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SPECIATION, SUBSPECIES DIVERGENCE, AND PARAPHYLY IN THE CINNAMON TEAL AND BLUE-WINGED TEAL

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Abstract. Divergent selection can lead to substantial morphological and behavioral differences despite slight differentiation in neutral genetic variation. We examined the evolutionary history of two closely related waterfowl, the Cinnamon Teal (*Anas cyanoptera*) and Blue-winged Teal (*A. discors*), that are morphologically distinct but paraphyletic in mitochondrial DNA (mtDNA) and share allozyme alleles. Sequences of mtDNA and two nuclear introns revealed that North American Cinnamon Teal ($n = 70$) and Blue-winged Teal ($n = 76$) are characterized by high genetic diversity, a large effective population size, and recent population expansion. In contrast, South American Cinnamon Teal ($n = 102$) have less genetic diversity and a smaller effective population size that has been more stable. We found 91 unique mtDNA haplotypes, only a few of which were shared by the two species or the three subspecies of the Cinnamon Teal, but the haplotypes were intermixed in a polyphyletic relationship, and we found no diagnostic phylogroups. Moreover, populations were more strongly differentiated in mtDNA ($\Phi_{ST} = 0.41$) than in the nuclear introns ($\Phi_{ST} = 0.04–0.06$). Analyses of isolation with migration indicated that sharing of haplotypes and alleles in the two continents is more likely attributable to incomplete lineage sorting than to gene flow, whereas estimates within each continent yielded higher migration rates. The oldest divergence was between North American Cinnamon Teal and the other taxa, whereas the Blue-winged Teal likely split from South American Cinnamon Teal more recently. Considerable overlap in confidence intervals for these divergences, however, suggests that these taxa diversified rapidly.

Key words: *Cinnamon Teal, Blue-winged Teal, genetic structure, speciation, multilocus, coalescent.*

Especiación, Divergencia entre Subespecies y Parafilia en *Anas cyanoptera* y *A. discors*

Resumen. La selección divergente puede conducir a la aparición de diferencias morfológicas y conductuales sustanciales a pesar de que la diferenciación en genes neutrales sea sutil. Examinamos la historia evolutiva de dos aves acuáticas cercanamente emparentadas, *Anas cyanoptera* y *A. discors*. Estas aves son morfológicamente distintas, pero son parafiléticas en cuanto a su ADN mitocondrial (ADNmt) y comparten alelos de aloenzimas. Análisis de secuencias de ADNmt y de dos intrones nucleares indicaron que las poblaciones norteamericanas de *A. cyanoptera* ($n = 70$) y de *A. discors* ($n = 76$) presentan alta diversidad genética y tamaños poblacionales efectivos grandes, y se han expandido recientemente. En contraste, las poblaciones suramericanas de *A. cyanoptera* ($n = 102$) presentan menor diversidad genética, un tamaño efectivo menor y han sido más estables. Encontramos 91 haplotipos únicos de ADNmt, de los cuales sólo unos pocos son compartidos por las dos especies o por las tres subespecies de *A. cyanoptera*. Sin embargo, los haplotipos están entremezclados en una relación polifilética y no encontramos filogrupos diagnósticos. Además, las poblaciones están más diferenciadas en el ADNmt ($\Phi_{ST} = 0.41$) que en los intrones nucleares ($\Phi_{ST} = 0.04–0.06$). Mediante análisis de aislamiento con migración, determinamos que los haplotipos y alelos compartidos entre los continentes serían atribuibles más probablemente a un proceso incompleto de purificación de linajes y no a la existencia de flujo genético, mientras que los estimados de flujo génico dentro de cada continente sugirieron tasas de migración más altas. La divergencia más antigua sucedió entre las poblaciones norteamericanas de *A. cyanoptera* y los demás taxones, mientras que *A. discors* probablemente se separó de las poblaciones suramericanas de *A. cyanoptera* más recientemente. Sin embargo, la superposición de los intervalos de confianza de los tiempos estimados para esos eventos de divergencia sugiere que los taxones se diferenciaron rápidamente.

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INTRODUCTION

Natural selection, sexual selection, and stochastic processes such as genetic drift and founder events are important evolutionary forces leading to divergence between populations and ultimately, in many cases, to speciation (Questiau 1999, Coyne and Orr 2004, Price 2008). As populations colonize new environments, particular traits become modified to exploit new resources or to gain advantages in social competition for contested resources such as food and mates (West-Eberhard 1983). Incipient species thus can develop distinct morphology or behavior in response to varying selection that results in premating and postmating isolation, with little or no differentiation in neutral genetic variation (Meyer 1993, Bernatchez et al. 1996, Schluter 1998, Seehausen and van Alphen 1998, Hendry 2001, Ödeen and Björklund 2003). These morphological and behavioral responses can cause incongruence between species limits based on phenotypic traits and gene genealogies, especially in recently diverged taxa (Funk and Omland 2003, Avise 2004, Buehler and Baker 2005, Joseph et al. 2006, Maley and Winker 2010). Furthermore, a major component of variation among closely related species or subspecies often results from differences in sexual ornaments used for mate recognition (West-Eberhard 1983, Price 1998, Questiau 1999, Johnsen et al. 2006). Such discrepancies between morphological and molecular data have resulted in questions regarding species' status; however, they provide a valuable opportunity to gain insight into species' biology and the evolutionary processes leading to speciation (Edwards et al. 2005, Omland et al. 2006, Johnsen et al. 2006, Joseph et al. 2006).

The Cinnamon Teal (*Anas cyanoptera*) and Blue-winged Teal (*A. discors*) are two species of closely related dabbling ducks that are particularly well suited for study of divergence and gene flow between paraphyletic species and subspecies with shallow genetic differentiation. These species differ conspicuously in body size, coloration, habitat choice, and aspects of their behavior (e.g., migratory behavior and territoriality; Gammonley 1996, Rohwer et al. 2002), but mitochondrial DNA (mtDNA) suggests a recent divergence (Kessler and Avise 1984, Johnson and Sorenson 1999, Kerr et al. 2007). Both species are widespread in the Western Hemisphere and are occasionally found in sympatry in western North America and in northern South America (Fig. 1). The Cinnamon Teal comprises five morphologically distinct subspecies inhabiting largely distinct geographic and ecological zones: *A. c. cyanoptera* (lowland South America and occasionally the high Andes), *A. c. orinomus* (endemic to the high Andes), *A. c. borreroi* (Colombian Andes), *A. c. tropica* (Colombian Andean lowlands), and *A. c. septentrionalium* (North America; Snyder and Lumsden 1951, American Ornithologists' Union 1957, Gammonley 1996, Wilson et al. 2010). Blue-winged Teal are found over most of North America but occur at low densities in western North America where they are sympatric with *A. c. septentrionalium*. Although Blue-winged Teal winter commonly in Central America and northern South America, only a few individuals occur year round in Colombia and Peru (Fjeldså and

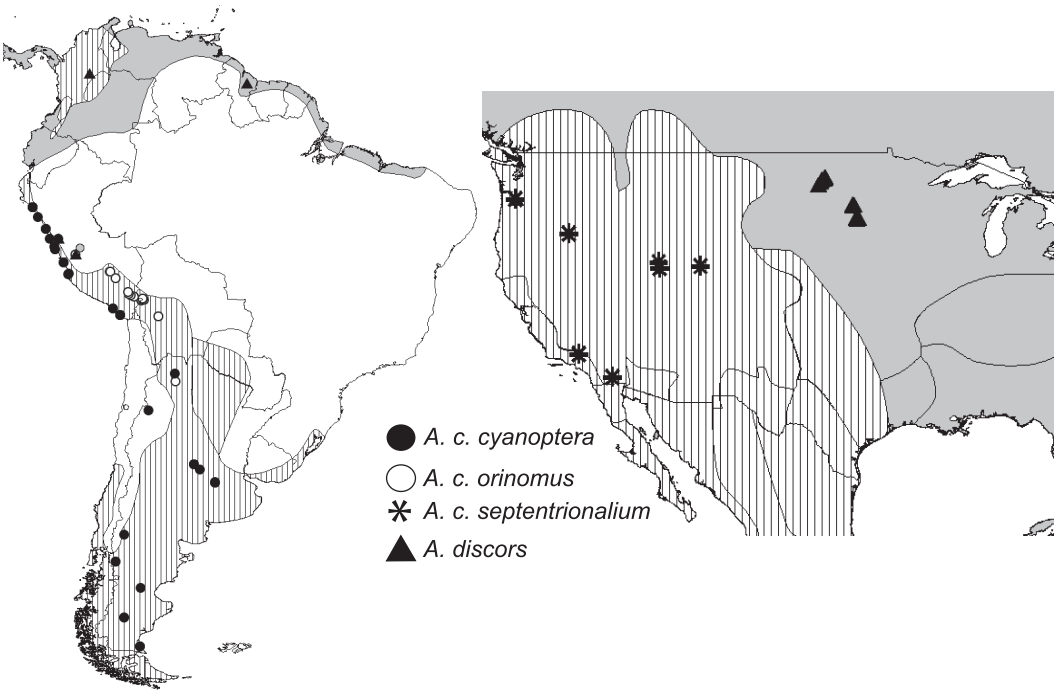

FIGURE 1. Sampling localities and geographic ranges (breeding and wintering) for the Cinnamon Teal (stripes: *Anas cyanoptera*) and Blue-winged Teal (gray: *Anas discors*) (Ridgely et al. 2003).

Krabbe 1990); a small breeding population was recently established in Colombia (G. Stiles pers. comm.).

The breeding plumages of male Cinnamon Teal and Blue-winged Teal are distinctive. Male Cinnamon Teal are reddish brown throughout, and male Blue-winged Teal have a characteristic steel-blue neck and head with a white facial crescent. Despite these striking differences in males' plumage, females and juveniles are difficult to distinguish, as is often the case for closely related birds (West-Eberhard 1983). In ducks, post-zygotic isolation is weak and hybridization is common (Tubaro and Lijtmaer 2002); most reproductive isolation occurs by other mechanisms that usually involve pre-mating behaviors. Hybridization between the Cinnamon Teal and Blue-winged Teal has been reported infrequently in the wild (only hybrid males can be recognized by plumage), perhaps because of limited overlap in their breeding distributions. However, the species interbreed freely in captivity (Delacour and Mayr 1945), suggesting that they diverged too recently for the evolution of strong pre- or post-mating isolating mechanisms.

Here we investigate the evolutionary histories of the Cinnamon and Blue-winged Teal on the basis of samples from throughout their breeding ranges by comparing sequences from the hyper-variable mtDNA control region and two independent nuclear loci. We evaluate whether there are distinct lineages or differences between Cinnamon Teal subspecies and Blue-winged Teal in frequency of haplotypes. We also use coalescence to examine the demographic history of this species complex (Nielsen and Wakeley 2001, Hey and Nielsen 2004). We compare times of divergence and gene flow within and between continents and between species to evaluate the roles these two factors play in the shallow genetic divergence and mitochondrial paraphyly of these taxa.

METHODS

SPECIMEN COLLECTION

We collected 52 vouchered specimens of *A. c. cyanoptera*, 50 of *A. c. orinomus*, 70 of *A. c. septentrionalium*, and 76 of *A. discors* in Argentina (2001, 2003, 2005), Bolivia (2001, 2005), Colombia (2004), Peru (2002), and the United States (2002, 2003; Fig. 1, Appendix 1). For the Cinnamon Teal, we used published subspecific morphological characters to classify each specimen to subspecies (Snyder and Lumsden 1951, Wilson et al. 2010). We excluded *A. c. borreroi* and *A. c. tropica* because they are critically endangered (Black 1998) and sufficient specimens of these subspecies do not exist.

DNA EXTRACTION, PCR, AND DNA SEQUENCING

We extracted genomic DNA from muscle tissue with a Qiagen DNeasy tissue kit (Qiagen, Valencia, California). We amplified 1272 bp of the mtDNA control region, phenylalanine tRNA, and part of the 12S rRNA gene with the overlapping primer pairs L78–H774 and L736–H1530 (Sorenson and Fleischer 1996, Sorenson et al. 1999) and two additional primers (L627: 5′–TAAGCCTGGACACACCTGCGTTATCG–3′; H693: 5′–CAGTGTCAAGGTGATTCCC–3′). PCR amplifications were carried out in a 50-μL volume with 2–100 ng genomic DNA, 0.5 μM each primer, 1.0 μM dNTPs, 10× PCR buffer, 2.5 μM $MgCl_2$, and 0.2 units Taq polymerase. PCR reactions began with 94 ºC for 7 min followed by 45 cycles of 94°C for 20 sec, 52 °C for 20 sec, and 72 °C for 1 min with a 7-min final extension at 72 °C. We gel-purified PCR products and sequenced both strands with BigDye Terminator Cycle sequencing kits on an ABI 3100 or 377 DNA sequencer (Applied Biosystems, Foster City, CA). Sequences from opposite strands were reconciled in Sequencher 4.1.2 (Gene Codes Corporation, Ann Arbor, MI).

We also sequenced two independent nuclear introns, ornithine decarboxylase (ODC1) intron five (353 bp) and α-enolase (ENO1) intron eight (312 bp) (Peters et al. 2008, McCracken et al. 2009a). We sequenced these two introns by the techniques described above with an annealing temperature of 60 °C and AmpliTaq Gold PCR Master Mix (Applied Biosystems, Foster City, CA). Sequences that contained double peaks, indicating the presence of two alleles, were coded with IUPAC degeneracy codes and treated as polymorphisms. We resolved insertions/deletions (indels) by comparing the unambiguous 5′ ends of sequences to the 3′ ambiguous ends of forward and reverse strands (Peters et al. 2007). Gaps resulting in shifted peaks in the chromatograms enabled us to resolve length polymorphisms within the sequences. We aligned all sequences by eye with the sequence alignment editor Se-Al 2.0a11 (Rambaut 2007) and deposited the sequences in GenBank (accession numbers GQ269364–GQ269567 and JF914362–JF914900).

GAMETIC PHASE OF ALLELE SEQUENCES

We used a two-step procedure to determine the gametic phase of each intron sequence that was heterozygous at two or more nucleotide positions. We first analyzed the diploid consensus sequences of each individual with Phase 2.1 (Stephens et al. 2001). Phase uses a Bayesian method to infer haplotypes from diploid genotypic data with recombination and the decay of linkage disequilibrium with distance. We analyzed each dataset by using the default values (100 main iterations, 1 thinning interval, 100 burn-in) followed by 1000 main iterations and 1000 burn-in (-X10 option) for the final iteration. The Phase algorithm was run five times automatically (-x5 option) from different starting points, selecting the result with the best overall goodness of fit. We next selected individuals with low allele-pair probabilities (<80%) and designed allele-specific primers to selectively amplify one allele (Bottema et al. 1993, Peters et al. 2005a). We then subtracted the resulting haploid allele sequence from the diploid consensus sequence to obtain the gametic phase of the second haplotype. We then analyzed each dataset five more times with Phase and the additional known allele sequences (-k option). We identified the

gametic phases of 92% ($n = 456$) of 495 individual autosomal sequences experimentally or with >95% posterior probability and 95% ($n = 469$) with >90% posterior probability.

GENETIC DIVERSITY AND POPULATION SUBDIVISION

Nucleotide diversity (π), expected and observed heterozygosities, and linkage disequilibrium between ODC1 and ENO1 were calculated in Arlequin 3.11 (Excoffier et al. 2005). Allelic richness was standardized to the smallest sample size ($n = 50$). Using the reduced median algorithm (Bandelt et al. 1995) to illustrate possible reticulations in the gene trees due to homoplasy or recombination, we constructed allelic networks in Network 4.5.1 (Fluxus Technology, Ltd.). Gaps were treated as a fifth state, and indels were treated as a single insertion or deletion regardless of length.

Preliminary analyses showed no significant genetic differentiation (Φ_{ST}) among populations within subspecies of *A. cyanoptera* or between North American and Colombian samples of *A. discors*. Therefore, we did all analyses at the level of the species or subspecies. To assess differences in population structure between *A. discors* and *A. cyanoptera* and among the subspecies of *A. cyanoptera*, we calculated pairwise Φ_{ST} for sequence data in Arlequin by using the best-fit nucleotide-substitution model, as identified in Modeltest 3.06 (Posada and Crandall 1998) under the Akaike information criterion (AIC; Akaike 1974). Additionally, we ran a hierarchical analysis of molecular variance (AMOVA) in Arlequin to analyze spatial variance in haplotypic and allelic frequencies between species and among populations. We adjusted *P*-values for multiple comparisons with permutations (3000) or Bonferroni corrections ($\alpha = 0.05$).

We used Structure 2.2.3 (Pritchard et al. 2000) to evaluate the number of genetic clusters (K) in our dataset. Structure assigns individuals to populations by maximizing Hardy–Weinberg equilibrium and minimizing linkage disequilibrium. For this analysis, we coded each mtDNA or nuclear DNA haplotype as a separate allele and analyzed mtDNA and nuclear sequences with an admixture model without a priori information about specimen identification or collection locality. The analysis was run for $K = 1$–15 populations with 100 000 burn-in iterations and 1 000 000 Markov chain Monte Carlo iterations; the analysis was repeated ten times to ensure consistency across runs. We used the ΔK method of Evanno et al. (2005) to determine the most likely number of groups at the uppermost level of population structure.

To test for past changes in effective population size, we calculated Fu's F_s (Fu 1997) and Tajima's D (Tajima 1989) on the basis of the site-frequency spectrum of segregating sites for mtDNA. Negative values of Tajima's D or Fu's F_s result when there is an excess of low-frequency polymorphisms, which can result from rapid population expansion or a selective sweep acting on linked polymorphisms. Conversely, a positive value for either test statistic can be indicative of a population decline. Additionally, we calculated mismatch distributions of mtDNA-haplotype data in Arlequin. Mismatch distributions that are multimodal in shape indicate a population that is at demographic equilibrium, whereas a unimodal distribution is consistent with a population that has undergone a recent expansion (Slatkin and Hudson 1991, Rogers and Harpending 1992). We used parametric bootstrapping based on the sum-of-square deviation (SSD) between observed and expected distributions to test the fit of the stepwise-expansion model. In addition, we used a coalescent model in LAMARC 2.1.3 (Kuhner 2006) to calculate the population-growth-rate parameter (g) for mtDNA from each Cinnamon Teal subspecies and the Blue-winged Teal (each population was treated independently). We used Bayesian analyses with 1 million recorded genealogies sampled every 50 steps, with a burn-in of 100 000 (10%) genealogies. Priors were flat with the upper limit for growth set to 15 000.

COALESCENT ANALYSES—GENE FLOW AND TIME OF DIVERGENCE

We used a coalescent model in IM (Hey and Nielsen 2004, Hey 2005) to determine whether patterns of differentiation between species and subspecies were the result of incomplete lineage sorting, gene flow, or a combination of both. We simultaneously estimated the following parameters scaled to the mutation rate: time since divergence between populations (t), immigration rates (m), and effective population sizes of ancestral (θ_A) and contemporary populations (θ_1 and θ_2). In addition, we ran each set of comparisons assuming constant population size and incorporating exponential population growth with the splitting parameter (s). We ran paired two-population analyses for a combined analysis of mtDNA and two nuclear loci, ODC1 and ENO1: (1) within North America (*A. c. septentrionalium* vs. *A. discors*), (2) within South America (*A. c. cyanoptera* vs. *A. c. orinomus*), and (3) between continents (*A. c. cyanoptera* vs. *A. discors* and *A. c. cyanoptera* vs. *A. c. septentrionalium*). We used within-continent comparisons to test hypotheses about patterns of gene flow between partially sympatric taxa. We used comparisons between continents to determine if shared haplotypes and mtDNA paraphyly resulted from incomplete lineage sorting or continuing gene flow and to test for the genetic signature of the direction of colonization (the splitting parameter, s; Hey 2005). The isolation-with-migration model assumes that the two populations being compared are each panmictic and are not exchanging genes with other populations or species (Hey and Nielsen 2004, Won et al. 2005), assumptions likely being violated. However, simulations suggest that IM is fairly robust to violations of those assumptions (Strasburg and Rieseberg 2010). In addition, the species tree for this group is unknown precluding a four-population analysis with IMa2. Thus, paired two-population analyses are the most suitable for analyzing patterns of divergence and gene flow within this species complex.

IM further assumes that loci are selectively neutral with no intralocus recombination. We tested for recombination within each nuclear intron with a four-gamete test in DNAsp version 4.10 (Rozas et al. 2003) and included the largest independently segregating block of sequence consistent with no recombination. ODC1 and ENO1 were truncated to the 5′ end positions 82–327 and 152–312, respectively. We defined inheritance scalars for mtDNA as 0.25 (maternally inherited) and for autosomal introns as 1.0 (biparentally inherited) to reflect differences in effective population sizes. We used the HKY model of mutation for mtDNA and infinite-sites model for the nuclear introns. We initially ran IM by using large, flat priors for each parameter. From the results of these runs, we defined narrower upper bounds for each parameter that encompassed the full posterior distributions from each initial run. However, estimates of current population sizes sometimes contained distinct peaks, but the tails did not approach zero. In those cases, we used priors that contained the peak and the point near where the distribution began flattening. Using those priors, we used a burn-in of 500 000 steps and recorded results every 50 steps for more than 10^6 steps. Effective sample sizes for each parameter exceeded 100. We repeated the analyses three times, using a different random number seed to verify that independent runs converged on the same values. We converted t to real time (t) by $t = t\mu$. We used mutation rates of 4.8×10^{-8} substitutions per site per year (s/s/y) for the mtDNA control region (Peters et al. 2005b), 1.0×10^{-9} s/s/y for ENO1, and 1.2×10^{-9} s/s/y for ODC1 (Peters et al. 2008). For conversions, we used the geometric mean of substitution rates of the three loci.

RESULTS

POPULATION STRUCTURE AND GENETIC DIVERSITY

The 248 Blue-winged Teal and Cinnamon Teal surveyed contained 91 unique haplotypes of the mtDNA control region, comprising 76 variable sites. No fixed differences were observed among subspecies or between species; rather, haplotypes were intermixed in a polyphyletic relationship (Fig. 2).

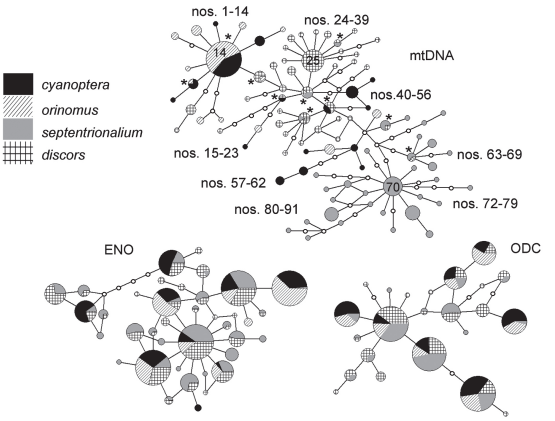

FIGURE 2. Unrooted allelic networks for mtDNA control region and two nuclear introns, ODC1 and ENO1. Sizes of circles are proportional to the frequency of each allele observed. Small white circles indicate putative ancestral alleles not sampled.

Ten haplotypes were shared by species or subspecies, five between *A. c. septentrionalium* and *A. discors* in North America, three between *A. discors* and the South American subspecies of the Cinnamon Teal, and two between the South American subspecies *A. c. cyanoptera* and *A. c. orinomus* (Fig. 2, Appendix 2). *A. c. septentrionalium* did not share any haplotypes with either of the South American subspecies. Overall, the genetic diversity of North American taxa was higher than that of South American taxa (Table 1).

The global Φ_{ST} for mtDNA control region was high, with 41% of the genetic diversity explained by differences among taxa ($\Phi_{ST} = 0.41$, $P < 0.001$). Inter-subspecies Φ_{ST} values ranged from 0.07 to 0.51 (Table 2). The highest Φ_{ST} was between *A. c. septentrionalium* and *A. discors* in North America, the lowest between *A. c. cyanoptera* and *A. c. orinomus* in South America. Variance in mtDNA haplotype frequencies among groups was maximized when samples were grouped by (sub)species ($\Phi_{CT} = 0.43$, $P < 0.001$) rather than geographic proximity ($\Phi_{CT} = 0.12$, $P = 0.14$).

We found 23 ODC1 alleles comprising 20 variable sites and 38 ENO1 alleles comprising 29 variable sites in the autosomal intron sequences. Most alleles were broadly shared among

TABLE 1. Number of haplotypes/alleles per population, observed (H_o) and expected (H_e) heterozygosity, allelic richness (r), and nucleotide diversity (π) for the mtDNA control region, ODC1, and ENO1 of the Blue-winged and Cinnamon Teal.

		mtDNA			ODC1				ENO1			
Population	n	No. haplotypes	r[a]	π	No. alleles	H_o/H_e (%)	r	π	No. alleles	H_o/H_e (%)	r	π
A. discors	76	38	35.0	0.003	19	73.7/72.9	16.2	0.006	28	96.1/91.0	24.2	0.013
A. c. septentrionalium	70	34	32.1	0.004	14	65.2/70.6	12.4	0.005	28	88.6/90.4	25.1	0.013
A. c. cyanoptera	52	16	16.0	0.003	7	80.8/79.4	7.0	0.008	9	76.9/85.6	9.0	0.013
A. c. orinomus	50	13	13.0	0.002	7	74.0/81.2	7.0	0.008	7	74.0/78.4	7.0	0.008

[a]Allelic richness based on smallest sample among subspecies and within subspecies.

TABLE 2. Pairwise Φ_{ST}[a] for mtDNA control region, ODC1, and ENO1 between three Cinnamon Teal subspecies and the Blue-winged Teal. Significant values are marked with an asterisk.

	mtDNA	ODC1	ENO1
discors			
–septentrionalium	0.51*	0.02*	0.00
–cyanoptera	0.25*	0.08*	0.04*
–orinomus	0.40*	0.03*	0.12*
septentrionalium			
–cyanoptera	0.43*	0.06*	0.06*
–orinomus	0.47*	0.04*	0.12*
cyanoptera			
–orinomus	0.07*	0.01	0.09*

[a]Best-fit nucleotide substitution models for mtDNA (HKY + I + G), ODC1 (K80 + I + G), and ENO1 (TVM + I).

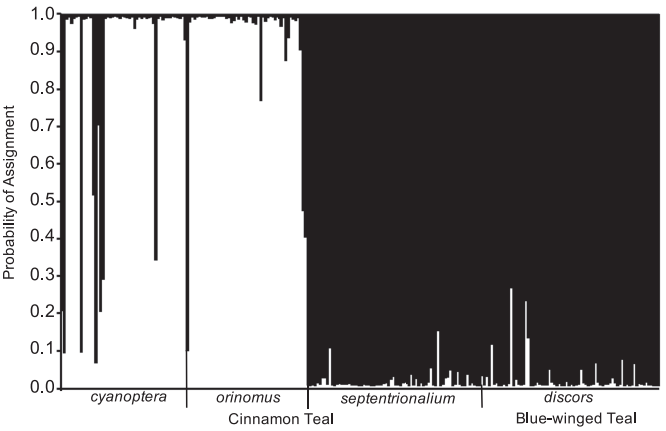

FIGURE 3. Structure 2.2 analysis showing posterior probability of assignment of individuals to each (K = 2) genetic cluster. White bar represents the estimated probability of assignment to cluster one, and black bar is the estimated probability of assignment to cluster two.

all four taxa (Fig. 2). Nucleotide diversity in the introns was consistently higher than in mtDNA, and heterozygosity ranged from 65.2 to 96.1% (Table 1). All taxa were in Hardy–Weinberg equilibrium, and we detected no linkage disequilibrium between ODC1 and ENO1, confirming that these loci are independent. Both introns were significantly structured between most taxa (Φ_{ST} = 0.00–0.12 for ENO1 and 0.00–0.08 for ODC1; Table 2). In contrast to that for mtDNA, the among-group variance for both nuclear introns combined was maximized when taxa were grouped on the basis of geographic proximity (i.e., North America versus South America; Φ_{CT} = 0.05, P = 0.01) rather than by (sub)species (Φ_{CT} = 0.03, P = 0.03), but the differences between the two models were small.

The Bayesian clustering analysis in Structure using mtDNA and both nuclear introns supported a two-population model (Fig. 3). Most specimens of *A. c. cyanoptera* (87%) and *A. c. orinomus* (94%) were assigned to one genetic cluster, whereas all those of *A. c. septentrionalium* and *A. discors* where assigned to a second cluster with high probability (98%). Seven specimens of *A. c. cyanoptera* assigned to the North American cluster with probability >66% were collected at lowland sites in Argentina (JT 011, JT 046, KGM 322, KGM 798, KGM 808) or the Peruvian coast (REW 081, REW 303). Three specimens of *A. c. orinomus* (KGM 441, REW 698, REW 708) were also assigned to the North American cluster with probability >50%. In summary, the majority of individuals were assigned to clusters corresponding to their geographic location in South America (*A. c. cyanoptera* and *A. c. orinomus*) or North America (*A. c. septentrionalium* and *A. discors*).

IM COALESCENT ANALYSES

In general, the population-size parameter (Θ) was larger for North American *A. c. septentrionalium* and *A. discors* (Fig. 4). Within the North American comparison, Θ was similar for *A. discors* and *A. c. septentrionalium* (7.79; 3.59–12.94 and 6.04; 2.75–15.25, respectively). Both population sizes were larger than the ancestral population size (3.31; 2.07–10.83), suggesting population expansions, but posterior distributions broadly overlapped. In the South American comparison, the population-size parameter was larger for *A. c. cyanoptera* (1.22; 0.49–4.67) than for *A. c. orinomus* (0.60; 0.24–2.02). Posterior distributions were smaller than the ancestral size (9.08; 3.23–44.23), suggesting population contractions following divergence.

The most probable estimate for the migration rate (m) between continents was low (0.00–1.35), and confidence intervals broadly overlapped zero in all directions, except into *A. c. septentrionalium* from *A. c. cyanoptera* (95% CI: 0.39–5.70; Fig. 4). Comparing the North American taxa yielded higher migration rates. Although confidence intervals overlapped broadly, the most probable estimates suggested that migration rates into *A. c. septentrionalium* (1.49; 0.39–5.76) were higher than into *A. discors* (0.49; ~0.00–3.34). In the South American comparison, IM suggested low migration into the highlands (0.33; 0.00–42.87), and we could not reject a hypothesis of no gene flow into *A. c. orinomus* from *A. c. cyanoptera*. However, no gene flow was rejected in the opposite direction as the posterior distribution of m into *A. c. cyanoptera* did not overlap with zero (18.05; 7.45–79.05).

TIME SINCE DIVERGENCE

The coalescent analyses suggested that the oldest divergence (t, scaled divergence times) was between *A. c. septentrionalium* and the other taxa, although there was broad overlap among comparisons (Fig. 5). The divergence between *A. c. septentrionalium* and *A. c. cyanoptera* peaked at 0.19 (0.11–0.77), suggesting a divergence of approximately 95 000 ybp (years before present; range 33 000–700 000). Posterior distributions of t for *A. discors* were similar to those for *A. c. septentrionalium* (0.14; 0.09–0.42) and *A. c. cyanoptera* (0.13; 0.07–0.26), which, when converted to years, suggested that *A. discors* diverged around 70 000 ybp (range 27 000–385 000 ybp; within-continent comparison) or 65 000 ybp

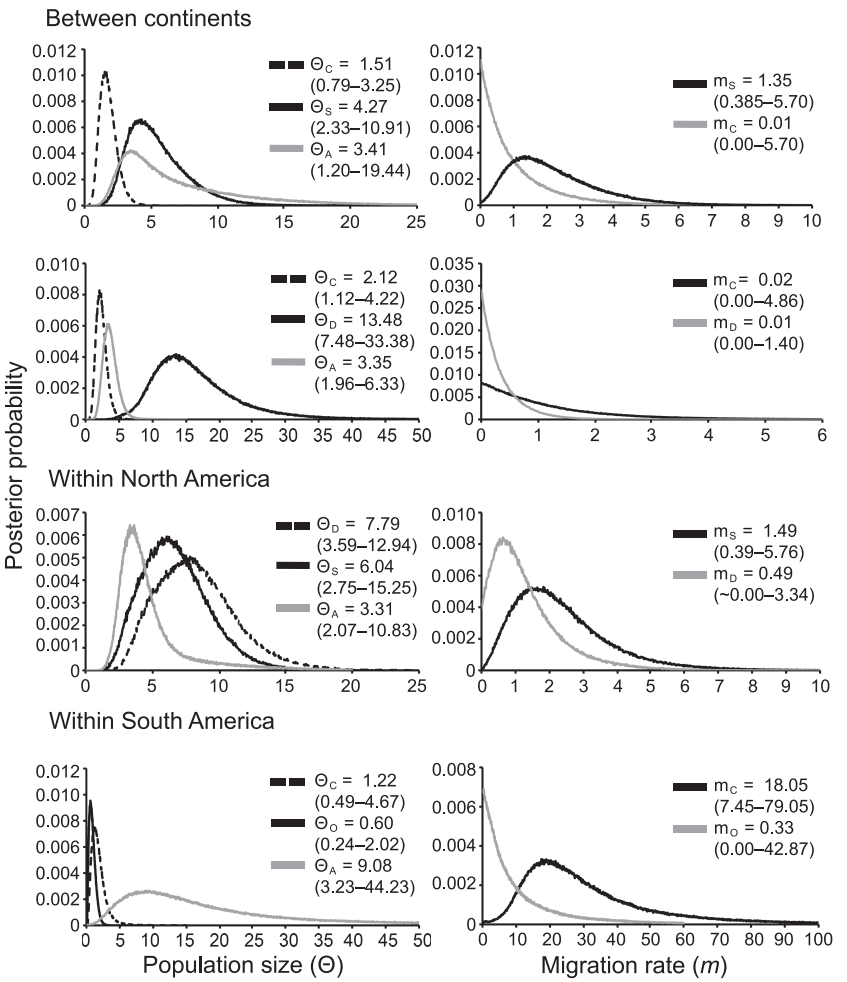

FIGURE 4. Posterior distributions of effective population size, Θ, and immigration rates, *m*, calculated with IM (scaled to the neutral mutation rate, μ). Peak estimates for each parameter are given, and the 95% highest posterior distribution is shown in parentheses. Letters correspond to subspecies of the Cinnamon Teal (C, *A. c. cyanoptera;* S, *A. c. septentrionalium;* O, *A. c. orinomus*), the Blue-winged Teal (D), or the ancestral population for each paired comparison (A).

(range 21 000–238 000 ybp; between-continent comparison). For the South American comparison, peak values spanned *t* of the other comparisons (0.13–0.20) and the tail of the distribution did not approach zero in all replicates; therefore an accurate estimate of divergence times could not be obtained.

Under an exponential-growth model, the posterior distribution of the splitting parameter, *s*, for the South American comparison peaked at 99.5 % (3.1–100%) as the percent of the South American ancestral population that contributed to *A. c. cyanoptera*. For all other comparisons, the distribution of *s* contained not a single peak but rather a plateau, and the highest likelihood appeared to be associated with a range of values indicating an ambiguous colonization.

HISTORICAL DEMOGRAPHY

In agreement with coalescent analyses, North American populations of *A. c. septentrionalium* and *A. discors* showed evidence of recent population expansion, as indicated by a single high-frequency haplotype accompanied by numerous rare mtDNA haplotypes (Fig. 2) and significantly negative values of Fu's F_s and Tajima's *D* (Fig. 6). Furthermore, the mismatch distributions for *A. c. septentrionalium* and *A. discors* were unimodal and fit the expansion model curve

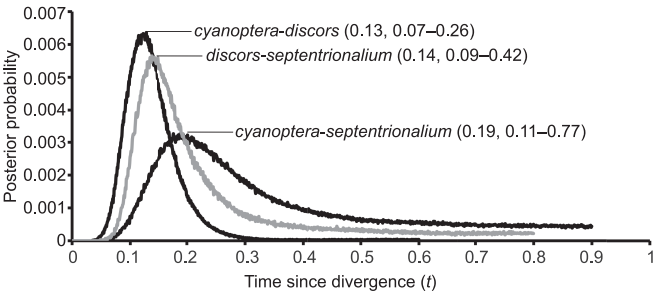

FIGURE 5. Posterior distribution of time since divergence (*t*), calculated in IM.

($P > 0.68$; Fig. 6). Recent population expansion also was supported by the population-growth-rate parameters (g) estimated by LAMARC for mtDNA, as 95% confidence limits did not contain zero.

In contrast, the mtDNA patterns of the South American subspecies (*A. c. cyanoptera* and *A. c. orinomus*) were consistent with long-term population stasis and a lack of clear demographic expansion. Neither Tajima's D nor Fu's F_s were significant for the mtDNA control region. The mismatch distributions were multimodal in shape, but the Harpending's raggedness index was not significant ($P > 0.66$). However LAMARC's estimate of the 95% confidence interval for population growth overlapped zero; the data were consistent with a stable population size (Fig. 6).

DISCUSSION

GENETIC STRUCTURE AMONG BLUE-WINGED TEAL AND CINNAMON TEAL

The male plumages of the Blue-winged and Cinnamon Teal differ markedly, whereas the subspecies of the Cinnamon Teal differ considerably in body size but only subtly in plumage (Snyder and Lumsden 1951, Wilson et al. 2008, 2010). Despite this phenotypic discord, previous studies based on more conservative regions of mtDNA found little or no genetic differentiation between these two species (Kessler and Avise 1984, Johnson and Sorenson 1999, Kerr et al. 2007), suggesting a recent divergence or high gene flow. In accord with these studies, we observed low genetic distances (0.3–0.6%) and no fixed differences between the species or among the subspecies. However, there were strong differences in haplotype frequencies in mtDNA ($\Phi_{ST} = 0.41$), similar to the differentiation observed among other subspecies and populations of waterfowl (McCracken et al. 2001, Peters et al. 2005b, Sonsthagen et al. 2011). Likewise, we found significant differentiation in nuclear introns (albeit lower levels, $\Phi_{ST} = 0.04–0.06$) that was similar to levels found between allopatric populations of other *Anas* ducks (Peters et al. 2008). Coalescent analyses of mtDNA and nuclear introns suggested that Blue-winged Teal have been diverging from South American Cinnamon Teal for at least 21 000 years and from North American Cinnamon Teal for at least 27 000 years (Fig. 5); therefore, it is unlikely that selectively neutral nuclear markers have had enough time to sort because of their coalescence time in association with a larger effective population size is longer than for mtDNA (Avise 2004, Zink and Barrowclough 2008).

Despite the lack of distinct mtDNA phylogroups indicating long-term isolation, the taxa shared few haplotypes. Furthermore, shared haplotypes were confined mostly to central or centrally connected positions within the network, suggesting the Blue-winged and Cinnamon Teal are at an

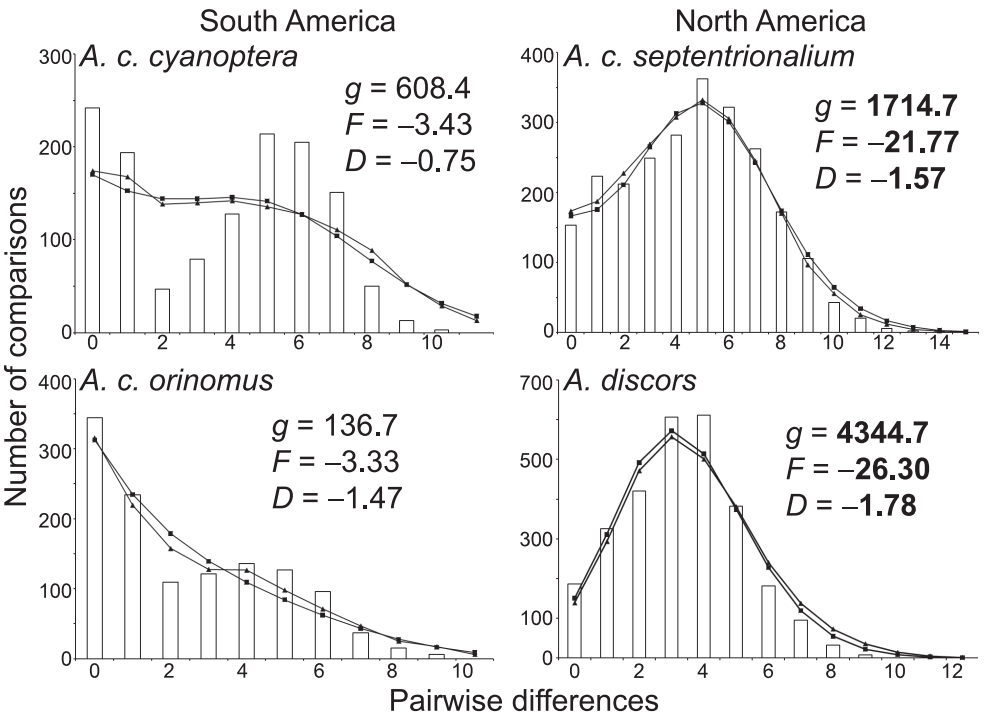

FIGURE 6. Results of mismatch distribution and population demographic parameters for North American and South American subspecies of the Cinnamon Teal (*Anas cyanoptera*) and Blue-winged Teal (*A. discors*). Bars represent the frequency of pairwise differences. The line with triangle depicts the theoretical distribution under a model of sudden expansion, whereas the line with square depicts the distribution under a model of spatial expansion. Significant P values for Fu's F_s (F, $P < 0.02$), Tajima's D (D, $P < 0.05$), and the population growth parameter (g) that did not overlap with zero are in bold type.

intermediate stage of divergence. These species appear to be approaching local fixation of haplotypes, leading to the eventual loss of ancestral haplotypes as taxa move towards reciprocal monophyly (Omland et al. 2006). The pattern within the nuclear network is similar, as alleles shared between continents tended to be at central positions, whereas more derived alleles tended to be taxon specific or shared within a continent. Limited sharing of alleles and haplotypes between continents suggests long-term genetic isolation between Northern Hemisphere and Southern Hemisphere taxa following divergence. Genetic isolation is also supported by the transcontinental migration rates peaking at or broadly overlapping zero, which is consistent with no gene flow between continents, except into North American *A. c. septentrionalium* from South American *A. c. cyanoptera*. The transcontinental gene flow might represent an ancient migration into North America, as current gene flow between *A. c. cyanoptera* and *A. c. septentrionalium* is unlikely because of completely segregated distributions (Evarts 2005, Camacho and Wilson 2011). However, large numbers of wintering Blue-winged Teal occur in sympatry with South American Cinnamon Teal as far south as Peru (Botero and Rusch 1988). Restricted gene flow between the continents could most likely be due to differences in the timing of the breeding cycle during periods of sympatry (Rohwer et al. 2002), indicated by the fact the three male Blue-winged Teal collected in Peru were not in breeding condition (left testis of nonbreeding individuals averaged 11 × 4 mm, that of breeding individuals 25 × 11 mm). Thus, the occurrence of mixed (sub) species pairs is probably rare and localized. Therefore, sharing of mtDNA haplotypes and nuclear alleles observed among species and subspecies from different hemispheres is more attributable to incomplete lineage sorting than to gene flow.

ORIGIN OF BLUE-WINGED TEAL AND CINNAMON TEAL

The geographic origin of many groups of dabbling ducks is difficult to determine because of their high dispersal ability. However, Johnson and Sorenson (1999) reported a general trend of Southern Hemisphere origin with multiple colonizations of the Northern Hemisphere. Cinnamon Teal appear to conform to this trend, suggested by the asymmetrical gene flow we found from South American Cinnamon Teal into North America. North American taxa are characterized by large effective population sizes that recently expanded, whereas South American subspecies have smaller effective population sizes that have not recently expanded. This contrast in demographic history could be explained by one or more colonizations of North America from South America followed by a population expansion in North America. However, recent population expansions are common among Northern Hemisphere birds (Zink 1997, Avise 2000) and are often interpreted as a postglacial expansion from Late Wisconsin refugia (see Lessa et al. 2003). Although the splitting parameter showed an ambiguous divergence between continents, population expansions in North America combined with asymmetrical gene flow into North America from South America support a South American origin for the Cinnamon Teal and Blue-winged Teal species complex.

Geographic isolation between North America and South America appears to have been a strong barrier to gene flow within these species after the initial colonization. In addition, east–west genetic differentiation is found among many widespread migratory birds in temperate North America (Milot et al. 2000, Kimura et al. 2002, Ruegg and Smith 2002, Newton 2003, Lovette et al. 2004, Peters et al. 2005b) and suggests two major glacial refugia on either side of the Rocky Mountains or Great Plains during the Pleistocene (Colbeck et al. 2008). Thus, North American Cinnamon Teal and Blue-winged Teal might descend from a common ancestor that colonized North America from South America, then diverged in allopatry on either side of the Rocky Mountains. Consistent with that hypothesis, the nuclear introns supported a greater similarity between pairs within continents than between continents, and the strong mtDNA divergence suggests at least two refugia.

Alternatively, there might have been multiple dispersals of a South American ancestor, independently giving rise to Blue-winged Teal and North American Cinnamon Teal. Multiple scenarios for colonization of North America have been proposed for several groups of species (Temple 1972, Weir et al. 2009), and this hypothesis might explain the closer mtDNA relationship of Blue-winged Teal to South American Cinnamon Teal (see also Johnson and Sorenson 1999). Furthermore, IM results suggested that *A. c. septentrionalium* is the most divergent lineage. Additional evidence of a closer affinity between Blue-winged Teal and South American Cinnamon Teal can be found in plumage patterns. Although in the Blue-winged Teal the male's breeding plumage is distinctive, the spotted body feathers bear a striking resemblance to an "archaeo-adult" spotted breeding plumage (first nuptial plumage) seen frequently in young male South American Cinnamon Teal (Snyder and Lumsden 1951) but absent in North American Cinnamon Teal. A closer relationship between the Blue-winged Teal and South American Cinnamon Teal suggests two independent colonizations of North America: one ~95 000 ybp giving rise to *A. c. septentrionalium* in western North America and another ~65 000 ybp giving rise to the Blue-winged Teal in central and eastern North America, followed by subsequent gene flow between two independently diverged populations. Regardless, additional loci are needed to test the single-colonization versus the dual-colonization hypothesis as confidence intervals for divergence times overlapped considerably.

WITHIN-CONTINENT DIVERGENCE

Within North America, at least two areas acted as temperate glacial refugia during the Pleistocene and were often separated by the Great Plains or Rocky Mountains (Gorman 2000, Milot et al. 2000, Ruegg and Smith 2002, Newton 2003, Shafer

et al. 2010). Concordance in phylogenetic breaks between closely related species identify suture zones clustered around mountain ranges, which have been proposed as barriers to gene flow during glacial and interglacial periods (Swenson and Howard 2004, 2005). The strong mtDNA divergence of the Cinnamon and Blue-winged Teal corresponds to an east–west divide. Concordant with the westward expansion of the Blue-winged Teal since the 1930s (Wheeler 1965, Connelly 1978), we observed a higher rate of migration into the Cinnamon Teal (~9 migrants per generation) than into the Blue-winged Teal (~4 migrants per generation), although confidence intervals overlapped broadly and symmetrical gene flow could not be rejected. Blue-winged Teal often occur with Cinnamon Teal (Connelly and Ball 1984), with mixed populations disproportionally represented by Cinnamon Teal (Bellrose 1980). Despite the species' being similar ecologically and behaviorally, hybridization is infrequent (Spencer 1953). Both males and females differ in plumage colors and vocalizations that are used in courtship as well as other social behaviors. These differences may serve as mate-recognition cues on shared wintering grounds where pairing occurs, thus decreasing hybridization.

In South America, the Andes impose not only a physical barrier but also extreme environmental selection associated with high elevation, and this likely restricts gene flow between populations resident at low and high elevations (Milá et al. 2009, McCracken et al. 2009a). Colonization within South America appears to have been from the lowlands to the highlands, conforming to the general trend observed in other Andean avifauna (Fjeldså 1985, Vuilleumier 1986, McCracken et al. 2009a). The cold, hypoxic conditions prevalent at high elevation likely require a physiological mechanism to deal with such environmental stressors, leading to both phenotypic and genetic differences in high-elevation populations of the Cinnamon Teal as well as other Andean waterfowl (Bulgarella et al. 2007, McCracken et al. 2009a, b, Wilson et al. 2010). Traits evolved in response to local adaptation could restrict dispersal from lowlands to highlands and vice versa (McCracken et al. 2009a, b). However, traits that are beneficial at high elevation (e.g., hemoglobin with high oxygen affinity) are well tolerated in the lowlands (Monge and León-Velarde 1991, León-Velarde et al. 1993, 1996), and our estimates of gene flow support asymmetrical gene flow into the lowlands from the highlands. We encountered and collected *A. c. cyanoptera* at the northern and southern limits of the Altiplano, which is outside the typical breeding distribution of *A. c. orinomus*, but not elsewhere in the Andes. Such sympatry could result in the intermixing of *A. c. cyanoptera* and *A. c. orinomus*. However, there is no direct evidence of *A. c. cyanoptera* breeding at high elevations (>3500 m), and there are no records of *A. c. orinomus* in the lowlands.

IM ASSUMPTIONS

Isolation-with-migration makes a number of assumptions (Hey and Nielsen 2004, Hey 2005), and many of these are violated to some extent in most systems (see Hey 2005, Peters et al. 2008), including within the Cinnamon Teal and Blue-winged Teal complex. Violating these assumptions could affect inferences from population-history parameters (Becquet and Przeworkski 2009). For example, IM assumes that the two populations being compared are panmictic and not exchanging genes with other populations. In particular, gene flow from a third species can cause divergence times to be overestimated and can result in spurious inferences of asymmetrical gene flow (Strasburg and Rieseberg 2010). These biases might be particularly important in pairwise comparisons of North and South American taxa, because the comparisons do not account for gene flow within continents. An alternative approach would be to use a four-population model in IMa2; however, that approach requires a priori information about the order of divergences, which is not known for these taxa. In addition, more independent loci will be required for parameters to be estimated under this more complex model. Despite these limitations, IM is generally fairly robust to small to moderate violations of those assumptions, so broad aspects of our pairwise comparisons are likely informative.

CONCLUSIONS

The Cinnamon and Blue-winged Teal are closely related species that differ substantially in plumage, and the Cinnamon Teal consists of morphologically distinct subspecies. We found strong differentiation in haplotype frequencies and little haplotype sharing between the species and among Cinnamon Teal subspecies. North American and South American Cinnamon Teal have limited contact, while Blue-winged Teal winter in partial sympatry with South American Cinnamon Teal. This limited overlap in breeding and/or winter distributions along with timing of breeding has likely restricted gene flow between the populations of the two continents following divergence. Although divergence times overlapped broadly, this result is expected in species complexes that have diverged rapidly, which is likely the case here. Where the Cinnamon and Blue-winged Teal are parapatric or partially sympatric within a continent, environmental selection associated with high altitude (South America) and sexual selection (North America) may have played a major role in their diversification.

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APPENDIX 1. Localities of specimens of *Anas cyanoptera* and *A. discors*. KGM, JT, and REW specimens are cataloged at the University of Alaska Museum.

A. c. septentrionalium

USA: Utah, Weber Co., 41° 14′ 59.7″ N, 112° 07′ 55.8″ W, 1275 m
REW 075

USA: Utah, Salt Lake Co., 40° 50′ 50.7″ N, 112° 01′ 50.9″ W, 1275 m
REW 077, 078, 079

USA: Oregon, Columbia Co., 45° 45′ 18.1″ N, 122° 50′ 51.4″ W, 1 m
REW 797, 398, 399, 400, 401, 402, 403, 404, 406

USA: California, Imperial Co., 33° 11′ 24.0″ N, 115° 35′ 18.5″ W, –68 m
REW 411, 412, 414, 416, 418, 419, 421

USA: California, Imperial Co., 33° 11′ 39.0″ N, 115° 34′ 46.2″ W, –73 m
REW 415, 420

USA: California, Kern Co., 34° 47′ 43.5″ N, 118° 07′ 11.3″ W, 693 m
REW 422, 423, 424, 425, 426, 427, 428, 429, 430, 431, 432, 433, 434, 435, 436, 437

(*continued*)

APPENDIX 1. Continued.

USA: Utah, Salt Lake Co., 40° 50′ 45.1″ N, 112° 01′ 41.7″ W, 1275 m
REW 438, 439, 440, 441, 442, 443, 444, 445, 446, 447, 448, 449, 450, 451, 452, 453, 454, 455, 456

USA: Colorado, Moffat Co., 40° 59′ 10.7″ N, 108° 59′ 10.5″ W, 1609 m
REW 457, 458

USA: Oregon, Harney Co., 48° 43′ 53.7″ N, 118° 50′ 25.3″ W, 1260 m
REW 459, 460, 461, 462, 463, 464, 465, 466, 467

A. c. cyanoptera

Argentina: Neuquen, Rio Collon Cura, R.N. 40, 40° 12′ 45″ S, 70° 38′ 58″ W, 625 m[a]
KGM 268

Argentina: Cordoba, Laguna La Felipa, 33° 04′ 17″ S, 63° 31′ 33″ W, 184 m[a]
KGM 310, 313, 311, 312

Argentina: Cordoba, S. Canals, 33° 36′ 23″ S, 62° 53′ 16″ W, 112 m[a]
KGM 322

Argentina: Jujuy, S. Purmamarca, 23° 49′ 13″ S, 65° 28′ 34″ W, 2141 m

(*continued*)

APPENDIX 1. Continued.

KGM 442
Peru: Dpto. Lima, S Huacho, 11° 10′ 12.9″ S, 77° 35′ 31.4″ W, 15 m
REW 081, 082
Peru: Dpto. Junín, Jauja, Laguna de Paca, 11° 44′ 14.5″ S, 75° 29′ 32.7″ W, 3506 m
REW 118, 122
Peru: Dpto. Ancash, Laguna Conococha, 10° 07′ 10.8″ S, 77° 17′ 00.7″ W, 4039 m
REW 164
Peru: Dpto. Lambayeque, ca. Puerto Eten, 06° 54′ 51.9″ S, 79° 52′ 22.4″ W, 13 m
REW 193, 194, 195, 196
Peru: Dpto. Lambayeque, Playa Monsefu, 06° 54′ 03.7″ S, 79° 53′ 42.4″ W, 12 m
REW 198, 199
Peru: Dpto. La Libertad, Magdalena de Cao, 07° 51′ 54.3″ S, 79° 20′ 51.2″ W, 23 m
REW 200
Peru: Dpto. Ancash, Chimbote, 09° 07′ 26.0″ S, 78° 33′ 11.3″ W, 15 m
REW 203, 204, 205
Peru: Dpto. Ancash, Puerto Huarmey, 10° 05′ 52.0″ S, 78° 09′ 10.3″ W, 14 m
REW 206
Peru: Dpto. Lima, Albufera de Medio Mundo, 10° 55′ 25.9″ S, 77° 40′ 10.8″ W, 14 m
REW 207
Peru: Dpto. Ica, Pisco, 13° 41′ 46.8″ S, 76° 13′ 07.3″ W, 7 m
REW 235
Peru: Dpto. Ica, Pisco, 13° 40′ 47.2″ S, 76° 12′ 56.6″ W, 9 m
REW 236
Peru: Dpto. Tacna, Ite, 17° 52′ 47.2″ S, 71° 01′ 05.9″ W, 10 m
REW 298, 299, 300, 301, 302, 303, 304
Peru: Dpto. Arequipa, Punta de Bombon-Islay, 17° 11′ 31.9″ S, 71° 46′ 19.4″ W, 8 m
REW 305, 306
Peru: Dpto. Lima, 2 km N. La Laguna, 12° 33′ 13.0″ S, 76° 42′ 42.1″ W, 9 m
REW 315, 316, 317
Argentina: Chubut, Laguna Terraplen, 42° 59′ 50.7″ S, 71° 30′ 55.1″ W, 630 m
KGM 712, 713
Argentina: Santa Cruz, Estancia La Angostura, 48° 38′ 33.9″ S, 70° 38′ 37.3″ W, 460 m
KGM 766, 767
Argentina: Santa Cruz, ca. Punta Loyola, 51° 37′ 35.7″ S, 69° 00′ 59.4″ W, –3 m
KGM 797, 798
Argentina: Santa Cruz, ca. Punta Loyola, 51° 36′ 54.9″ S, 68° 59′ 26.6″ W, 0 m
KGM 799
Argentina: Chubut, S. Lago Colhue Huapi, 45° 38′ 49.6″ S, 68° 56′ 45.1″ W, 256 m
KGM 808
Argentina: Catamarca, Antofogasta de la Sierra, Laguna La Alumbrera, 26° 06′ 46.4″ S 67° 25′ 26.7″ W, 3338 m
KGM 1110

(*continued*)

APPENDIX 1. Continued.

Argentina: Catamarca, Embalse Las Cortaderas, 27° 33′ 21.2″ S, 68° 08′ 41.9″, 3369 m
KGM 1142
Argentina: Buenos Aires, 34° 52′ 27″ S, 61° 23′ 19.2″, 86 m
JT 011
Argentina: Buenos Aires, 34° 53′ 15″ S, 61° 21′ 51″, 86 m
JT 046, 047
A. c. orinomus
Argentina: Salta, NE La Caldera, 24° 33′ 01″ S, 65° 22′ 15″ W, 1468 m
KGM 441
Bolivia: Dpto. La Paz, Lago Titicaca, 16° 11′ 45″ S, 68° 37′ 28″ W, 3808 m
KGM 485, 486, 487
Bolivia: Dpto. La Paz, Lago Titicaca, 16° 20′ 13″ S, 68° 41′ 20″ W, 3854 m
KGM 499
Bolivia: Dpto. Oruro, Lago Uru Uru, 18° 02′ 03″ S, 67° 08′ 46″ W, 3735 m
KGM 527, 528, 529, 530, 531, 532, 533, 534, 535
Bolivia: Dpto. La Paz, Lago Titicaca, 16° 25′ 28″ S, 68° 51′ 43″ W, 3850 m
KGM 557
Bolivia: Dpto. La Paz, Lago Titicaca, Cohani, 16° 21′ 03″ S, 68° 37′ 40″ W, 3839 m
KGM 559, 560
Bolivia: Dpto. La Paz, Lago Titicaca, Cohani, 16° 21′ 02″ S, 68° 37′ 48″ W, 3840 m
KGM 561, 562
Bolivia: Dpto. La Paz, Lago Titicaca, Cohani, 16° 21′ 07″ S, 68° 38′ 06″ W, 3845 m
KGM 563, 564, 565, 566
Peru: Dpto. Junin, Jauja, Laguna de Paca, 11° 44′ 14.5″ S, 75° 29′ 32.7″ W, 3506 m
REW 125, 126
Peru: Dpto. Cusco, Laguna Chacan, 13° 26′ 02.6″ S, 72° 07′ 49.6″ W, 3533 m
REW 238, 239, 240, 241, 242
Peru: Dpto. Cusco, ca. Chinchero, 13° 25′ 49.3″ S, 72° 03′ 41.7″ W, 3789 m
REW 248
Peru: Dpto. Cusco, Urubamba Valley, 13° 25′ 22.9″ S, 72° 02′ 38.2″ W, 3743 m
REW 253, 254
Peru: Dpto. Cusco, ca. Laguna Pomacanchi, 14° 06′ 51.9″ S, 71° 27′ 56.6″ W, 3781 m
REW 255, 256, 257, 258, 259
Peru: Dpto. Puno, Lago Titicaca, Jaru Jaru, 15° 59′ 05.6″ S, 69° 36′ 24.3″ W, 3,824 m
REW 268, 269
Peru: Dpto. Puno, Lago Titicaca, ca. Puno, 15° 52′ 01.2″ S, 69° 56′ 21.3″ W, 3,830 m
REW 271
Peru: Dpto. Puno, Lago Umayo, Sillvstani, 15° 42′ 45.8″ S, 70° 09′ 00.0″ W, 3,853 m
REW 272
Peru: Dpto. Puno, Deustva, 15° 33′ 50.0″ S, 70° 14′ 33.1″ W, 3,871 m

(*continued*)

APPENDIX 1. Continued.

REW 284, 285, 286
A. discors
USA: South Dakota, Day Co.
REW 001, 002, 003, 004, 005, 006, 007, 008, 009, 010, 011, 013, 014, 015
USA: South Dakota, Kingsbury Co.
REW 021, 022, 023, 028, 029, 032, 033, 034, 035, 036, 037
USA: North Dakota, Kidder Co.
REW 038, 039, 040, 041, 042, 043, 044, 045, 046, 047, 048, 049, 050, 052, 053, 054, 056, 061, 062, 063, 065, 066, 067, 068
USA: Oregon, Columbia Co., 45° 45′ 18.1″ N, 122° 50′ 51.4″ W, 1 m
REW 405

(*continued*)

APPENDIX 1. Continued.

Peru: Dpto. Junin, Jauja, Laguna de Paca, 11° 44′ 14.5″ S, 75° 29′ 32.7″ W, 3506 m
REW 121, 124
Peru: Dpto. Ancash, Laguna Conococha, 10° 07′ 10.8″ S, 77° 17′ 00.7″ W, 4039 m
REW 163
Guyana
ANSP 8442
Colombia
F(23), M(16)1–M(16)4, M(19)1–M(19)3, M(24)1–M(24)8, M(9)1–M(9)6

[a]These elevation values are interpolated from the U.S. Geological Survey's GTOPO30 (http://eros.usgs.gov); all other elevations were measured with a GPS receiver.

APPENDIX 2. Geographic areas, sampling sites, number of each mtDNA control region haplotype observed, and total sample size per area included in the present study.

Geographic area	Sampling site	Haplotypes observed (count)	*n*
A. c. cyanoptera			
Peru	coastal regions	12 (4), 14 (15), 40 (3), 41 (1), 43 (1), 61 (3), 62 (2)	29
Peru	Andes (highland)	14 (2), 40 (1)	3
Argentina	Catamarca (highland)	8 (2)	2
Argentina	Jujuy (highland)	42 (1)	1
Argentina	Patagonia	3(1), 8 (1), 9 (1), 14 (1), 23 (1), 57 (2), 59 (1), 62 (1)	9
Argentina	Córdoba and Buenos Aires	14 (3), 20 (1), 40 (2), 43 (1), 60 (1)	8
A. c. orinomus			
Peru	Altiplano and puna region	2 (1), 4 (2), 7 (1), 8 (1), 14 (12), 15 (1), 22 (1), 54 (2), 58 (2)	23
Bolivia	Altiplano	1 (2), 2 (3), 5 (2), 6 (1), 13 (1), 14 (13), 22 (1), 54 (1), 58 (2)	26
Argentina	Salta	14 (1)	1
A. c. septentrionalium			
Utah	Salt Lake Co.	19 (1), 56 (1), 63 (1), 65 (1), 67 (1), 69 (2), 70(7), 71 (1), 75 (1), 76 (1), 78 (1), 79 (1), 83 (1), 86 (1), 87 (4)	25
Colorado	Moffat Co.	77 (1), 94 (1)	2
Oregon	Columbia Co. and Harney Co.	32 (1), 55 (2), 65 (1), 66 (1), 69 (1), 70 (1), 72 (1), 73 (1), 77 (4), 78 (1), 81 (1), 89 (1), 90 (1), 91 (1)	18
California	Imperial Co. and Kerns Co.	19 (1), 44 (1), 55 (1), 64 (1), 67 (2), 68 (1), 70 (6), 74 (1), 77 (3), 80 (1), 82 (1), 83 (1), 85 (1), 87 (3), 88 (1)	25
A. discors			
North Dakota	Kidder Co.	10 (2), 15 (1), 18 (1), 19 (2), 24 (1), 25 (8), 28 (1), 29 (1), 34 (1), 43 (1), 44 (1), 46 (1), 47 (1), 51 (1), 55 (1)	24
South Dakota	Day Co. and Kingsbury Co.	10 (2), 11 (1), 17 (2), 24 (1), 25 (5), 30 (1), 31 (1), 32 (1), 37 (1), 38 (1), 39 (1), 43 (1), 44 (1), 45 (1), 49 (1), 50 (2), 52 (1), 53 (1)	25
Oregon	Columbia Co.	25 (1)	1
Colombia	Barranquilla	15 (3), 16 (2), 19 (1), 20 (1), 21 (1), 24 (1), 25 (3), 26 (1), 27 (1), 28 (1), 31 (1), 33 (1), 36 (1), 43 (1), 44 (1), 48 (1), 65 (1)	22
Guyana		35 (1)	1
Peru	Andes (highland)	25 (1), 44 (1), 46 (1)	3