Plumage and body size differentiation in Blue-winged teal and Cinnamon teal

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ABSTRACT

Blue-winged Teal (*Anas discors*) and Cinnamon Teal (*A. cyanoptera septentrionalium*) are two closely related North American dabbling duck species that are ecological equivalents. Cinnamon Teal are primarily restricted to regions west of the Great Plains, whereas Blue-winged Teal occur primarily in the central and eastern part of the continent, only recently expanding westward. Males of the two species exhibit striking plumage color differences, while females are difficult to differentiate by plumage, and it is unclear if interspecific size differences exist between either sex due to inconsistencies in previous reports. Here we reassess body size differences, and quantify plumage color differences using avian color discrimination modeling. Like previous studies, significant differences were found for bill morphology; mean bill length was 7–10% longer in Cinnamon Teal. Based on avian visual modeling of plumage reflectance data, color differences not visible to human vision were found between species for several female feather patches (e.g. breast coloration) and male wing speculum coloration, potentially representing previously unrecognized interspecific signals to the avian visual system. Although color reflectance data yielded higher accuracy than morphometrics for identifying females, body size measurements (in addition to plumage to a lesser degree) also proved to be reliable in correctly classifying males of each species. In combination, morphometrics and plumage reflectance data represent useful identification tools for avian species that are otherwise difficult to distinguish.

Keywords: *plumage divergence, morphology, Cinnamon Teal, Blue-winged Teal, species identification*

1. INTRODUCTION

Blue-winged Teal (*Anas discors*) and Cinnamon Teal (*A. cyanoptera*) are widespread waterfowl species in the Western Hemisphere. Similarities in courtship displays (McKinney, 1970) and ecological requirements (Connelly and Ball, 1984) as well as low genetic distances and lack of distinct mitochondrial DNA (mtDNA) phylogroups have led researchers to hypothesize that the two species have diverged recently (Kessler and Avise, 1984; Johnson and Sorenson, 1999; Kerr *et al.*, 2007; Wilson *et al.*, 2011). Cinnamon Teal are composed of five subspecies ranging throughout the Americas. The North American subspecies (*A. c. septentrionalium*) breeds west of the Great Plains and into central Mexico (Gammonley, 1996; Evarts, 2005). The Blue-winged Teal is monotypic and breeds primarily in the north-central United States and Prairie Provinces of Canada (Rohwer *et al.*, 2002). Within the last 75 years, Blue-winged Teal have expanded their breeding range west of the Great Plains, where they were not known to occur prior to 1860 (Wheeler, 1965; Connelley Jr, 1978). Both species can now be observed on the same ponds at many locations throughout western North America, and some hybridization occurs in areas of sympatry (Harris and Wheeler, 1965; Bolen, 1978; Lokemoen and Sharp, 1981). Although secondary contact on the breeding grounds has occurred only recently in their evolutionary history, Cinnamon Teal and Blue-winged Teal co-occur on wintering areas. Like most migratory waterfowl, Cinnamon Teal and Blue-winged Teal form pair bonds on the wintering grounds; therefore a mechanism has likely been in place for individuals to differentiate between members of each species (McKinney, 1992).

Blue-winged Teal and Cinnamon Teal exhibit pronounced variation in male breeding body coloration, but reportedly show little variation in body size, or in plumage among non-breeding males, females, and juveniles. Cinnamon Teal males are reddish brown throughout, and Blue-winged Teal males have a characteristic steel blue neck and head with a white facial crescent. Some differences regarding the overall tone of female coloration have been suggested with Cinnamon Teal females described as more reddish brown (Wallace and Ogilvie, 1977), however such a subtle distinction would likely require observing the two species side by side with a reference specimen. Palmer (1976) furthermore noted that female plumages are quite variable among individuals within each species, thus suggesting

overall color tone may not be a reliable indicator of species identification. As in plumage characters, females of these two species can be difficult to tell apart based solely on body size measurements. Previous reports have suggested that culmen length and other bill length measures are potential discriminating characters, as it has been noted that Cinnamon Teal bills are slightly longer and of a more spatula shape than Blue-winged Teal with no overlap in measurements (Spencer, 1953; Stark, 1979). However, Johnsgard (1975) reported that there is overlap in bill measurements, and, thus, bill characteristics may not be adequate to correctly identify species.

Due to the inconsistencies across studies, we reassess body size variation between Blue-winged Teal and North American Cinnamon Teal and report novel plumage coloration differences based on spectral reflectance data. Objective measurements of color using reflectance spectrophotometry are necessary, given that birds see plumage colors differently than humans (Cuthill *et al.*, 2000; Vorobyev, 2003; Bennett and Thery, 2007; Hart and Hunt, 2007), including sensitivity to UV reflectance, which is a prevalent aspect of avian plumage (Eaton and Lanyon, 2003). Furthermore, human visual assessment and interpretations of feather coloration might be inadequate, given that models of avian color discrimination suggest human vision often does not see plumage color differences that potentially are visible to birds (Vorobyev *et al.*, 1998; Eaton, 2005; Hastad *et al.*, 2005; Benites *et al.*, 2007). Hence, we tested for plumage color differences between Blue-winged Teal and Cinnamon Teal from the visual perspective of the birds, for six color patches on males and eight color patches on females. Our main goal with respect to body size data was to rigorously reassess morphometric variation among these two species, using recently collected and measured specimens to avoid biases due to specimen shrinkage (Winker 1993, 1996; Wilson and McCracken, 2008). Overall, our results represent a more thorough quantification of plumage and morphological differences between Blue-winged Teal and Cinnamon Teal, and offer diagnosable characters for species identification.

2. METHODS

2.1 Morphometrics

Body measurements were taken from adult Cinnamon Teal (10 females, 50 males) from California, Colorado, Oregon, and Utah, and adult Blue-winged Teal (13 females, 34 males) from North Dakota, Oregon, and South Dakota, USA (2002–2003) that were part of a larger genetics study (Appendix 1; Wilson *et al.* 2011). We took nine body-size measurements from each bird: wing chord length (carpal joint to longest primary feather unflattened, ± 1 mm), tail length (base of the uropygial gland on back to tip of the center tail feather, ± 1 mm),

exposed culmen length, bill length at nares (anterior edge of nares to tip of nail), tarsus bone length (tarsometatarsus), bill height (height of upper mandible at anterior edge of nares), bill width (width of upper mandible at anterior edge of nares) (all ± 0.1 mm), and body mass (± 5 g). Measurements were taken the same day individuals were collected prior to preparation as museum specimens. Body mass was not used for comparisons as individuals were in different reproductive states, which influenced body mass differences (*e.g.* some females were in the laying stage but others were not).

Statistical analyses were performed with Statistica 9.1 Software (StatSoft, 2010). All traits were tested for normality with Kolmogorov-Smirnov tests and were normally distributed ($Ps > 0.05$). A multivariate analysis of variance (MANOVA) was performed to evaluate overall differences between species. Analysis of variance (ANOVA) and pairwise comparisons for each individual measurement were performed using a general linear model with Bonferroni correction for multiple comparisons. We tested the diagnosability of species using the method of Patten and Unitt (2002), which focuses on the extent of overlap rather than detecting mean differences. Diagnosability of species was tested for each measurement separately at the 75% level to determine if at least 75% of the distribution of data points for one species lies outside the distribution of the other species. An index value (D_{ij}) ≥ 0 indicates that species *i* is diagnosable from species *j*. Reciprocal tests were performed to determine whether species *i* is diagnosable from species *j* and species *j* is diagnosable from species *i*.

We also performed a forward step-wise general discriminant analysis to evaluate whether the Cinnamon Teal and Blue-winged Teal could be accurately identified using a subset of morphometric variables. The reliability of the discriminant analysis was assessed using a cross-validation procedure. Cross-validation samples give a less biased error rate in classification, because it does not include observations that are used to create the classification function. The cross-validation sample consisted of ten individuals from each species for males, and two females due to the lower sample size.

2.2 Colorimetric plumage measurements

To evaluate potential plumage color differences between Blue-winged Teal (eight females, 10 males) and Cinnamon Teal (12 females, 12 males), we collected reflectance data using an Ocean Optics S2000 fiber optic spectrophotometer following methods described in Wilson *et al.* (2008). Plumage color data were not collected concurrent with collection of morphometric data from freshly collected specimens. At the time plumage data were collected, round study skins were not available for most of these particular individuals, and thus, plumage measurements were taken from round

study skins housed at the University of Alaska Museum (12 Cinnamon Teal males), Smithsonian Institution National Museum of Natural History (10 Blue-winged Teal males), and the Field Museum of Natural History (all female specimens). In addition, we were able to measure, and include data from, 43 Blue-winged Teal males (33 used in morphometric data) and 17 Cinnamon Teal males (all used in morphometric data) for all wing-patch measurements (Appendix 1).

Plumage spectral properties of museum skins may change over time due to fading (Endler and Théry, 1996; Hausmann *et al.*, 2003), thus potentially not representing accurately the color of living birds. However, it has been shown that specimens collected within the last 50 years change little in color (Armenta *et al.*, 2008), and even studies including very old specimens do not report effects of specimen age on plumage color (Benites *et al.*, 2010; Seddon *et al.*, 2010). While the collection dates for most of the male specimens were from 2001 or 2002, specimen age did range from 1896 to 2002. Hence, we performed all analyses using all individuals and using only the most recent individuals (< 50 years) and results did not change, indicating that year of collection did not bias our results. In addition, linear regression of each reflectance variable against the year of specimen collection showed no significant relationship (all $P > 0.05$); therefore the results shown are from all individuals.

Measurements were taken from male specimens at six different feather patches: cheek, crown, blue wing patch, white greater wing coverts, speculum, and tertials; and from female specimens at eight feather patches: cheek, crown, blue wing patch, white greater wing coverts, speculum, tertials, breast, and flanks. All homologous male and all homologous female feather patches measured appear identical to human vision, or very similar in coloration (*e.g.* breast coloration of females), between Cinnamon Teal and Blue-winged Teal, except for male cheek (cinnamon color in Cinnamon Teal *versus* bluish grey in Blue-winged Teal). This latter plumage patch was included to serve as a representative value of color difference within avian perceptual color space, corresponding to a clear difference in human visual assessment of color, by which to compare other avian color space values (see below).

We subsequently calculated color difference (ΔS) between Blue-winged Teal and Cinnamon Teal for each plumage patch within each sex using the Vorobyev-Osorio (1998) color discrimination model, with detailed methods described by Eaton (2005) and Wilson *et al.* (2008). Briefly, the model calculates a linear distance (ΔS) between two colors (*e.g.* reflectance measurements from the same patch of a female Cinnamon Teal and a female Blue-winged Teal) in avian perceptual color space, defined by the spectral sensitivity functions of the four different single-cone cell photoreceptors, and the signal-to-noise ratio of each of these photoreceptors (see Vorobyev *et al.*, 1998). Thus, Q1 represents the receptor

quantum catch of the violet sensitive cone (VS), Q2 the short-wave sensitive cone (SWS), Q3 the middle-wave sensitive cone (MWS), and Q4 the long-wave sensitive cone (LWS). The units of ΔS are jnd (just noticeable differences), where 1.0 jnd is, by definition, the threshold value for discrimination of colors (Vorobyev *et al.*, 1998). Thus, ΔS values < 1.0 jnd indicate two colors are visually indistinguishable, whereas values ≥ 1.0 jnd indicate the magnitude of discrimination above the threshold (Vorobyev *et al.*, 1998; Vorobyev, 2003; Siddiqi *et al.*, 2004). Generally, at jnd = 1.0 for threshold, two colors are barely distinguishable under ideal conditions, and as jnd becomes larger two colors are more easily discernable under worsening viewing conditions (Siddiqi *et al.*, 2004).

2.3 Statistical analysis of spectral data

Average coloration for each feather patch within species and sexes was used in the color discrimination model, and thus differences interpreted by the model might not be biologically functional if the variance in coloration of two homologous feather patches overlaps to the point that it is not a reliable visual indicator of taxonomy. To test the reliability of color indicators, MANOVAs and ANOVAs with Bonferroni correction for multiple comparisons were performed for each feather patch within each sex to evaluate overall differences in color between species and differences in the visual signal of each avian cone-cell type (Q1–Q4) for color from each plumage patch. To assess the reliability of plumage coloration in species identification between species and to determine which feather patches best discriminate species, we used a forward stepwise general discriminant analysis with cross-validation sample of two males and two females to assess reliability, as in the morphometric analysis.

3. RESULTS

3.1 Morphometrics

Overall morphology differed between species (Wilks' $\lambda = 0.38$, $F_{(8, 96)} = 19.83$, $P < 0.0001$) and between sexes (Wilks' $\lambda = 0.52$, $F_{(8, 96)} = 11.18$, $P < 0.0001$). There was no significant interaction between species and sex (Wilks' $\lambda = 0.91$, $F_{(8, 96)} = 1.15$, $P = 0.338$). Mean differences between species were restricted to three bill measurements (culmen length, length at nares, and bill width) for both males and females, with Cinnamon Teal approximately 7–10 % larger on average (Table 1). Using the diagnosability index (D_{ij}), Blue-winged Teal and Cinnamon Teal were not diagnosable from each other as all index values were less than zero for both males and females except male Blue-winged Teal was diagnosable from Cinnamon Teal in culmen length;

Table 1 Body size (mm) and body mass (g) measurements for Cinnamon Teal (*Anas cyanoptera septentrionalium*) and Blue-winged Teal (*A. discors*)

Sex	*A. c. septentrionalium*[a]			*A. discors*[a]			P[b]	Diagnosability index[c]
	Mean	SE	Range	Mean	SE	Range		
Males								
Mass	361.8	3.33	310–420	386.1	4.69	330–460	–	–
Wing chord	188.8	0.87	168–201	187.6	0.70	180–199	1.00	−19.1/−12.4
Tarsus	31.01	0.15	28.1–33.4	30.50	0.16	29.1–32.5	1.00	−3.1/−2.3
Tail	80.47	0.58	66.0–87.0	73.51	1.03	62.9–84.6	**< 0.001**	−8.7/−9.4
Nare	35.00	0.17	32.4–37.1	32.30	0.30	29.6–37.4	**< 0.001**	−1.8/−2.0
Culmen	45.63	0.20	42.5–47.9	41.31	0.22	37.7–44.7	**< 0.001**	−0.6/0.3
Bill height	13.39	0.08	12.3–15.1	13.74	0.18	12.1–15.9	0.40	−1.7/−2.5
Bill width	16.76	0.07	15.7–17.8	15.74	0.13	13.7–17.2	**< 0.001**	−0.8/−1.0
Females								
Mass	363.5	14.20	315–430	410.4	9.63	335–465	–	–
Wing chord	180.7	1.60	171–187	177.2	1.38	171–186	0.76	−14.2/−13.2
Tarsus	30.69	0.55	29.2–34.9	30.05	0.17	29.1–31.2	1.00	−4.7/−2.2
Tail	76.30	2.02	67.0–86.0	72.90	1.32	66.9–81.4	0.69	−17.9/−13.7
Nare	32.74	0.48	30.5–35.1	30.37	0.38	27.9–32.5	**< 0.001**	−2.8/−2.3
Culmen	43.10	0.61	40.1–46.0	39.65	0.62	37.1–44.3	**< 0.001**	−3.2/−4.1
Bill height	12.59	0.23	11.1–13.8	12.88	0.25	12.1–14.5	1.00	−2.4/−2.6
Bill width	16.13	0.25	15.0–17.4	14.95	0.13	14.1–15.7	**< 0.001**	−1.4/−0.6

[a]Sample sizes: *A. c. septentrionalium* (50 male, 10 female), *A. discors* (34 male, 13 female).
[b]Bonferroni corrected P values ($P_{adjusted}$ < 0.05). Significant comparisons included in bold.
[c]Diagnosability index ($D_{septentrionalium/discors}/D_{discors/septentrionalium}$).

Table 2 Stepwise discriminant function coefficients for identification of male and female Cinnamon Teal (*Anas cyanoptera septentrionalium*) and Blue-winged Teal (*A. discors*) using morphometric and plumage reflectance data

	Male				Female	
			Morphometrics			
	A. c. septentrionalium	*A. discors*			*A. c. septentrionalium*	*A. discors*
Intercept	−1102.00	−991.86		Intercept	−275.87	−236.43
Culmen	22.62	20.06		Bill width	34.10	31.57
Tail	3.04	2.50				
Wing chord	4.89	5.12				
% Correctly Classified	94.0	100.0		% Correctly Classified	70.0	92.3
			Plumage			
	Wing only				Full body/wing only	
Intercept	−11.65	−13.95		Intercept	−37.15/−17.34	−21.74/−6.05
Q2 speculum	0.05	0.03		Q4 crown	−0.02/–	0.04/–
Q3 speculum	0.01	0.03		Q3 speculum	−1.25/−0.48	0.66/−0.06
				Q4 speculum	0.94/0.39	−0.44/0.08
				Q1 cheek	−0.21/–	0.04/–
				Q2 cheek	0.24/–	−0.04/–
% Correctly Classified	76.5	81.5		% Correctly Classified	100.0	100.0

however, Cinnamon Teal males were not diagnosable from Blue-winged Teal males (Table 1).

The final discriminant function included three variables (culmen, tail length, wing chord) for males and only one variable (bill width) for females (Table 2). Overall, male Cinnamon Teal and Blue-winged Teal were correctly assigned in 94.0% and 100.0% of cases, respectively. Female classification was lower, with Cinnamon Teal and Blue-winged Teal classified correctly in 70.0% and 92.3% of cases, respectively. All cross-validation samples were correctly assigned for both males and females.

3.2 Color divergence

As expected, color difference in avian perceptual color space between Cinnamon Teal and Blue-winged Teal was greatest for cheek color of males (ΔS = 11.4 jnd), which corresponds to an easily distinguishable difference in coloration to human vision. Unexpectedly, there were also color differences most likely large enough to be visually discernable to birds (ΔS = ~3 jnd) for several plumage patches that are visually identical to the human eye: male speculum, female breast, and female cheek (Tables 3–4). All other patches were very near, or less than, the threshold for discrimination as different colors in avian perceptual color space, with the exception of female flank which had ΔS = 1.99 jnd. We observed statistical differences between Cinnamon Teal and Blue-winged Teal for at least one photoreceptor signal (*i.e.* quantum catches, Q_1–Q_4; Tables 3–4) for coloration taken from each of the following plumage patches: all male patches, except tertial; and for females, crown, breast, speculum, and tertial.

Final discriminant analysis showed that speculum (Q1 and Q2) best discriminated species for male wings, and crown (Q4), speculum (Q3 and Q4), and cheek (Q1 and Q2) best discriminated species for females (Table 2). When only female wing reflectance measurements were used, speculum (Q3 and Q4) showed the best predictability. Males were correctly classified in 76.5% and 81.4% of cases for Cinnamon Teal and Blue-winged Teal, respectively. All Blue-winged Teal males used in the

Table 3 Average receptor quantum catches (Qi) of each of the four single cone cell types, and color discriminability (ΔS) using the Vorobyev-Osorio color discrimination model for each feather patch on male Cinnamon Teal (Anas cyanoptera septentrionalium) and Blue-winged Teal (A. discors). ΔS > 1.0 just noticeable difference indicates distinguishable differences in color to the avian visual system under ideal viewing conditions

Feather	A. discors Mean (SE)	A. c. septentrionalium Mean (SE)	P^a	ΔS
Blue wing patch				
Q1[b]	2495.55 (64.5)	2134.0 (101.0)	0.004	0.49
Q2	1607.11 (39.0)	1393.2 (63.7)	0.005	
Q3	1199.37 (27.2)	1055.7 (47.1)	0.008	
Q4	1372.99 (29.3)	1230.2 (56.1)	0.017	
Speculum border				
Q1	3837.96 (86.7)	4232.0 (226.0)	0.050	0.61
Q2	2825.89 (68.4)	3123.0 (141.0)	0.038	
Q3	2340.03 (60.0)	2603.0 (105.0)	0.027	
Q4	2973.70 (78.0)	3320.0 (126.0)	0.022	
Speculum				
Q1	534.14 (16.7)	491.0 (23.6)	0.16	3.24
Q2	340.22 (10.5)	330.7 (18.4)	0.69	
Q3	631.23 (19.8)	515.4 (27.9)	0.002	
Q4	529.31 (22.0)	470.4 (23.7)	0.13	
Crown				
Q1	278.41 (26.9)	408.5 (28.5)	0.007	0.09
Q2	213.92 (19.9)	314.8 (24.7)	0.009	
Q3	208.45 (18.9)	307.1 (26.9)	0.014	
Q4	328.82 (30.1)	481.6 (47.7)	0.025	
Cheek				
Q1	674.26 (40.1)	381.5 (30.9)	< 0.001	11.4
Q2	517.07 (27.1)	321.6 (26.1)	< 0.001	
Q3	467.07 (22.8)	388.9 (29.0)	0.04	
Q4	671.93 (31.8)	854.2 (50.7)	0.005	
Blue tertial				
Q1	2163.49 (68.3)	2144.0 (107.0)	0.88	0.49
Q2	1433.62 (43.2)	1375.9 (70.3)	0.48	
Q3	1022.91 (31.8)	971.0 (45.1)	0.35	
Q4	1094.26 (27.4)	1049.4 (48.1)	0.42	

[a]Bonferroni adjusted *P*-value.
[b]Q1 is receptor quantum catch of the violet sensitive cone (VS), Q2 the short-wave sensitive cone (SWS), Q3 the middle-wave sensitive cone (MWS), and Q4 the long-wave sensitive cone (LWS).

Table 4 Average receptor quantum catches (Qi) of each of the four single cone cell types, and color discriminability (ΔS) using the Vorobyev-Osorio color discrimination model for each feather patch on female Cinnamon Teal (*Anas cyanoptera septentrionalium*) and Blue-winged Teal (*A. discors*). ΔS > 1.0 just noticeable difference indicates distinguishable differences in color to the avian visual system under ideal viewing conditions

Feather	A. discors Mean (SE)	A. c. septentrionalium Mean (SE)	P^a	ΔS
Crown				
Q1[b]	447.9 (45.4)	324.4 (22.8)	0.016	1.05
Q2	356.6 (38.6)	259.0 (17.8)	0.020	
Q3	348.7 (37.9)	259.7 (17.7)	0.029	
Q4	543.8 (58.1)	422.8 (28.7)	0.054	
Cheek				
Q1	1188.0 (123.0)	908.7 (78.9)	0.059	2.92
Q2	1053.0 (105.0)	892.8 (69.1)	0.20	
Q3	1023.7 (97.5)	941.1 (67.5)	0.48	
Q4	1511.0 (136.0)	1465.0 (101.0)	0.79	
Breast				
Q1	1292.0 (119.0)	853.8 (45.8)	< 0.001	3.41
Q2	1143.2 (90.8)	834.9 (43.2)	0.003	
Q3	1135.6 (78.9)	911.9 (45.5)	0.017	
Q4	1715.0 (105.0)	1488.5 (70.6)	0.078	
Flank				
Q1	470.0 (41.0)	439.4 (32.4)	0.56	1.99
Q2	412.3 (38.0)	410.7 (29.1)	0.97	
Q3	439.6 (38.1)	462.6 (31.2)	0.65	
Q4	734.6 (57.7)	806.3 (50.4)	0.37	
Blue wing patch				
Q1	1735.0 (135.0)	1481.8 (55.0)	0.064	1.26
Q2	1169.7 (84.0)	1033.9 (35.4)	0.11	
Q3	920.0 (57.0)	835.8 (25.0)	0.15	
Q4	1102.8 (58.3)	1042.0 (28.0)	0.31	
Speculum border				
Q1	2169.0 (310.0)	2276.0 (282.0)	0.81	1.04
Q2	1614.0 (219.0)	1787.0 (222.0)	0.60	
Q3	1383.0 (178.0)	1563.0 (188.0)	0.52	
Q4	1822.0 (223.0)	2083.0 (239.0)	0.46	
Speculum				
Q1	278.6 (25.2)	402.9 (36.9)	0.023	0.92
Q2	225.5 (19.3)	325.1 (28.9)	0.020	
Q3	219.5 (17.3)	315.4 (25.9)	0.013	
Q4	313.7 (26.0)	477.2 (36.6)	0.004	
Blue tertial				
Q1	194.4 (16.9)	282.4 (27.1)	0.026	0.54
Q2	162.3 (13.0)	233.3 (21.0)	0.021	
Q3	168.0 (12.5)	240.4 (19.6)	0.013	
Q4	261.9 (19.3)	388.3 (29.8)	0.005	

[a]Bonferroni adjusted *P*-value.
[b]Q1 is receptor quantum catch of the violet sensitive cone (VS), Q2 the short-wave sensitive cone (SWS), Q3 the middle-wave sensitive cone (MWS), and Q4 the long-wave sensitive cone (LWS).

cross-validation sample ($n = 5$) were correctly classified, while only 66.7% (two out of three) of Cinnamon Teal were. For females, all individuals for both models (full body and wing only), including the cross-validation sample ($n = 2$), were correctly classified based on color variables across plumage patches.

4. DISCUSSION

Blue-winged Teal and Cinnamon Teal are very similar in both morphology and plumage characters making species identification difficult, especially among female individuals. As with other studies (Spencer, 1953; Stark, 1979), we confirm interspecific mean differences in bill morphology. However, there was overlap in each measurement, which is not surprising as on average differences only correspond to a 3 mm (length) and 1 mm (width) difference and habitat use and feeding strategies are virtually identical (Connelly and Ball, 1984). Although being morphologically similar in size, Blue-winged Teal and Cinnamon Teal males show strikingly divergent plumage, not only in overall body coloration, but also in head and neck coloration. This was clearly reflected in our color discrimination analyses, with male cheek reflectance measurements yielding a large distance in avian perceptual color space between the two species (ΔS = 11.4 jnd). This, of course, corresponds with a difference in coloration that humans easily perceive as distinct (see plate 20 in Kear, 2005). In addition to the large male plumage divergences, from the visual perspective of a duck we found that several female plumage patches showed color differences between species, although to a lesser degree than male color differences. This is often the case between closely related avian species where a major component of variation often results from differences in sexual ornaments used for mate recognition with little variation among juvenile and female plumages (West-Eberhard, 1983; Price, 2008).

4.1 Biological plumage differences between species

Plumage is an integral part of signaling behavior of waterfowl, and color patches have evolved to increase the effectiveness of displays in social situations such as pair formation (McKinney, 1992; Price, 2008). As with many closely related dabbling duck species, Cinnamon Teal and Blue-winged Teal males perform the same display repertoire and the accompanying vocal and plumage signals are often used for mate recognition (Johnsgard, 1963; McKinney, 1970). In both species, the speculum is used in a common courtship display (lateral dabbling), along with other distinguishing plumage traits such as cheek and flank feathers. Although wing coloration of the two species is indistinguishable to human vision, the interspecific color difference (ΔS = 3.24 jnd) of the speculum likely represents a novel species-specific plumage signal in males. Furthermore, the color divergence between species in the green speculum was absent in females (ΔS < 1 jnd), suggesting that sexual selection might play a role in evolution of speculum color divergence in male Blue-winged Teal and Cinnamon Teal.

Previous descriptions of female Blue-winged Teal and Cinnamon Teal reported overall body and head coloration differences, although these lacked rigorous quantification (Spencer, 1953; Wallace and Ogilive, 1977; Bellrose, 1980). From an avian visual perspective, we quantified interspecific differences in cheek, breast, and flank plumage coloration that should be visually distinguishable to the birds, given their respective linear distances in avian perceptual color space between homologous feather patches (*i.e.* ΔS values, Table 4). These objective plumage color differences support previous subjective descriptions of female coloration. Statistically, only color variables representing the breast plumage were different between females of the two species, with intraspecific variation being too large for cheek and flank color (Table 4). These ambiguous results between statistical analyses of color and color discrimination model analyses might reflect the confusing historical descriptions of plumage variability among and within these teal species (Palmer, 1976).

Active mate choice by both males and females are common in dabbling ducks (McKinney, 1992) as females preferred certain males (Williams, 1982) and males have been shown to prefer to court certain females while ignoring others (Weidmann, 1956; Bezzel, 1959; Lebret, 1961; Wishart, 1983). Thus, these differences in female coloration (e.g. breast plumage) could potentially serve as recognition cues for potential mates (e.g. species recognition), and thus, might reinforce divergence through decreasing hybridization events, assuming hybrids have lower fitness due to such factors such as susceptibility to parasitism (Mason and Clark, 1990) or disadvantages in securing a mate (Morton, 1998; Sorenson *et al.*, 2010). It has been noted that in captivity Blue-winged Teal and Cinnamon Teal readily interbreed and stocks become completely intermixed (Delacour, 1956). Although hybrids in the wild have been noted (Anderson and Miller, 1953; Bolen, 1978, 1979), the frequency of hybridization in areas where both species co-occur is not well documented, which in part could be due to the difficulty in distinguishing females and juveniles of these two species (see Randler 2004). Ideally, behavioral choice experiments are needed to confirm female plumage signals as biologically functional species identifiers.

4.2 Identification of species

Aside from male breeding plumage, Blue-winged Teal and Cinnamon Teal have historically been difficult to differentiate, and this confusion in part has likely played a role in lack of accurate population and harvest estimates especially for Cinnamon Teal as counts of these two species are combined during aerial surveys, banding records, and waterfowl parts surveys (Gammonley, 1996; Rohwer *et al.*, 2002; Raftovich *et al.*, 2010). In addition, identification of females based on an accompanying male can be misleading as these two species do hybridize (Phillips, 1975), although the extent and frequency of

hybridization has not been well documented since the Blue-winged Teal's expansion to the west.

Differences between species have been reported as potential discriminating variables, particularly in bill measurements. However, there is no consensus across reports indicating that a single measurement or plumage feature can accurately differentiate these two species. In agreement with Johnsgard (1975), but in contrast with Stark (1979), we found considerable overlap in bill measurements as well as other measurements, indicated by the lack of diagnosability, *e.g.* less than 75% of individuals from Blue-winged Teal lie outside the range of Cinnamon Teal and vice versa. Using a multivariate discriminate function (wing chord, tail, and culmen length), males could be correctly identified with high accuracy (96.4%). Even though this model is based on adult males, this model can be applicable to immature males of eight weeks or older when full growth is essentially obtained (Stark, 1979). Females were particularly problematic to identify. The low power for female assignment could be attributable to low sample size. However, variation in Blue-winged Teal measurements typically overlapped the means of Cinnamon Teal measurements. Therefore, it is unlikely that a larger sample size would substantially increase accuracy of the assignments. Also differences between species in bill measurements were extremely small (< 3mm); therefore any error in measuring, even 1 mm, could cause a misidentification.

Plumage features such as overall color tone, facial pattern, and presence of eye stripe have also been proposed as possible discriminating characteristics. However most of the descriptions are subjective such as more "reddish brown" or "streakier" and would require comparing both species side by side. Using plumage reflectance data to quantify color differences allows for the potential to accurately identify individuals without reference specimens and takes away observer subjectivity in such factors as what constitutes more "reddish brown". Plumage coloration did show higher accuracy in identification between females than did morphometrics. The typical reddish brown was evident in all Cinnamon Teal females, but female coloration in Blue-winged Teal was variable, as indicated by others (*e.g.* Palmer, 1976). However, the discriminate function based on reflectance data from cheek, crown, and speculum correctly assigned all females to species (Table 2). In addition, males could be assigned with high accuracy based on wing coloration (although not 100% as in females). Whereas identification requiring precise bill measurements where any error in measurement could result in misidentification, plumage reflectance data have the potential to provide additional confirmation on species identification or accurately identify problematic individuals.

The fiber optic spectrophotometer we used for data collection, or any portable spectrophotometer, along with a laptop can be employed in a field setting (technical details available from MDE) to collect plumage color reflectance data from captured ducks in the hand, or used in a lab setting to collect data from whole specimens or parts (*e.g.* wing and tail feathers from the United States Fish and Wildlife Service parts collection component of waterfowl harvest survey). These data could then be compared to any set of reflectance measurements taken from positively identified Blue-winged and Cinnamon Teal specimens and used for species identification. Thus, the use of plumage reflectance information may serve as a useful new tool for wildlife managers, in combination with morphometrics, to more accurately identify individuals of unknown species.

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APPENDIX 1

Catalog numbers of *Anas cyanoptera* and *A. discors* specimens used in this study. REW specimens are cataloged at University of Alaska Museum, FMNH are archived at Field Museum of Natural History, and NMNH are stored at the National Museum of Natural History, Smithsonian Institution

A. cyanoptera septentrionalium

REW 075, REW 077, REW 078, REW 079, REW 397, REW 398, REW 399, REW 400, REW 401, REW 402, REW 403, REW 404, REW 406, REW 411, REW 412, REW 414, REW 416, REW 418, REW 419, REW 421, REW 415, REW 420, REW 422, REW 423, REW 424, REW 425, REW 426, REW 427, Receptor 428, REW 429, REW 430, REW 431, REW 432, REW 433, REW 434, REW 435, REW 436, REW 437, REW 438, REW 439, REW 440, REW 441, REW 442, REW 443, REW 444, REW 445, REW 446, REW 447, REW 448, REW 449, REW 450, REW 451, REW 452, REW 453, REW 454, REW 455, REW 456, REW 457, REW 458, REW 459, REW 460, REW 461, REW 462, REW 463, REW 464, REW 465, REW 466, REW 467, FMNH 156461, FMNH 156467, FMNH 160137, FMNH 160138, FMNH 400419, FMNH 400423, FMNH 400425, FMNH 401430, FMNH 408121, FMNH 408124, FMNH 417207, FMNH 417698

A. discors

REW 001, REW 002, REW 003, REW 004, REW 005, REW 006, REW 007, REW 008, REW 009, REW 010, REW 011, REW 013, REW 014, REW 015, REW 021, REW 022, REW 023, REW 028, REW 029, REW 032, REW 033, REW 034, REW 035, REW 036, REW 037, REW 038, REW 039, REW 040, REW 041, REW 042, REW 043, REW 044, REW 045, REW 046, REW 047, REW 048, REW 049, REW 050, REW 052, REW 053, REW 054, REW 056, REW 061, REW 062, REW 063, REW 065, REW 066, REW 067, REW 068, REW 405, NMNH 466871, NMNH 365057, NMNH 340178, NMNH 565093, NMNH 302973, NMNH 565092, NMNH 482013, NMNH 482013, NMNH 152862, NMNH 152863, FMNH 126948, FMNH 126951, FMNH 246446, FMNH 324805, FMNH 324807, FMNH 324808, FMNH 324810, FMNH 324811, FMNH 324812, FMNH 370857, FMNH 379421, FMNH 387784