samples from North America ($N = 10$–56 per taxon; Supplementary Material Table S1) were included in our analyses (BioProject PRJNA541567, accessions SAMN11587829–115187923; Brown et al., 2020; Sonsthagen et al., 2019). All ddRAD-seq library preparation with restriction enzymes (SbfI and EcoRI) and Illumina HiSeq 2500 single-end sequencing at the Tufts University Core Genomics Facility followed those outlined in Sonsthagen et al. (2019). One North American mallard (*Anas platyrhynchos*) was sequenced and included in alignments to serve as an outgroup in nuclear phylogenetic analyses. Detailed sample information is provided in Sonsthagen et al. (2021) and supplementary material Table S1.

We used the computational pipeline described by DaCosta & Sorenson (2014; Python scripts available at http://github.com/BU-RAD-seq/ddRAD-seq-Pipeline) and following steps outlined in Lavretsky et al. (2015a) to cluster filtered reads into putative loci based on sequence similarity. Following alignment of reads to putative loci, genotypes were inferred for individual samples at each locus. Finally, genomic positions were determined by perfect BLAST hit to a reference mallard sequence (Huang et al., 2013; chromosomal assembly provided by T. Farault, unpubl. data; Kraus et al., 2011), which permitted separation of autosomal and Z-linked sex chromosome loci in downstream analyses, including properly coding the latter as having two alleles in males (homogametic sex) and one allele in females (heterogametic sex). Finally, to further limit the effect of sequencing error, a minimum sequencing depth of 5 reads were required to score an allele, such that a minimum of 10 reads was required to score a locus as homozygous or heterozygous. Any allele with < 5x coverage was scored as missing data. Due to potential biases in ddRAD-seq datasets from allelic drop outs due to variability in the sequence similarity across enzymatic cut-sites (Lowry et al., 2017), loci with $< 20\%$ missing genotypes across all samples, as well as within species, were retained for downstream analyses. Thus, all loci were represented by at least one member of each species. Final output files (e.g., fasta, NEXUS, ADMIXTURE, fineRADstructure) were generated using custom python scripts (Lavretsky et al., 2016).

2.2. Mitogenomes - DNA extraction, library preparation, and data processing

Mitochondria were isolated from heart or breast muscle using a Qproteome Mitochondria Isolation Kit and DNA extraction carried out using a DNeasy blood and tissue kit for a single individual per sea duck species, following manufacturer's protocol (Qiagen, Valencia, CA, USA). Libraries were prepared using Nextera sample preparation and Nextera index kits (Illumina, San Diego, CA, USA). Next-generation sequencing followed manufacturer's protocol on a MiSeq Desktop Sequencer (2×150 bp or 2×250 bp read-length configuration). Sample demultiplexing

and adaptor trimming were performed using MiSeq Reporter Software (Illumina). Mitogenomes were assembled in Geneious Prime (Biomatters, Limited, Auckland, New Zealand) by mapping reads to a reference (*Mergus squamatus*, GenBank accession NC016723) using medium–low sensitivity setting and minimum mapping quality set to > 99.999%. In addition, we conducted Sanger sequencing of regions where coverage was consistently low (<10x) across species using methods described in Sonsthagen et al. (2007) and primer pairs listed in Supplemental Table S2. Consensus sequences were constructed for each sample using the highest threshold setting with a minimum of 10x coverage across base-pairs. Mitogenomes are accessioned in GenBank and accession numbers by sample can be found in Sonsthagen et al. (2021). A published mallard mitogenome (GenBank Accession No. EU755253; Tu et al., 2012) was included and served as as an outgroup in our phylogenetic analysis.

2.3. Population structure

Population structure analyses were conducted on all samples, permitting us to identify hybrids (i.e., contemporary hybridization) with a bi-allelic SNP dataset filtered in PLINK (Purcell et al., 2007) for singletons (i.e., minimum allele frequency (–maf 0.005), any SNP missing ≥ 20% of data across samples (–geno 0.2), as well as any SNPs found to be in linkage disequilibrium (LD) (–indep-pairwise 2 1 0.5). One of the two SNPs was randomly excluded if a LD correlation factor (r^2) > 0.5 was obtained. All analyses were done without *a priori* information on population or species identity.

First, we visualized variation among samples with a principal component analysis (PCA) employing the "dudi.pca" function in the R package *adegenet* (Jombart, 2008). Next, maximum likelihood estimates of population assignments across samples were estimated in the program ADMIXTURE v.1.3 (Alexander and Lange, 2011; Alexander et al., 2009). Datasets were formatted for the ADMIXTURE analyses using PLINK (Purcell et al., 2007) and following steps outlined in Alexander et al. (2012). Each ADMIXTURE analysis was run with a 10-fold cross validation (CV) and with a quasi-Newton algorithm employed to accelerate convergence (Zhou et al., 2011). ADMIXTURE analysis used a block relaxation algorithm for point estimation and terminated once the change in the log-likelihood of the point estimations increased by < 0.0001. We ran ADMIXTURE for *K* populations of 1 through 25, with 25 iterations per each value of *K*. The optimum *K* was based on the average of CV-errors across the iterations per *K* value; however, additional values of *K* were examined to test for further structural resolution across analyses. We used the R package PopHelper (Francis, 2016) to convert ADMIXTURE outputs into CLUMPP input files at each *K* value, and determine the robustness of the assignments of individuals to populations at each *K* value with the program CLUMPP v.1.1 (Jakobsson and Rosenberg, 2007). In CLUMPP, we employed the Large Greedy algorithm and 1000 random permutations. Final admixture proportions for each *K* value and per sample assignment probabilities (Q estimates; the log likelihood of group assignment) were based on CLUMPP analyses of all 25 replicates per *K* value.

Third, we assessed patterns of co-ancestry using fineRADstructure (Malinsky et al., 2018b), which includes the programs RADpainter v 0.1 and finestructure (Lawson et al., 2012). In short, fineRADstructure derives a matrix of co-ancestry coefficients based on the distribution of identical or nearest neighbor haplotypes among samples. Each individual's co-ancestry at each locus is equally divided among all other individuals with identical haplotypes, or in the case of a unique allele, all other individuals with the "nearest neighbor" haplotype. Thus, rare haplotypes defined by rare SNPs, which are on average of more recent origin (Kimura and Ohta, 1973), contribute the most to the co-ancestry index, providing a measure that emphasizes recent co-ancestry. This analysis is completed without *a priori* information about population or species identity. A burn-in of 100,000 iterations, followed by 100,000 Markov chain Monte Carlo iterations were completed, followed by tree building using default parameters. To visualize the results, we used the R scripts fineradstructureplot.r and finestructurelibrary.r (available at http://cichlid.gurdon.cam.ac.uk/fineRADstructure.html).

Finally, composite pairwise species estimates of relative divergence (Φ_{ST}) for autosomal and Z-Sex chromosome linked ddRAD-seq loci, and nucleotide diversity per species were calculated in the R package PopGenome (Pfeifer et al., 2014) using a concatenated dataset for each marker-type and excluding any contemporary hybrids; insertions/deletions were treated as missing data. Note that any identified hybrids were excluded to limit the influence of contemporary hybridization on estimating genetic differentiation and diversity at the species level.

2.4. Phylogenomics

Three separate analyses were conducted to reconstruct evolutionary relationships based on autosomal bi-allelic SNPs derived from the all species dataset or variation from sequenced mitogenomes. Once again, contemporary hybrids identified in population structure analyses (see above) were excluded to provide a more accurate phylogenetic reconstruction, and testing for ancestral or historical gene flow events. All trees were rooted using a North American mallard.

For autosomal ddRAD-seq loci, we first analyzed all possible samples and a bi-allelic SNP dataset filtered in PLINK (Purcell et al., 2007) for singletons (i.e., minimum allele frequency (–maf 0.005), any SNP missing ≥ 20% of data across samples (–geno 0.2), as well as any SNPs found to be in linkage disequilibrium (LD) (–indep-pairwise 2 1 0.5) in the program TreeMix version 1.12 (Pickrell and Pritchard, 2012). In addition to establishing phylogenetic relationships, TreeMix was used to test for gene flow in a phylogenetic context. Specifically, TreeMix simultaneously estimates a maximum likelihood (ML) species tree and the direction and weight (*w*) of gene flow among taxa based on allele frequencies. Analyses were run across each independent bi-allelic SNP (-k 1), with global rearrangement occurring during tree building (-global). Node support was based on a 1,000 bootstraps using the python treemix_tree_with_bootstraps.py script (https://github.com/mgharvey/misc_python/blob/master/bin/TreeMix/treemix_tree_with_bootstraps.py). Burn-in was set to 10% of the total number of sampled trees, and final species trees were constructed using TreeAnnotator and viewed in FigTree v1.4.0 (http://tree.bio.ed.ac.uk/software/figtree). Next, the optimum number of added migration edges without overconfidence in the phylogenetic model was based on adding migration edges until ≥ 98% of the variance was explained (Pickrell and Pritchard, 2012). Statistical significance of each migration edge was further assessed using the standard error and associated significant p-value as estimated in TreeMix program (-se) that is based on jackknifing across SNPs, and through the fourpop (f_4) statistic (see below).

In addition to the TreeMix tree, we employed the SNAPP function (Leaché et al., 2014) in the program *BEAST v. 2.5.2 (Bouckaert et al., 2014) to reconstruct a species tree based on SNPs. In short, SNAPP uses bi-allelic SNPs to derive a posterior distribution of putative species trees through estimating the probability of allele frequency changes across nodes given the data. Due to the exponential increase in computational demand with sample and locus size with species tree reconstructions using Bayesian methods, we used the best five samples per species (i.e., those samples with the smallest proportion of missing data), and randomly sampled one bi-allelic SNP per ddRAD-seq locus that had a MAF of 0.03, and again used PLINK to filter for missingness and linkage disequilibrium (LD). For SNAPP, we employed the Hasegawa-Kishino-Yano (HKY) substitution model (Hasegawa et al., 1985) with a gamma distribution across sites, and with five of these having some proportion of invariable sites. We employed a strict clock. SNAPP analysis was run for 100,000,000 iterations, with a burn-in of 250,000 steps, and sampling occurring every 1,000 iterations, to ensure that the effective sample sizes (ESS) across parameters were ≥ 100. Burn-in was set to 10% of the total number of sampled trees, and final species trees was constructed using TreeAnnotator and viewed in FigTree v1.4.0 (htt

p://tree.bio.ed.ac.uk/software/figtree). The program DensiTree (Bouckaert, 2010) was used to visualize the entire posterior set of trees from the SNAPP analysis.

Finally, we reconstructed a mitogenome Bayesian tree using the MrBayes (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003) plugin in Geneious v. 10.0.5 (https://www.geneious.com). MrBayes was run with an HKY site substitution model, a gamma distribution across sites, and with 4 of these having some proportion of invariable sites. MrBayes was run for 500,000 MCMC steps, with a burn-in of 250,000 steps, and sampling occurred every 500 iterations, for a total of 10,000 possible sampled trees. We ensured that the average standard-deviation between runs was ≤ 0.01, and the effective sample sizes (ESS) across parameters were ≥ 100. The final mitogenome tree was based on a burn-in set to 10% of the total number of sampled trees.

2.5. Testing for gene flow in a phylogenetic context

In addition to testing for gene flow directly in TreeMix, we used the *f*4-statistic (Keinan et al., 2007) as implemented in the fourpop software, and *f*3-statistic (Reich et al., 2009) as implemented in the threepop software within TreeMix to further test for ancestral gene flow, or whether any single species is extensively admixed, respectively. Standard errors used to determine variance for each calculated statistic was done by jackknifing across SNPs as implemented in the TreeMix program. First, the *f4*-statistic (Keinan et al., 2007) tests all possible four taxon combinations (e.g., A,B; C,D). Typically, informative comparisons exist under a specific phylogenetic scenario in which the outgroup and non-sister lineage (i.e., lineage of interest) is separate from two parental sister species (i.e., Outgroup, $P_{non\text{-}sister}$; P_1, P_2). In the absence of introgression, genealogical discordance (i.e., shared alleles restricted to non-sister taxon pairs → $P_{non\text{-}sister}$ with P_1 or P_2) as a result of incomplete lineage sorting (ILS) or recurrent mutations are expected to be approximately equal in abundance across the genome (Green et al. 2010; Durand et al. 2011). Thus, a significant difference in the excess of shared variation between $P_{non\text{-}sister}$ with either P_1 and/or P_2 would result in a non-zero f4-statistic, and be evidence for the genetic exchange between $P_{non\text{-}sister}$ and either parental taxa. Specifically, a significant *f4*-statistic (i.e., Z score $< |3|$; $p < 0.0001$) in which the Z score was positive or negative would suggest an access of shared variation between $P_{non\text{-}sister}$ and P_1 or P_2, respectively. In the end, these tests identify when the relationships among taxa are fully described by a simple tree model, or whether including gene flow provides a significantly improved tree. Following, we estimate admixture proportions using an *f4*-ratio test for any putatively admixed group (see Patterson et al., 2012). We focused on four population analyses with mallards as an outgroup only, as this allowed us to infer the proportional contribution of parental taxa into a putative hybrid taxon based on a *f*4-ratio test for any group that appeared to be admixed (Reich et al., 2009). Next, we calculated the *f*3-statistic across all possible population triplets (e.g., A; B,C). For example, a negative *f*3-statistic with a significant Z-score (Z score < -3; $p < 0.0001$) would support that population A is the product of admixture between B and C (Reich et al. 2009). These tests were also used to determine the significance of migration edges identified during tree building in TreeMix. Note that whereas the *f*4-statisic is often best at detecting subtle gene flow at evolutionary scales, the *f*3-statistic is known to perform better for more recent and those that are highly admixed (i.e., 50:50 genomes; Patterson et al., 2012).

3. Results

When analyzing all sea duck samples together, we recovered 1,009 autosomal loci (138,813 base-pairs) and 31 Z-chromosome linked loci (4,534 base-pairs) from the ddRAD-seq that met our filtering and missing data criteria.

3.1. Population structure & molecular diversity

All population structure analyses (Fig. 1) were done with 13,007 (of 18,866) bi-allelic autosomal SNPs that met our filtering and missing data criteria, including a per SNP allelic presence of > 98% across samples. For PCA, plotting the first two principal component axes, we recovered three main clusters that included: (a) harlequin ducks (*Histrionicus histrionicus*), (b) all eider species and long-tailed ducks (*Clangula hyemalis*), (c) bufflehead, along with scoter, merganser, and goldeneye species (Fig. 1C). An optimum population *K* of 18 was recovered in the ADMIXTURE analysis of all species (Fig. 1A, B). Increasing *K* values to 20 provided additional resolution by identifying some intra-specific structure. We note that other than the single F1 Barrow's × common goldeneye hybrid, we are unable to assign hybrid status to other samples with confidence at these high values of *K* in ADMIXTURE. Rather, we found that comparing co-ancestry assignments from fineRADstructure analyses were more interpretable in identifying individuals with admixed ancestries (Fig. 2). Specifically, individuals were considered to be putative hybrids if they had co-ancestry assignment across individuals of a separate species, and which were visibly higher than the average interspecific co-ancestry assignment for the rest of the individuals of that specific species. Moreover, we note that hybrids tended to form a basal relationship with the genetically most closely-related group of individuals within the dendrogram (Fig. 2). In general, co-ancestry analyses recovered all major sea duck groups as observed in our PCA (Fig. 1C) and ADMIXTURE analyses (Fig. 1A). In total, we recovered 18 samples with multi-species co-ancestry, which we infer to likely represent putative contemporary hybrids and include the following 12 combinations: (a) F1 Barrow's × common goldeneye ($N = 1$), (b) Barrow's goldeneye backcrossed with bufflehead ($N = 1$), (c) bufflehead backcrossed with white-winged scoter ($N = 3$), (d) common eider backcrossed with common goldeneye ($N = 1$), (e) common eider backcrossed with harlequin duck ($N = 3$), (f) harlequin duck backcrossed with common merganser and bufflehead ($N = 2$), (g) king eider backcrossed with surf scoter ($N = 1$), (h) long-tailed duck backcrossed with black scoter ($N = 1$), (i) long-tailed duck backcrossed with bufflehead ($N = 2$), (j) long-tailed duck backcrossed with harlequin duck and surf or white-winged scoter) ($N = 1$), (k) long-tailed duck backcrossed with true Eider ($N = 1$), and (l) red-breasted merganser backcrossed with king or spectacled eider ($N = 1$). In addition, all long-tailed duck samples showed similar levels of shared co-ancestry with the main Eider Clade, and all ten Steller's eider samples had equally high co-ancestry assignment to long-tailed ducks and the main Eider Clade.

To achieve true species comparisons, all putative hybrids recovered from population structure analyses were excluded in estimates of relative divergence and calculated nucleotide diversity. First, with the exception of true Eider Clade taxa (composite Φ_{ST} range ~ 0.10–0.20), composite estimates of relative differentiation among species were generally high (composite $\Phi_{ST} > 0.60$) across pair-wise species comparisons (Fig. 3A). Although composite Φ_{ST} estimates based on Z-sex chromosome ddRAD-seq loci tended to be higher than those based on autosomal ddRAD-seq loci, the Z:Autosomal (Z:A) Φ_{ST} ratio was mostly around 1 (highest Z:A Φ_{ST} ratio of 2), which are all close to neutral expectations based on Z-sex chromosome loci having three-fourths the effective population size of autosomal markers (i.e., ΦST Z:Autosomal $\leq$ 1.33; Lavretsky et al., 2015a; Lavretsky et al., 2016; Fig. 3). These results suggest that evolutionary processes are similarly shaping the genetic variation across the Z-sex and autosomal chromosomes, which is in contrast to those Z:A Φ_{ST} ratios found in other ducks (Lavretsky et al., 2019). Finally, an average nucleotide diversity of 0.0024 and 0.0017 was recovered for autosomal and the Z-sex chromosome, respectively across sea ducks (Fig. 3B). Although the majority of species were recovered with calculated nucleotide diversity close to these averages, Barrow's goldeneye had the lowest, whereas long-tailed ducks had the highest calculated nucleotide diversities for both marker types. In general, Z-sex linked diversity was either comparable or had about half the

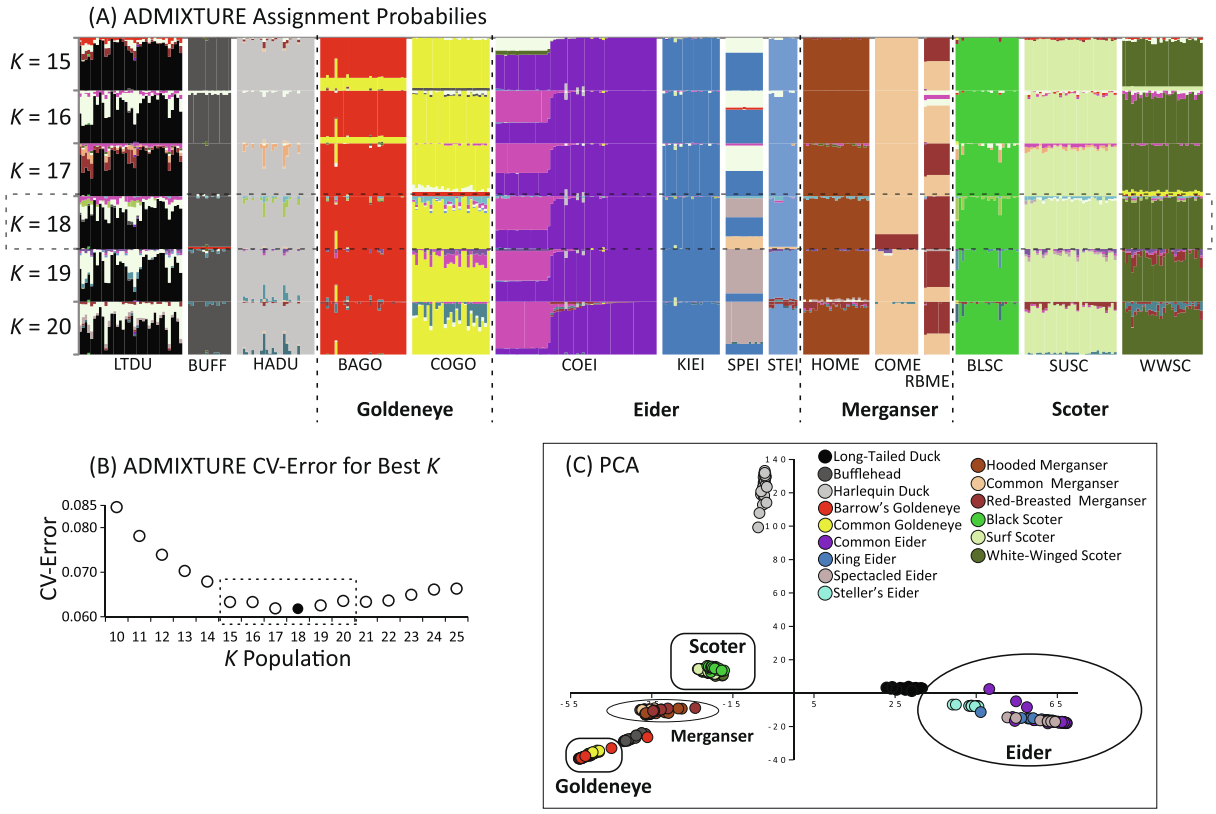

Fig. 1. Individual assignments and clustering of sampled sea ducks based on a 13,007 bi-allelic ddRAD-seq autosomal SNP dataset, and visualized as (**A**) ADMIXTURE likelihood assignment probabilities based on *K* of 15–20 populations (**B**; note the optimum *K* population was 18), and (**C**) the first two components of the principal component analysis (PCA). Samples are color coded by original species identity (Supplementary Materials Table S1).

diversity than that recovered from ddRAD-seq autosomal loci.

3.2. Phylogenomics & species relationships

Based on ddRAD-seq autosomal data, species tree reconstruction using SNAPP (based on 972 bi-allelic ddRAD autosomal SNPs and 5 samples per species) or TreeMix (based on 13,007 bi-allelic SNPs across autosomal markers and all samples per species) recovered well supported and near identical relationships that were also well supported (posterior support ≥ 85%) in the Bayesian mitogenome tree (Fig. 4; Supplementary Materials Fig. S1). Note again that samples recovered as putative contemporary hybrids were excluded from analyses (see genetic assignments in Supplementary Materials Table. S1). In general, we recovered four major clades making up two taxonomic lineages. The first lineage has harlequin ducks sister to three clades that include (a) Barrow's and common goldeneye (Bufflehead/Goldeneye Clade) as sister taxa, with bufflehead basal to that clade, (b) three species of merganser, with hooded mergansers being most diverged (Merganser Clade), and (c) three species of scoters in which surf scoters and white-winged scoters are sister taxa (Scoter Clade). The second major lineage has long-tailed ducks sister to the four eider species. However, whereas we recovered a sister relationship either between common and king eider (SNAPP Nuclear & mitogenome; Fig. 4) or spectacled eider (Nuclear SplitsTree (Supplementary Materials Fig. S1) and the fineRADstructure dendrogram (Fig. 2)) within the true Eider Clade, Steller's eiders remained a distant lineage to these true Eiders.

We note that the lower posterior support within the SNAPP nuclear species tree is likely due to using a much reduced genomic and per-taxon sample representation (i.e., 972 bi-allelic ddRAD autosomal SNPs and 5 samples per species) as compared to the TreeMix species tree (based on 13,007 bi-allelic SNPs across autosomal markers and all samples per species) (Supplementary Materials Fig. S1). We also caution interpretation of branch lengths between the SNAPP nuclear and mitogenome species trees as the variance in sampling efforts in the different analyses likely bias these (Lavretsky et al., 2014). However, despite the lower posterior support and variation in branch lengths within the SNAPP species tree, the taxonomic relationships were identical across trees in which the TreeMix nuclear and mitogenome species trees offered very high (>85%) support across nodes (Fig. 4; Supplementary Materials Fig. S1). Thus, given similarity we conclude that the recovered relationships are robust (Fig. 4; Supplementary Materials Fig. S1).

3.3. Testing for ancestral gene flow in a phylogenetic context

TreeMix analyses were used to estimate the direction and magnitude of gene flow among taxa. First, rooted phylogenetic relationships among sea ducks were robust, with bootstrap support ≥ 95% across all nodes (Supplementary Materials Fig. S1). Importantly, we found that a tree without migration explained > 99% of the model variation (Supplementary Materials Fig. S1), and thus was already robust given the data. Moreover, adding up to ten migration edges, we tended to find statistically insignificant (p-value > 0.01) support across identified edges. Despite TreeMix results, we report several significant *f*4-statistics (Supplementary Materials Table S3), with evidence suggesting ancestral gene flow between the Scoter and Merganser clades, as well as the Scoter and Bufflehead/Goldeneye clades. Following, we conducted an *f*4-ratio test for these two clades, as well as between true Eiders, Steller's eider, and long-tailed ducks that showed some forms of admixture in co-ancestry plots (Fig. 2). For each of the comparisons, we calculated ratios based on all possible sister relationships as each of the Scoter, Bufflehead/Goldeneye, and Eider clades include three closely related species based on phylogenetic results (Fig. 4; Supplementary Materials Fig. S1). Whereas *f*4-ratios were near identical when assessed using sister species of the introgressing clade, those obtained when combined

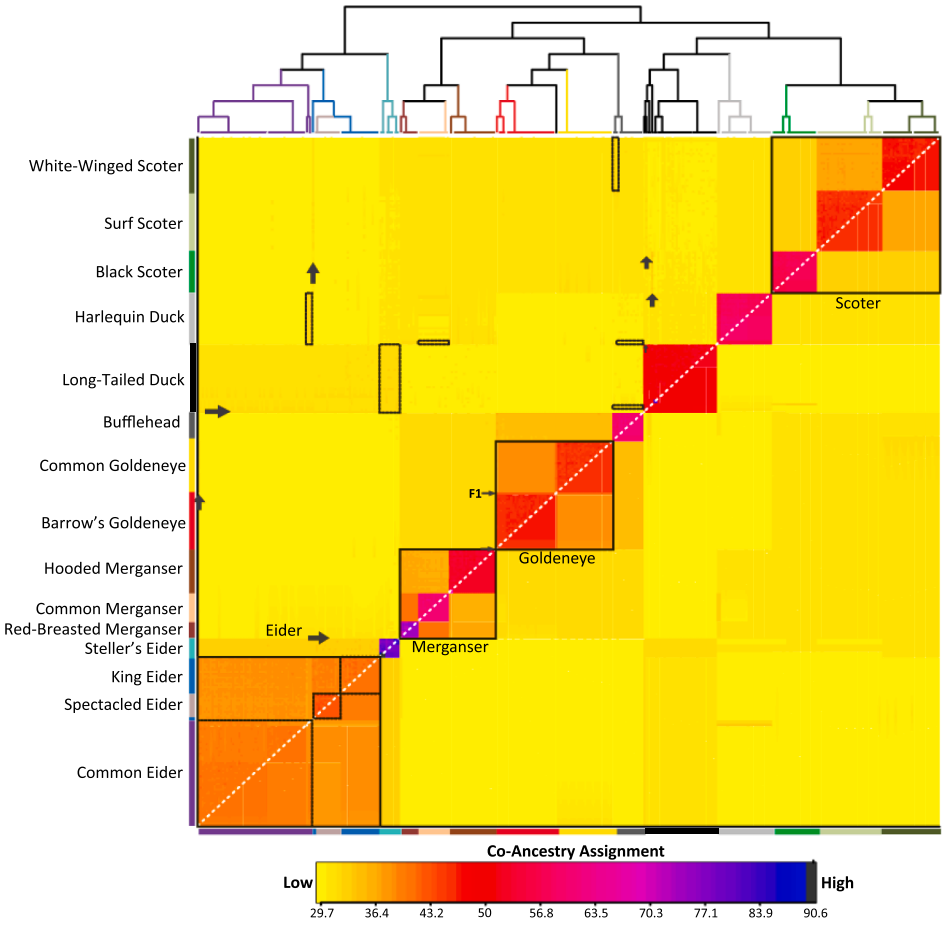

Fig. 2. A matrix of individual (above the diagonal) and average (below the diagonal) co-ancestry coefficients along with the resulting dendrogram from the fineRADstructure analysis of sampled sea ducks that were based on a 13,007 bi-allelic ddRAD-seq autosomal SNP dataset. Note that co-ancestry ranges from low (yellow) to high (black) as indicated by the color scale. Samples are color coded by original species identity (Supplementary Materials Table S1). Note that arrows and dotted lines identify samples showing higher than average interspecific co-ancestry, and thus, identify those samples as putative hybrids. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

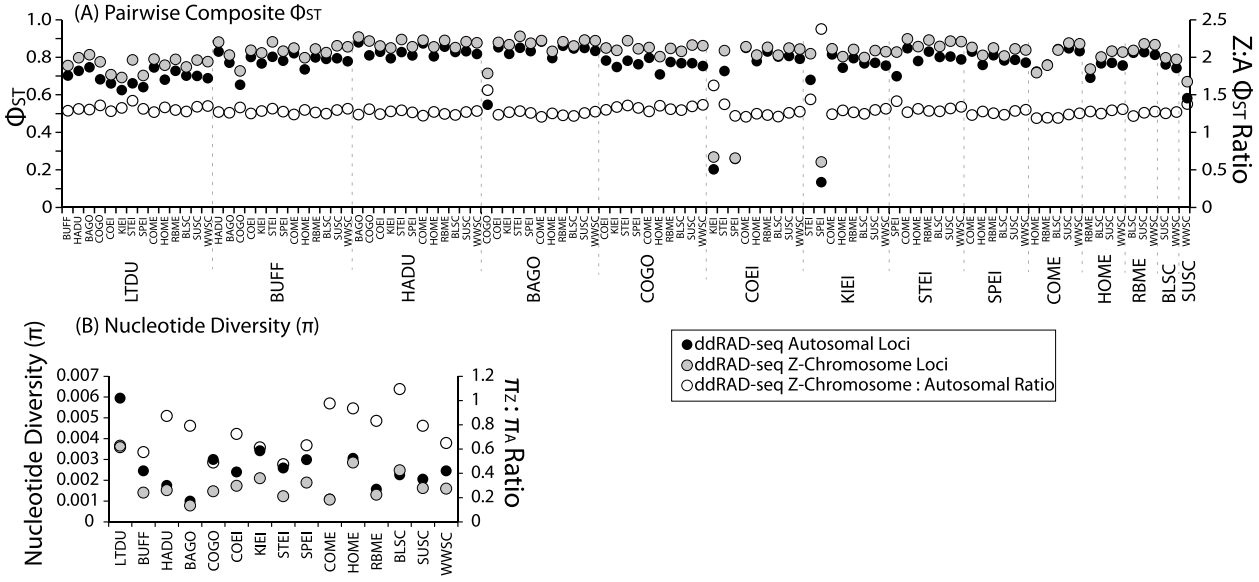

Fig. 3. (**A**) Pair-wise species estimates of relative differentiation (Φ_{ST}), and (**B**) per-species calculated nucleotide diversity across concatenated datasets of each ddRAD-seq linked Z-sex or autosomal chromosomes across sampled sea duck species. Note that the ratio of ddRAD-seq linked Z-sex versus autosomal Φ_{ST} estimates are provided for reference as well.

with the most divergent lineage of Scoter (i.e., black scoter) or Bufflehead/Goldeneye (i.e., bufflehead) clades were consistently 1.5–3 fold higher (Supplementary Materials Table S4); the same effect was not evident when assessing species of the Merganser or Eider clades. The increase is either a result of higher shared variants with these specific species, or a potential bias towards higher gene flow when violating phylogenetic relationships for these clades. Consequently, we considered *f4*-ratios based on the five taxon sets including sister species for

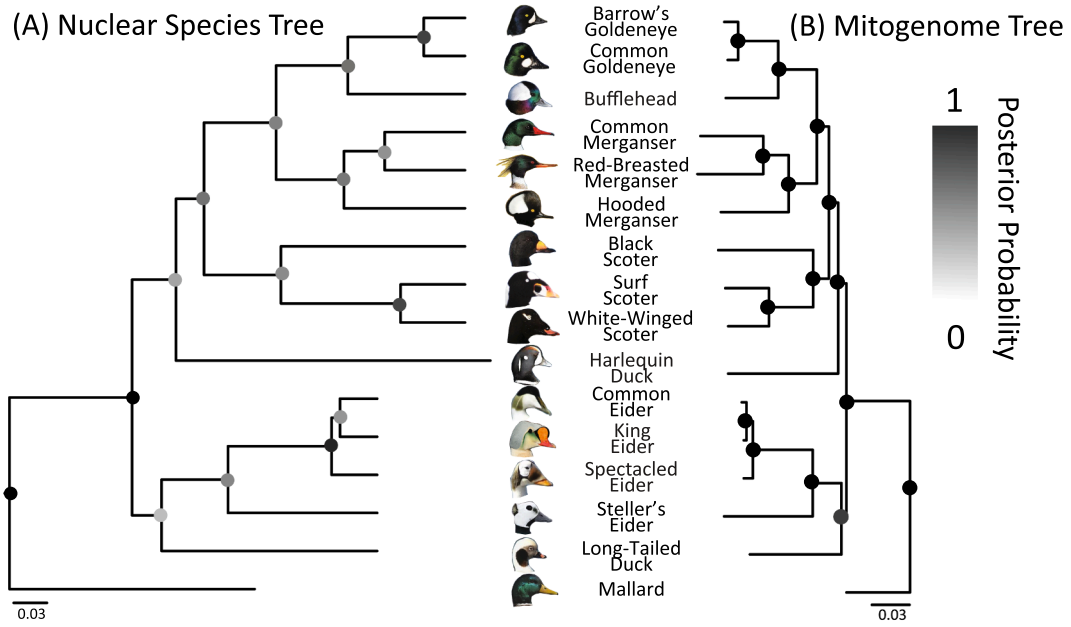

Fig. 4. Phylogenetic relationships as determined from species tree reconstructions from (**A**) ddRAD-seq autosomal SNPs and analyzed in the program SNAPP, and (**B**) mitogenomes analyzed in the program MrBayes. Note that individuals of potential admixed ancestry were excluded from analyses (see genetic assignment column in Supplementary Materials Table S1). Nodal posterior supports are presented in grey scale.

Scoter (i.e., surf and white-wing scoters) or Bufflehead/Goldeneye (i.e., common and Barrow's goldeneye) clades in final admixture proportions. Doing so, we recovered (1) an average 10% (range = 9.7%–11%) and 14% (range = 13%–15%) of ancestry shared due to gene flow into species of the Scoter and Bufflehead/Goldeneye clades, respectively, from species of the alternative clade, and (2) an average 9.1% (range = 6.2%–12%) and 10% (range = 9%–11%) of ancestry shared due to gene flow into species of the Scoter and Merganser clades, respectively, from species of the alternative clade (Supplementary Materials Table S4). Next, although *f4*-ratios for long-tailed ducks when compared to true Eiders or Steller's eider were uninformative (>1; Supplementary Materials Table S4), we found that ~ 7% and 23–24% of the genetic variation within long-tailed ducks was explained by gene flow from any of the true Eider species or Steller's eiders, respectively. Moreover, given that co-ancestry plots suggested that Steller's eider's to be an admixture of true Eiders and long-tailed ducks, we obtained an estimate of true Eider and long-tailed duck ancestry in Steller's eider calculated as α and 1- α (see Patterson et al., 2012). We recovered 94%–98% of the genetic variation within Steller's eider due to be ancestry from the three true Eider species, and thus, we infer the remaining 2%–6% of genetic variation was due to ancestry with long-tailed ducks (Supplementary Materials Table S4). Finally, all *f3*-statistics were insignificant (Supplementary Materials Table S5), establishing that none of the lineages are recently or adversely admixed (Patterson et al., 2012); and which corresponds with the relatively low levels of genetic contribution estimated (Supplementary Materials Table S4) from any of the comparisons with significant *f4*-statistics (Supplementary Materials Table S3).

4. Discussion

4.1. Population structure, evolution, and hybridization among sea ducks

Here, we provide the most comprehensive comparative genomic study of sea ducks (tribe Mergini) to date. In general, we find strong interspecific structure across sampled ddRADseq nuclear sequences (Figs. 1 & 2), with all species showing $\Phi_{ST} > 0.2$, and most having > 0.6 relative differentiation despite marker-type (i.e., autosomal versus Z-sex chromosome; Fig. 3A). Although identifying hybrid samples was difficult in ADMIXTURE (Fig. 1A), our comparative workflow in assessing co-ancestry estimates from the fineRADstructure analysis identified at least 18 possible hybrids (Fig. 2), with all but one involving a generational backcross. Thus, despite strong genomic differentiation among species, viable hybrids and subsequent backcrossed offspring are being produced. These results attest to the amount of time required for post-zygotic isolation to evolve (Fitzpatrick, 2004; Price and Bouvier, 2002), and the importance of prezygotic mechanisms that isolate avian species (Grant and Grant, 1997a; Price, 2008; Randler, 2006). In general, the genomes of birds are small and have shown little change as compared to mammalian genomes (Ellegren, 2010), providing the capacity for even highly diverged species to form viable hybrid offspring (Griffin et al., 2008).

Due to aspects of sea duck behavior (seasonal monogamy, absence of forced copulation, and territoriality), hybridization among species is generally considered rare (Johnsgard, 1960; McKinney et al., 1983); however, lack of detection may be attributable to remoteness of habitats utilized throughout the annual cycle. Despite the ecological and biological attributes evoked to consider hybridization unlikely among sea ducks, hybrids between 13 species pairs have been reported in the wild (Ottenburghs, 2019; Ottenburghs et al., 2015); and we recovered hybrid pairings that directly attest to two of these, with an additional three involving a species of the same genus (Fig. 2). However, because all but one of the 18 identified contemporary hybrids—which comprise 12 unique combinations—appear to be generational backcrosses, when hybridization does occur, it is still quite infrequent. Specifically, among the lineages, bufflehead (8), harlequin ducks (6), and long-tailed ducks (5) were found in 13 (of 18) pairing events, with long-tailed ducks and bufflehead accounting for four of each of the 12 unique combinations. Although hybridization may result from mis-imprinting, which is often the consequence of nest or brood parasitism (Randler, 2005), it is unlikely this mechanism is involved in most of the observed cases of hybrids and in particular between cavity and non-cavity nesting species (e.g., bufflehead × long-tailed duck). However, the geographic location of hybrids observed suggests that the spatial distribution on wintering and nesting areas (i.e., full or partial sympatry) and local population size

likely influences the potential for a hybridization event to occur (i.e. Hubb's Principle, Hubbs, 1955). For example, hybrids between common eider and harlequin duck were only found on the east coast of North America. The eastern population of harlequin ducks underwent a drastic population decline in the 1980 s (Environment Canada 2007) with < 2,000 observed wintering on the east coast (Baldassarre, 2014). Furthermore, and unlike other waterfowl species, common eiders (Swennen et al., 1979) and harlequin ducks (average 1:1 male/female with low of 0.72 male/female; Mittelhauser et al., 2002) both show population sex-ratios that are not male-biased, which may facilitate interspecies pairing. Specifically, the surplus of males in other areas (see references in Baldassarre, 2014) may account for the lack of hybrids observed outside the eastern region. In addition, all long-tailed duck × bufflehead hybrids involve a small nesting population of long-tailed ducks in interior Alaska, which comprises only a small percentage of the nesting areas. Although most species in general are rather abundant on the regional scale, the scarcity of one species on the local scale may explain these unexpected hybrid combinations.

4.2. Importance of ancestral gene flow among sea ducks

We provide evidence that gene flow not only occurs among contemporary species, but may have served as an important mechanism in the evolution of several sea duck species. While TreeMix analyses did not recover statistically significant migration events nor *f3*-statistics that suggests none of the lineages are adversely admixed, we uncovered consistent evidence—significant f_4-statistics and co-ancestry assignments (Supplementary Materials Table S3)—that suggests gene flow has occurred in the evolution of several sea duck lineages. Importantly, f_4-ratios identified ~ 10% of the genetic variation within the Goldeneye/Bufflehead and Merganser clades to be due to gene flow from each of the three scoters species, and that 10% of the genetic variation within the Scoter clade was due to gene flow from each the Goldeneye/Bufflehead and Merganser clades (Supplementary Materials Table S4). Given near identical proportions were recovered despite the compared species in any of the f_4-ratio tests suggests that bouts of gene flow likely occurred between the ancestors of each of these clades, rather than any specific species. Finding that gene flow has contributed to the evolutionary history of several sea duck lineages is not surprising, given that hybridization continues today (e.g., 3 white-winged scoter × bufflehead; Fig. 2). Next, co-ancestry analyses (Fig. 3) and phylogenetic placements (Fig. 4) of both long-tailed ducks and Steller's eiders suggests that each may share unique histories. First, across long-tailed duck samples we recovered high co-ancestry assignment with the true Eider Clade (Fig. 2), suggesting that the lineage leading to long-tailed duck likely had genetic contributions from eiders during their evolutionary history. An ancestral gene flow event is supported through consistent f_4-ratios recovering that ~ 7% of the genetic diversity of long-tailed ducks is best explained by gene flow from eiders, and regardless of which of the three species were analyzed (Supplementary Materials Table S4). We also cannot discount the significant *f4*-ratio suggesting that 23–24% of the genetic diversity of long-tailed ducks was a result of gene flow from Steller's eider as also determined through f_4-ratios. In fact, despite estimated North American census sizes similar to other sea duck species of about two million (Robertson and Savard, 2020), long-tailed ducks have the highest levels of calculated autosomal and Z-linked chromosomal genetic diversity (Fig. 3B). Given that five sampled long-tailed ducks were demarcated as putative hybrids, including an apparent backcrossed individual of true Eider × long-tailed duck, we posit that extensive species-level gene flow with the main Eider Clade in some distant past may explain the high genetic diversity calculated for long-tailed ducks as also observed within *Anser* geese species (Ottenburghs et al., 2016). Why long-tailed ducks readily engage in interspecific mating remains unknown. Future work will benefit from increased geographical and temporal sampling of both long-tailed ducks and true Eiders to determine the true rates of hybridization between these species, and whether such events are tied with particular geography or seasonal affects.

4.3. Hybrid origin for Steller's eider?

The population genetic analyses showed that co-ancestry assignment of all Steller's eiders was to both long-tailed ducks and the true Eider lineage (Fig. 2), and the overall pattern was similar to another putative hybrid species, the Hawaiian duck (Lavretsky et al., 2015b; Wells et al., 2019). This begs the question of whether the Steller's eider represents a species of hybrid origin (i.e., hybrid species), or an eider × long-tailed duck hybrid swarm. We hypothesize that the genetic combination of the two parental species (i.e., long-tailed duck × true Eider) in a single genome may explain how Steller's eider may possess higher than expected nucleotide diversity given that this species has one of the smallest census sizes among sea ducks in North America (BirdLife International, 2016). In fact, through f_4-ratio tests, we infer that 94%–98% of the genetic variation within Steller's Eider is due to ancestry with the three true Eider species, and thus, the remaining 2%–6% is ancestry with long-tailed ducks (Supplementary Materials Table S4). Although the relatively few Steller's eiders sampled here ($N = 10$) likely limited the statistical support across several analyses, the non-significant *f3*-statistic (Supplementary Materials Table S5) is consistent if the Steller's eider's genome is largely eider with a small proportion of long-tailed duck. Although we currently cannot discern which of the Eiders contributed to the genetics of Steller's eider, the consistent f_4-ratio tests across all three true eider species suggests that the ancestral gene flow event may have occurred early in species divergence. In the end, given that shared ancestry between long-tailed ducks and all the true Eiders (Fig. 2), including consistent f_4-ratios (Supplementary Materials Table S4) points to an ancestral gene flow event between these two, we hypothesize that this event(s) resulted in the movement of genetic material from true Eiders to long-tailed ducks, and that the resulting hybrids may have diverged into what we consider Steller's eider today. If a hybrid origin of Steller's eider is the case, then its unique morphology (e.g., plumage) and behavior (e.g. courtship displays; Johnsgard, 1965), which is not intermediate between any of the true Eiders and long-tailed duck, could be due to transgressive segregation where hybrid population/species exhibit extreme traits outside the parental forms (Rieseberg et al., 1999). Alternatively, the observed genomic pattern could be the result of separate introgressive hybridization events, similar to that proposed for the red-breasted goose (*Branta ruficollis*; Ottenburghs et al., 2017b), between Steller's eider and long-tailed duck and between Steller's eider and the ancestor of the true Eiders. Although we do not find significant gene flow from Steller's eider to true Eiders, *f4*-ratio tests do provide evidence of gene flow from Steller's eider into the long-tailed duck lineage. In the end, while we cannot definitively identify the source of the shared genetic variation, we provide strong evidence for a complex evolutionary history of shared variation between true Eiders, long-tailed ducks, and Steller's eider that will require additional sampling of individuals and genomes to fully understand.

While efforts to increase individual and genome sampling will be needed to better understand how gene flow may have influenced the evolutionary history of Steller's eiders, we do present further evidence based on the nuclear genome supporting Steller's eider is distinct from true Eiders (Figs. 1-3) and our mitogenome analysis corroborates results from Buckner et al. (Buckner et al., 2018). We note that the Labrador duck (*Camptorhyncus labradorius*) and Steller's eider are sister species based on mitochondrial DNA (Buckner et al., 2018), and share some morphological characteristics such as a soft-edge bill and gray feet not present in the true Eiders. Inclusion of genomic data from this extinct species may further help provide insight into the evolutionary origins of both the Steller's eider and Labrador duck.

4.4. Conclusions

Although researchers have known for decades that genetic introgression occurs in wild species, its frequency and distribution has been underappreciated, and only recently have we understood gene flow to be an important mechanism in species' evolutionary history, including in birds (Rheindt and Edwards, 2011). Introgression is thought to have maintained and increased genetic variation, including advantageous novelty (Noor et al., 2000; Seehausen, 2004), and this is particularly important during times of large-scale climate change, which is rapidly altering ecosystems and possibly the relationships within and among species communities. Indeed, our own species is thought to have undergone complicated histories of climate change associated introgression with multiple hominid lineages, in some cases resulting in the capture of locally-adapted alleles by colonizing humans (Green et al., 2010; Reich et al., 2010; Sankararaman et al., 2016). Coupling multi-species comparisons with population and phylogenomics provided valuable insight into the evolutionary history of the sea duck tribe, Mergini. Though we identify contemporary hybrids between multiple species pairs, the rate of introgression appears to be minimal at the evolutionary scale for most species. However, our research provides evidence that an ancestral gene flow event between long-tailed ducks and true Eiders not only resulted in the movement of genetic material into the former species, but potentially resulted in the origin of a novel species, the Steller's eider, via hybrid speciation. These results attest to the power of coupling population-level and partial genome sampling to unravel evolutionary histories that would otherwise remain hidden. Once believed to be a minor player in species evolution, inter-species gene flow and its impact across different biological lineages will likely continue to come to light as sequencing technologies and attendant analytical techniques become ever more readily available and streamlined for non-model systems.

CRediT authorship contribution statement

Philip Lavretsky: Conceptualization, Data curation, Formal analysis, Writing - original draft, Writing - review & editing. **Robert E. Wilson:** Conceptualization, Data curation, Formal analysis, Writing - original draft, Writing - review & editing. **Sandra L. Talbot:** Conceptualization, Writing - original draft, Writing - review & editing. **Sarah A. Sonsthagen:** Conceptualization, Funding acquisition, Data curation, Formal analysis, Writing - original draft, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data archiving:

Mitochondrial Genomes: GenBank accession numbers MW849278 - MW849292.

Illumina ddRAD-Seq Reads: NCBI's Sequence Read Archive BioProject PRJNA718623: BioSample Accession Numbers SAMN18543280 - SAMN18543506.

Sample information: Sonsthagen et al. 2021.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ympev.2021.107164.

References

Alexander, D.H., Lange, K., 2011. Enhancements to the ADMIXTURE algorithm for individual ancestry estimation. BMC Bioinf. 12, 246.
Alexander, D.H., Novembre, J., Lange, K., 2009. Fast model-based estimation of ancestry in unrelated individuals. Genome Res. 19, 1655–1664.
Alexander, D.H., Novembre, J., Lange, K., 2012. Admixture 1.22 Software Manual.
Amaral, A.R., Lovewell, G., Coelho, M.M., Amato, G., Rosenbaum, H.C., 2014. Hybrid speciation in a marine mammal: The clymene dolphin (*Stenella clymene*). PLoS ONE 9, e83645 http://doi.org/83610.81371/journal.pone.0083645.
Anderson, E.M., Dickson, R.D., Lok, E.K., Palm, E.C., Savard, J.L., Bordage, D., Reed, A., 2020. Surf Scoter (*Melanitta perspicillata*), version 1.0. Birds of the World. Cornell Lab of Ornithology, Ithaca, NY, USA.
Anderson, M.G., Rhymer, J.M., Rohwer, F.C., 1992. Philopatry, dispersal, and the genetic structure of waterfowl populations. Ecol. Manage. Breeding Waterfowl 365–395.
Baldassarre, G., 2014. Ducks, Geese, and Swans of North America. Johns Hopkins University Press.
Barton, N.H., Hewitt, G.M., 1989. Adaption, speciation and hybrid zones. Nature 341, 497–503.
Bouckaert, R., Heled, J., Kühnert, D., Vaughan, T., Wu, C.-H., Xie, D., Suchard, M.A., Rambaut, A., Drummond, A.J., 2014. BEAST 2: a software platform for Bayesian evolutionary analysis. PLoS Comput. Biol. 10, e1003537.
Bouckaert, R.R., 2010. DensiTree: making sense of sets of phylogenetic trees. Bioinformatics 26, 1372–1373.
Brelsford, A., Milá, B., Irwin, D.E., 2011. Hybrid origin of Audubon's warbler. Mol. Ecol. 20, 2380–2389.
Brown, J.I., Lavretsky, P., Wilson, R.E., Haughey, C.L., Boyd, W.S., Esler, D., Talbot, S.L., Sonsthagen, S.A., 2020. High site fidelity does not equate to population structure for common goldeneye and barrow's goldeneye in North America. J. Avian Biol. 51, e02600.
Buckner, J.C., Ellingson, R., Gold, D.A., Jones, T.L., Jacobs, D.K., 2018. Mitogenomics supports an unexpected taxonomic relationship for the extinct diving duck *Chendytes lawi* and definitively places the extinct Labrador Duck. Mol. Phylogenet. Evol. 122, 102–109.
Campbell, C.R., Poelstra, J., Yoder, A.D., 2018. What is speciation genomics? The roles of ecology, gene flow, and genomic architecture in the formation of species. Biol. J. Linn. Soc. 124, 561–583.
Canada, E., 2007. Management Plan for the Harlequin Duck (*Histrionicus histrionicus*) Eastern Population, in Atlantic Canada and Québec [Proposed]. Environment Canada, Ottawa, Species at Risk Act Management Plan Series, p. 32.
Consortium, H.G., 2012. Butterfly genome reveals promiscuous exchange of mimicry adaptations among species. Nature 487, 94–98.
Cutter, A.D., Payseur, B.A., 2013. Genomic signatures of selection at linked sites: unifying the disparity among species. Nat. Rev. Genet. 14, 262–274.
DaCosta, J.M., Sorenson, M.D., 2014. Amplification biases and consistent recovery of loci in a double-digest RAD-seq protocol. PLoS ONE 9, e106713.
Dobzhansky, T., 1940. Speciation as a stage in evolutionary divergence. Am. Nat. 74, 312–321.
Eadie, J.M., Savard, J.-P.L., 2015. Breeding systems, spacing behavior, and reproductive behavior of sea ducks. Ecology and Conservation of North American Sea Ducks. In: Savard, J.-.P.L., Derksen, D.V., Esler, D., Eadie, J.M. (Eds.), Studies in Avian Biology. CRC Press, New York, pp. 365–415.
Eadie, J.M., Savard, J.L., Mallory, M.L., 2020. Barrow's Goldeneye (*Bucephala islandica*), version 1.0. In: Poole, A.F., Gill, F.B. (Eds.), Birds of the World. Cornell Lab of Ornithology, Ithaca, NY, USA.
Ellegren, H., 2010. Evolutionary stasis: the stable chromosomes of birds. Trends Ecol. Evol. 25, 283–291.
Ellegren, H., 2014. Genome sequencing and population genomics in non-model organisms. Trends Ecol. Evol. 29, 51–63.
Finley, J.K., Huot, S., 2010. Interspecific mate choice and hybridism in the bufflehead, Bucephala albeola. Can. Field-Naturalist 124, 28–31.
Fitzpatrick, B.M., 2004. Rates of evolution of hybrid inviability in birds and mammals. Evolution 58, 1865–1870.
Fontaine, M.C., Pease, J.B., Steele, A., Waterhouse, R.M., Neafsey, D.E., Sharakhov, I.V., Jiang, X., Hall, A.B., Catteruccia, F., Kakani, E., 2015. Extensive introgression in a malaria vector species complex revealed by phylogenomics. Science 347, 1258524.
Francis, R.M., 2016. Pophelper: an R package and web app to analyse and visualize population structure. Mol. Ecol. Resour. 17, 27–32.
Goudie, R.I., Robertson, G.J., Reed, A., 2020. Common Eider (*Somateria mollissima*), version 1.0. In: Billerman, S.M. (Ed.), Birds of the World. Cornell Lab of Ornithology, Ithaca, NY, USA.
Grant, P.R., Grant, B.R., 1992. Hybridization of bird species. Science 256, 193–197.
Grant, P.R., Grant, B.R., 1997a. Genetics and the origin of bird species. PNAS 94, 7768–7775.
Grant, P.R., Grant, B.R., 1997b. Hybridization, sexual imprinting, and mate choice. Am. Nat. 149, 1–28.

Grant, P.R., Grant, B.R., 2020. Triad hybridization via a conduit species. Proc. Natl. Acad. Sci. 117, 7888–7896.
Green, R.E., Krause, J., Briggs, A.W., Maricic, T., Stenzel, U., Kircher, M., Patterson, N., Li, H., Zhai, W., Fritz, M.H.-Y., 2010. A draft sequence of the Neandertal genome. Science 328, 710–722.
Greenwood, P.J., 1980. Mating systems, philopatry and dispersal in birds and mammals. Anim. Behav. 28, 1140–1162.
Griffin, D.K., Robertson, L.B., Tempest, H.G., Vignal, A., Fillon, V., Crooijmans, R.P., Groenen, M.A., Deryusheva, S., Gaginskaya, E., Carré, W., 2008. Whole genome comparative studies between chicken and turkey and their implications for avian genome evolution. BMC Genomics 9, 168.
Hartman, P.J., Wetzel, D.P., Crowley, P.H., Westneat, D.F., 2012. The impact of extra-pair mating behavior on hybridization and genetic introgression. Theor. Ecol. 5, 219–229.
Hasegawa, M., Kishino, H., Yano, T.-A., 1985. Dating of the human-ape splitting by a molecular clock of mitochondrial DNA. J. Mol. Evol. 22, 160–174.
Hedrick, P.W., 2013. Adaptive introgression in animals: examples and comparison to new mutation and standing variation as sources of adaptive variation. Mol. Ecol. 22, 4606–4618.
Hermansen, J.S., SÆther, S.A., Elgvin, T.O., Borge, T., Hjelle, E., SÆTre, G.-P., 2011. Hybrid speciation in sparrows I: phenotypic intermediacy, genetic admixture and barriers to gene flow. Mol. Ecol. 20, 3812–3822.
Hoskin, C.J., Higgie, M., McDonald, K.R., Moritz, C., 2005. Reinforcement drives rapid allopatric speciation. Nature 437, 1353–1356.
Huang, Y., Li, Y., Burt, D.W., Chen, H., Zhang, Y., Qian, W., Kim, H., Gan, S., Zhao, Y., Li, J., 2013. The duck genome and transcriptome provide insight into an avian influenza virus reservoir species. Nat. Genet. 45, 776–783.
Hubbs, C.L., 1955. Hybridization between fish species in nature. Syst. Zool. 4, 1–20.
Huelsenbeck, J.P., Ronquist, F., 2001. MRBAYES: Bayesian inference of phylogenetic trees. Bioinformatics 17, 754–755.
Iverson, S.A., Esler, D., Rizzolo, D.J., 2004. Winter philopatry of harlequin ducks in Prince William Sound, Alaska. The Condor 106, 711–715.
Jacobsen, F., Omland, K.E., 2011. Increasing evidence of the role of gene flow in animal evolution: hybrid speciation in the yellow-rumped warbler complex. Mol. Ecol. 20, 2236–2239.
Jakobsson, M., Rosenberg, N.A., 2007. CLUMPP: a cluster matching and permutation program for dealing with label switching and multimodality in analysis of population structure. Bioinformatics 23, 1801–1806.
Jarvis, E.D., Mirarab, S., Aberer, A.J., Li, B., Houde, P., Li, C., Ho, S.Y., Faircloth, B.C., Nabholz, B., Howard, J.T., 2014. Whole-genome analyses resolve early branches in the tree of life of modern birds. Science 346, 1320–1331.
Johnsgard, P.A., 1960. Hybridization in the *Anatidae* and its taxonomic implications. The Condor 62, 25–33.
Johnsgard, P.A., 1965. Handbook of waterfowl behavior: Tribe Aythyini (Pochards).
Jombart, T., 2008. Adegenet: a R package for the multivariate analysis of genetic markers. Bioinformatics 24, 1403–1405.
Kear, J., 2005. Bird Families of the World: Ducks. Oxford University Press, Oxford, UK, Geese and Swans.
Kearns, A.M., Restani, M., Szabo, I., Schrøder-Nielsen, A., Kim, J.A., Richardson, H.M., Marzluff, J.M., Fleischer, R.C., Johnsen, A., Omland, K.E., 2018. Genomic evidence of speciation reversal in ravens. Nat. Commun. 9, 1–13.
Keinan, A., Mullikin, J.C., Patterson, N., Reich, D., 2007. Measurement of the human allele frequency spectrum demonstrates greater genetic drift in East Asians than in Europeans. Nat. Genet. 39, 1251–1255.
Keller, I., Wagner, C., Greuter, L., Mwaiko, S., Selz, O., Sivasundar, A., Wittwer, S., Seehausen, O., 2012. Population genomic signatures of divergent adaptation, gene flow and hybrid speciation in the rapid radiation of Lake Victoria cichlid fishes. Mol. Ecol. 22, 2848–2863.
Kimura, M., Ohta, T., 1973. The age of a neutral mutant persisting in a finite population. Genetics 75, 199–212.
Kleindorfer, S., O'Connor, J.A., Dudaniec, R.Y., Myers, S.A., Robertson, J., Sulloway, F.J., 2014. Species collapse via hybridization in Darwin's tree finches. Am. Nat. 183, 325–341.
Kraus, R., Kerstens, H., Van Hooft, P., Crooijmans, R., Van Der Poel, J., Elmberg, J., Vignal, A., Huang, Y., Li, N., Prins, H., Groenen, M., 2011. Genome wide SNP discovery, analysis and evaluation in mallard (*Anas platyrhynchos*). BMC Genomics 12, 150.
Kunte, K., Shea, C., Aardema, M.L., Scriber, J.M., Juenger, T.E., Gilbert, L.E., Kronforst, M.R., 2011. Sex chromosome mosaicism and hybrid speciation among tiger swallowtail butterflies. PLoS Genet. 7, e1002274.
Lavretsky, P., Dacosta, J.M., Hernández-Baños, B.E., Andrew Engilis, J., Sorenson, M.D., Peters, J.L., 2015a. Speciation genomics and a role for the Z chromosome in the early stages of divergence between Mexican ducks and mallards. Mol. Ecol. 24, 5364–5378.
Lavretsky, P., DaCosta, J.M., Sorenson, M.D., McCracken, K.G., Peters, J.L., 2019. ddRAD-seq data reveal significant genome-wide population structure and divergent genomic regions that distinguish the mallard and close relatives in North America. Mol. Ecol. 28, 2594–2609.
Lavretsky, P., Engilis, A., Eadie, J.M., Peters, J.L., 2015b. Genetic admixture supports an ancient hybrid origin of the endangered Hawaiian duck. J. Evol. Biol. 28, 1005–1015.
Lavretsky, P., McCracken, K.G., Peters, J.L., 2014. Phylogenetics of a recent radiation in the mallards and allies (Aves: *Anas*): Inferences from a genomic transect and the multispecies coalescent. Mol. Phylogenet. Evol. 70, 402–411.
Lavretsky, P., McInerney, N.R., Mohl, J., Brown, J.I., James, H., McCracken, K.G., Fleischer, R., 2020. Assessing changes in genomic divergence following a century of human mediated secondary contact among wild and captive-bred ducks. Mol. Ecol. 29, 578–595.
Lavretsky, P., Peters, J.L., Winker, K., Bahn, V., Kulikova, I., Zhuravlev, Y.N., Wilson, R. E., Barger, C., Gurney, K., Mccracken, K.G., 2016. Becoming pure: identifying generational classes of admixed individuals within lesser and greater scaup populations. Mol. Ecol. 25, 661–674.
Lawson, D.J., Hellenthal, G., Myers, S., Falush, D., 2012. Inference of population structure using dense haplotype data. PLoS Genet. 8, e1002453.
Leaché, A.D., Fujita, M.K., Minin, V.N., Bouckaert, R.R., 2014. Species delimitation using genome-wide SNP data. Syst. Biol. 63, 534–542.
Lijtmaer, D.A., Mahler, B., Tubaro, P.L., 2003a. Hybridization and postzygotic isolation patterns in pigeons and doves. Evolution 57, 1411–1418.
Lijtmaer, D.A., Mahler, B., Tubaro, P.L., Dunn, P., 2003b. Hybridization and postzygotic isolation patterns in pigeons and doves. Evolution 57, 1411–1418.
Livezey, B.C., 1986. A phylogenetic analysis of recent Anseriform genera using morphological characters. Auk 103, 737–754.
Livezey, B.C., 1997. A phylogenetic analysis of basal Anseriformes, the fossil *Presbyornis*, and the interordinal relationships of waterfowl. Zool. J. Linn. Soc. 121, 361–428.
Lowry, D.B., Hoban, S., Kelley, J.L., Lotterhos, K.E., Reed, L.K., Antolin, M.F., Storfer, A., 2017. Breaking RAD: an evaluation of the utility of restriction site-associated DNA sequencing for genome scans of adaptation. Mol. Ecol. Resour. 17, 142–152.
Malinsky, M., Svardal, H., Tyers, A.M., Miska, E.A., Genner, M.J., Turner, G.F., Durbin, R., 2018a. Whole-genome sequences of Malawi cichlids reveal multiple radiations interconnected by gene flow. Nat. Ecol. Evol. 2, 1940.
Malinsky, M., Trucchi, E., Lawson, D., Falush, D., 2018b. RADpainter and fineRADstructure: population inference from RADseq data. Mol. Biol. Evol. 35, 1284–1290.
Mallet, J., 2007. Hybrid speciation. Nature 446, 279–283.
Mallory, M.L., 2015. Site fidelity, breeding habitats, and the reproductive strategies of sea ducks. Ecology and Conservation of North American Sea Ducks. In: Savard, J.-.P. L., Derksen, D.V., Esler, D., Eadie, J.M. (Eds.), Studies in Avian Biology. CRC Press, New York, NY, USA.
Martin, P.R., DiLabio, B.M., 1994. Natural hybrids between the Common Goldeneye, *Bucephala clangula*, and Barrow's Goldeneye, *B. islandica*. Canadian Field Naturalist 108, 195–198.
Mavarez, J., Linares, M., 2008. Homoploid hybrid speciation in animals. Mol. Ecol. 17, 4181–4185.
McKinney, F., Derrickson, S.R., Mineau, P., 1983. Forced copulation in waterfowl. Behaviour 86, 250–294.
Meyer, M., Kircher, M., Gansauge, M.-T., Li, H., Racimo, F., Mallick, S., Schraiber, J.G., Jay, F., Prüfer, K., de Filippo, C., 2012. A high-coverage genome sequence from an archaic Denisovan individual. Science 338, 222–226.
Miller, W., Schuster, S.C., Welch, A.J., Ratan, A., Bedoya-Reina, O.C., Zhao, F., Kim, H.L., Burhans, R.C., Drautz, D.I., Wittekindt, N.E., 2012. Polar and brown bear genomes reveal ancient admixture and demographic footprints of past climate change. PNAS 109, E2382–E2390.
Mittelhauser, G.H., Drury, J.B., Corr, P.O., 2002. Harlequin Ducks (*Histrionicus histrionicus*) in Maine, 1950–1999. Northeastern Naturalist 9, 163–182.
Noor, M.A., Johnson, N.A., Hey, J., 2000. Gene flow between *Drosophila pseudoobscura* and *D. persimilis*. Evolution 54, 2174–2175.
Ottenburghs, J., 2019. Multispecies hybridization in birds. Avian Res. 10, 20.
Ottenburghs, J., Kraus, R.H., Hooft, P., Wieren, S.E., Ydenberg, R.C., Prins, H.H., 2017a. Avian introgression in the genomic era. Avian Res. 8, 30.
Ottenburghs, J., Megens, H.-J., Kraus, R.H., Madsen, O., van Hooft, P., van Wieren, S.E., Crooijmans, R.P., Ydenberg, R.C., Groenen, M.A., Prins, H.H., 2016. A tree of geese: A phylogenomic perspective on the evolutionary history of True Geese. Mol. Phylogenet. Evol. 101, 303–313.
Ottenburghs, J., Megens, H.-J., Kraus, R.H., van Hooft, P., van Wieren, S.E., Crooijmans, R.P., Ydenberg, R.C., Groenen, M.A., Prins, H.H., 2017b. A history of hybrids? Genomic patterns of introgression in the True Geese. BMC Evol. Biol. 17, 201.
Ottenburghs, J., Ydenberg, R.C., Van Hooft, P., Van Wieren, S.E., Prins, H.H., 2015. The Avian Hybrids Project: gathering the scientific literature on avian hybridization. Ibis 157, 892–894.
Patterson, N., Moorjani, P., Luo, Y., Mallick, S., Rohland, N., Zhan, Y., Genschoreck, T., Webster, T., Reich, D., 2012. Ancient admixture in human history. Genetics 192, 1065–1093.
Pearce, J.M., Talbot, S.L., Petersen, M.R., Rearick, J.R., 2005. Limited genetic differentiation among breeding, molting, and wintering groups of the threatened Steller's eider: the role of historic and contemporary factors. Conserv. Genet. 6, 743–757.
Pearce, J.M., Talbot, S.L., Pierson, B.J., Petersen, M.R., Scribner, K.T., Dickson, D.L., Mosbech, A., 2004. Lack of spatial genetic structure among nesting and wintering King Eiders. The Condor 106, 229–240.
Peters, J.L., Bolender, K.A., Pearce, J.M., 2012. Behavioural vs. molecular sources of conflict between nuclear and mitochondrial DNA: the role of male-biased dispersal in a Holarctic sea duck. Mol. Ecol. 21, 3562–3575.
Pfeifer, B., Wittelsbürger, U., Ramos-Onsins, S.E., Lercher, M.J., 2014. PopGenome: An efficient swiss army knife for population genomic analyses in R. Mol. Biol. Evol. 31, 1929–1936.
Pickrell, J.K., Pritchard, J.K., 2012. Inference of population splits and mixtures from genome-wide allele frequency data. PLoS Genet. 8, e1002967.
Price, T.D., 2008. Speciation in Birds. Roberts and Company, Greenwood Village CO.
Price, T.D., Bouvier, M.M., 2002. The evolution of F1 postzygotic incompatibilities in birds. Evolution 56, 2083–2089.

Purcell, S., Neale, B., Todd-Brown, K., Thomas, L., Ferreira, M.A., Bender, D., Maller, J., Sklar, P., De Bakker, P.I., Daly, M.J., 2007. PLINK: a tool set for whole-genome association and population-based linkage analyses. Am. J. Hum. Genet. 81, 559–575.
Randler, C., 2005. Do forced extrapair copulations and interspecific brood amalgamation facilitate natural hybridisation in wildfowl? Behaviour 477–488.
Randler, C., 2006. Behavioural and ecological correlates of natural hybridization in birds. Ibis 148, 459–467.
Reich, D., Green, R.E., Kircher, M., Krause, J., Patterson, N., Durand, E.Y., Viola, B., Briggs, A.W., Stenzel, U., Johnson, P.L., 2010. Genetic history of an archaic hominin group from Denisova Cave in Siberia. Nature 468, 1053.
Reich, D., Thangaraj, K., Patterson, N., Price, A.L., Singh, L., 2009. Reconstructing Indian population history. Nature 461, 489–494.
Rentsch, J.D., Leebens-Mack, J., 2012. Homoploid hybrid origin of *Yucca gloriosa*: intersectional hybrid speciation in Yucca (*Agavoideae, Asparagaceae*). Ecol. Evol. 2, 2213–2222.
Rheindt, F.E., Edwards, S.V., 2011. Genetic introgression: an integral but neglected component of speciation in birds. Auk 128, 620–632.
Rieseberg, L.H., Archer, M.A., Wayne, R.K., 1999. Transgressive segregation, adaptation and speciation. Heredity 83, 363–372.
Rieseberg, L.H., Raymond, O., Rosenthal, D.M., Lai, Z., Livingstone, K., Nakazato, T., Durphy, J.L., Schwarzbach, A.E., Donovan, L.A., Lexer, C., 2003. Major ecological transitions in wild sunflowers facilitated by hybridization. Science 301, 1211–1216.
Robertson, G.J., Savard, J.L., 2020. Long-tailed Duck (*Clangula hyemalis*), version 1.0. In: Billerman, S.M. (Ed.), Birds of the World. Cornell Lab of Ornithology, Ithaca, NY, USA.
Ronquist, F., Huelsenbeck, J.P., 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19, 1572–1574.
Rundle, H.D., Nosil, P., 2005. Ecological speciation. Ecol. Lett. 8, 336–352.
Rutledge, L.Y., Devillard, S., Boone, J.Q., Hohenlohe, P.A., White, B.N., 2015. RAD sequencing and genomic simulations resolve hybrid origins within North American *Canis*. Biol. Lett. 11, 20150303.
Sankararaman, S., Mallick, S., Patterson, N., Reich, D., 2016. The combined landscape of Denisovan and Neanderthal ancestry in present-day humans. Curr. Biol. 26, 1241–1247.
Scherer, V.S., Hilsberg, T., 1982. Hybridisierung und verwandtschaftsgrade innerhalb der Anatidae – eine systematische un evolutionstheoretische betrachtung. J. für Ornitologie 123, 357–380.
Schluter, D., 2009. Evidence for ecological speciation and its alternative. Science 323, 737–741.
Schumer, M., Rosenthal, G.G., Andolfatto, P., 2014. How common is homoploid hybrid speciation? Evolution 68, 1553–1560.
Seehausen, O., 2004. Hybridization and adaptive radiation. Trends Ecol. Evol. 19, 198–207.
Seehausen, O., 2006. Conservation: losing biodiversity by reverse speciation. Curr. Biol. 16, R334–R337.
Silverman, E.D., Saalfeld, D.T., Leirness, J.B., Koneff, M.D., 2013. Wintering sea duck distribution along the Atlantic Coast of the United States. J. Fish Wildlife Manage. 4, 178–198.
Sonsthagen, S.A., Talbot, S.L., McCracken, K.G., 2007. Genetic characterization of common eiders breeding in the Yukon-Kuskokwim Delta, Alaska. The Condor 109, 878–893.
Sonsthagen, S.A., Talbot, S.L., Scribner, K.T., McCracken, K.G., 2011. Multilocus phylogeography and population structure of common eiders breeding in North America and Scandinavia. J. Biogeogr. 38, 1368–1380.
Sonsthagen, S.A., Wilson, R.E., Lavretsky, P., Talbot, S.L., 2019. Coast to coast: High genomic connectivity in North American scoters. Ecol. Evol. 9, 7246–7261.
Swennen, C., Duiven, P., Reyrink, L., 1979. Notes on the sex ratio in the common eider *Somateria mollissima* (L.). Ardea 67, 54–61.
Talbot, S.L., Sonsthagen, S.A., Pearce, J.M., Scribner, K.T., 2015. Phylogenetics, phylogeography, and population genetics of North American sea ducks (tribe: Mergini). Ecology and Conservation of North American Sea Ducks. In: Savard, J.-.P. L., Derksen, D.V., Esler, D., Eadie, J.M. (Eds.), Studies in Avian Biology. CRC Press, New York, pp. 29–61.
Sonsthagen, S.A., Wilson, R.E., Lavretsky, P., Talbot, S.L., 2021. Genomic data of North American Sea Ducks. US Geological Survey data release; https://doi.org/10.5066/F7T43RK9.
Taylor, E.B., Boughman, J.W., Groenenboom, M., Sniatynski, M., D, D.S., Gow, J.L., 2006. Speciation in reverse: morphological and genetic evidence of the collapse of a three-spined stickleback (Gasterosteus aculeatus) species pair. Mol. Ecol. 15, 343–355.
Trefry, S.A., Dickson, D.L., Hoover, A.K., 2007. A common eider x king eider hybrid captured on the Kent Peninsula. Nunavut. Arctic 251–254.
Tu, J., Si, F., Xing, X., Yue, Z., Yang, F., 2012. Determination and analysis of complete mitochondrial genome sequence of mallard (*Anas platyrhychos)*. Mitochondrial DNA 23, 283–285.
Vallender, R., Robertson, R., Friesen, V., Lovette, I., 2007. Complex hybridization dynamics between golden-winged and blue-winged warblers (*Vermivora chrysoptera* and *Vermivora pinus*) revealed by AFLP, microsatellite, intron and mtDNA markers. Mol. Ecol. 16, 2017–2029.
Vonlanthen, P., Bittner, D., Hudson, A.G., Young, K.A., Müller, R., Lundsgaard-Hansen, B., Roy, D., Piazza, S.D., Largiader, C.R., O, O.S., 2012. Eutrophication causes speciation reversal in whitefish adaptive radiations. Nature 482, 357–362.
Webb, W.C., Marzluff, J.M., Omland, K.E., 2011. Random interbreeding between cryptic lineages of the Common Raven: evidence for speciation in reverse. Mol. Ecol. 20, 2390–2402.
Wells, C.P., Lavretsky, P., Sorenson, M.D., Peters, J.L., DaCosta, J.M., Turnbull, S., Uyehara, K.J., Malachowski, C.P., Dugger, B.D., Eadie, J.M., Engilis, A.J., 2019. Persistence of an endangered island endemic, an introduced congener, and multiple hybrid swarms across the main Hawaiian Islands. Mol. Ecol. 28, 5203–5216.
White, T.P., Veit, R.R., 2020. Spatial ecology of long-tailed ducks and white-winged scoters wintering on Nantucket Shoals. Ecosphere 11, e03002.
Zhou, H., Alexander, D., Lange, K., 2011. A quasi-Newton acceleration for high-dimensional optimization algorithms. Statist. Comput. 21, 261–273.