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# COLOR DIVERGENCE AMONG CINNAMON TEAL (*ANAS CYANOPTERA*) SUBSPECIES FROM NORTH AMERICA AND SOUTH AMERICA

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**Divergencia de coloración en las subespecies del Pato Colorado (*Anas cyanoptera*) de Norteamérica y Sudamérica.**

**Key words:** *Anas cyanoptera*, Cinnamon Teal, color vision, plumage divergence.

## INTRODUCTION

Plumage is an integral part of signaling behavior of waterfowl, especially during courtship and pair formation. There is a vast array of display repertoires among dabbling ducks (genus *Anas*) with many species performing the same displays. While many closely related species perform displays in similar form, the accompanying vocal and plumage signals differentiate species (McKinney 1970). Modifications in display frequencies have been proposed to evolve in association with slight plumage or morphological differences (Johnsgard 1960, McKinney 1961, McKinney 1965). In addition, color patches have evolved to increase the effectiveness of the displays in social situations such as pair-formation, hostile or territorial encounters, maintaining contact with mate, and flock activities (McKinney 1970, Price 2007).

Cinnamon Teal (*Anas cyanoptera*) is composed of five subspecies (*A. c. borreroi*, *A. c. cyanoptera*, *A. c. orinomus*, *A. c. septentrionalium*, and *A. c. tropica*; Synder & Lumdsen 1951), and each performs a variety of movements during social courtship that are accompanied by postures using different plumage areas. The color of the "cinnamon" feathers in males are known to be variable among and within subspecies (Synder & Lumdsen 1951), however color of other plumage patches among subspecies appear identical to human visual assessment (Delacour 1956, Blake

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1977, Johnsgard 1978, Evarts 2005). During Cinnamon Teal displays, such as Turn-back-of-head and lateral dabbling, differences in color of feather patches could potentially provide information about subspecies identification or male quality, since plumage is known to be important in avian signaling and mate choice (e.g., Cooke & McNally 1975, Klint 1980, Holmberg *et al.* 1989, Weidmann 1990, Sorenson & Derrickson 1994, Omland 1996a, 1996b; Bridge & Eaton 2005).

However, all birds studied to date see plumage colors differently than humans (Cuthill *et al.* 2000, Bennett & Thery 2007, Hart & Hunt 2007), and recent analyses of plumage colors quantified through spectrophotometry suggest birds might detect plumage color differences not detectable through human vision (Eaton 2005, Benites *et al.* 2007). Thus, human visual assessment of feather coloration is inadequate for proper study and interpretation of many biological questions. To overcome this problem, herein, we test for color differences from the visual perspective of the birds, using a model of avian color discrimination (Vorobyev & Osorio 1998). For several plumage patches which appear identical in coloration to humans, including those used during courtship displays, we quantify both male and female plumage color differences (i.e., divergence) among the three most widespread and abundant Cinnamon Teal subspecies (*A. c. cyanoptera*, *A. c. orinomus*, and *A. c. septentrionalium*). The other subspecies are not common, and museum collections lack very recently collected specimens needed for comparisons in this study.

## METHODS

*Study species.* In general, the male breeding plumage consists of a reddish brown to bright reddish chestnut color. The abdomen color ranges from brownish to black, and crown is typically black. The wings have blue upper-wing coverts (wing patch) and a metallic green speculum that is duller on females and are separated by white greater wing coverts. Although the coloration of males within and among subspecies is variable, there are some general trends that have been used in conjunction with morphological measurements to distinguish subspecies (Synder & Lumdsen 1951). Male *A. c. septentrionalium* tends to have more cinnamon red color than the other subspecies and lacks the spots on the breast, flanks, and belly that can be found on *A. c. cyanoptera* (Blake 1977). *A. c. cyanoptera* is usually a rich chestnut color. *A. c. tropica* and *A. c. borreroi* generally have a darker overall chestnut color with a higher frequency of spotting. The chestnut color of *A. c. orinomus* is typically lighter than *A. c. cyanoptera*. Female coloration range from mottled tan brown to red brown and tone is also quite variable ranging from pale to moderately dark (Gammonley 1996). *A. c. tropica* and *A. c. borreroi* are generally darker than the other subspecies. *A. c. orinomus* females tend to have darker streaking and are more reddish than *A. c. cyanoptera*. *A. c. septentrionalium* females are extremely variable in both color and tone (Blake 1977, Gammonley 1996).

*Spectral analysis of plumage colors.* In 2004*,* we measured 17 adult *A. c. orinomus* (7 females, 10 males), 29 *A. c. cyanoptera* (8 females, 21 males) and 15 *A. c. septentrionalium* (3 female, 12 males) collected from Argentina (2001, 2003), Peru (2002), and western United States (2002-2003). To avoid any potential bias introduced from color degradation from older specimens, we only used very recently collected specimens. Voucher specimens are archived at the University of Alaska Museum (Fairbanks, Alaska). All individuals were determined to be in complete breeding plumage and there was no evidence of color fading. Feather patch locations measured were chosen based on

TABLE 1. Color discriminability of ($\Delta S$) among Cinnamon Teal subspecies (*Anas cyanoptera orinomus*, 7 females, 10 males; *A. c. cyanoptera*, 8 females, 21 males; and *A. c. septentrionalium*, 3 female, 12 males) using the Vorobyev-Osorio color discrimination model. Values > 1.0 just noticeable differences indicate distinguishable differences using the avian visual system under ideal viewing conditions.

| | Pairwise comparisons | | |
|---|---|---|---|
| | *cyanoptera* vs *orinomus* | *cyanoptera* vs *septentrionalium* | *orinomus* vs *septentrionalium* |
| Male | | | |
| Crown | 1.07 | 3.30 | 2.25 |
| Cheek | 1.76 | 1.32 | 2.42 |
| Breast | 1.30 | 1.19 | 0.82 |
| Blue wing patch | 0.29 | 1.03 | 0.76 |
| White wing covert | 0.25 | 0.37 | 0.59 |
| Speculum | 0.61 | 3.16 | 3.57 |
| Blue tertial | 0.12 | 0.34 | 0.39 |
| Female | | | |
| Blue wing patch | 0.59 | 1.65 | 2.23 |
| Speculum | 1.03 | 1.56 | 2.58 |

their overall visibility during social displays (McKinney 1970) and conspicuousness when compared to surrounding feathers. Streaked or barred regions of the plumage were not used because those patches are smaller than the ~4 mm$^2$ measuring area, and thus, reliable measurements could not be made. Measurements were taken of seven different feather locations for males: crown, cheek, breast, blue wing patch, white greater wing coverts, green speculum, and blue tertial feathers. Due to the streakiness of female plumage, only two readings (blue wing patch and green speculum) were taken, both from the wing.

Spectral reflectance data were collected with an Ocean Optics S-2000 spectrometer (Dunedin, FL, USA) equipped with an R200-7-UV/VIS reflectance probe (fiber diameter = 200 microns) and a PX-2 pulsed xenon light source. Data collected were calibrated against a Spectralon white reflectance standard with the following settings: msec = 100, average = 10. These settings determined the pulse rate of the light source, and the number of scans averaged per spectrum saved, respectively. The reflectance probe was housed in a black rubber tube, which blocked ambient light, maintained the distance from the probe to the feather surface constant (approximately 2 mm), and achieved a 90-degree measurement angle relative to the feather surface. The spectrometer was recalibrated after all measurements were taken for each individual specimen. Raw reflectance data were averaged to yield percent light reflected every 10 nm between 300 and 700 nm, using the SAS statistical software package (SAS Institute, Cary, North Carolina, USA).

*Avian visual system modeling.* We evaluated color divergence among three of the *A. cyanoptera* subspecies for each feather patch using the Vorobyev-Osorio (1998) color discrimination model. The model calculates a distance in avian color space ($\Delta S$), defined by the quantum catches of each receptor type in the avian retina. Thus, $Q_1$ represented the receptor quantum catch of the violet sensitive cone (VS), $Q_2$ the short-wave sensitive cone (SWS), $Q_3$ the middle-wave sensitive cone (MWS), and $Q_4$ the long-wave sensitive cone (LWS). The model assumes only that discrimination

TABLE 2. Average receptor quantum catches of each of the four cones for each feather patch on male Cinnamon Teal (*Anas cyanoptera*) subspecies.

| Feathers | *A. c. orinomus* (n = 10) | *A. c. cyanoptera* (n = 21) | *A. c. septentrionalium* (n = 12) | *P*[1] |
|---|---|---|---|---|
| | Mean (SE) | Mean (SE) | Mean (SE) | |
| Crown | | | | |
| $Q_1$[2] | 371.3 (25.8) | 341.5 (13.6)* | 408.5 (28.5)* | 0.071 |
| $Q_2$ | 269.0 (22.1) | 237.1 (9.7)* | 314.8 (24.7)* | 0.007 |
| $Q_3$ | 247.8 (20.6) | 215.5 (8.7)* | 307.1 (26.9)* | 0.001 |
| $Q_4$ | 365.7 (32.8)^ | 307.1 (13.7)* | 481.6 (47.7) ^* | 0.001 |
| Breast | | | | |
| $Q_1$ | 546.0 (47.6) | 523.9 (27.6) | 563.6 (30.7) | 0.684 |
| $Q_2$ | 398.6 (32.9) | 386.7 (21.8) | 427.9 (24.6) | 0.506 |
| $Q_3$ | 398.6 (28.4) | 404.3 (22.9) | 441.6 (26.5) | 0.503 |
| $Q_4$ | 769.2 (40.9) | 808.9 (41.4) | 826.8 (45.2) | 0.721 |
| Cheek | | | | |
| $Q_1$ | 362.2 (38.2) | 306.5 (12.2)* | 381.5 (30.9)* | 0.057 |
| $Q_2$ | 282.1 (27.3) | 238.9 (10.8)* | 321.6 (26.1)* | 0.010 |
| $Q_3$ | 311.5 (24.3)^ | 278.7 (13.2)* | 388.9 (29.0)^* | 0.001 |
| $Q_4$ | 675.8 (37.3)^ | 642.3 (27.9)* | 854.2 (50.7)^* | 0.001 |
| Blue wing patch | | | | |
| $Q_1$ | 2010.0 (128.0) | 2372.0 (136.0) | 2071.0 (126.0) | 0.138 |
| $Q_2$ | 1282.4 (70.9) | 1494.1 (80.1) | 1352.0 (78.6) | 0.183 |
| $Q_3$ | 956.6 (46.4) | 1104.1 (54.9) | 1023.1 (56.9) | 0.202 |
| $Q_4$ | 1080.4 (50.3) | 1246.2 (59.6) | 1184.5 (66.3) | 0.209 |
| White wing covert | | | | |
| $Q_1$ | 4377.0 (224.0) | 4610.0 (195.0) | 4278.0 (318.0) | 0.579 |
| $Q_2$ | 3141.0 (187.0) | 3360.0 (137.0) | 3145.0 (200.0) | 0.544 |
| $Q_3$ | 2583.0 (161.0) | 2775.0 (114.0) | 2625.0 (147.0) | 0.558 |
| $Q_4$ | 3261.0 (212.0) | 3505.0 (147.0) | 3347.0 (176.0) | 0.592 |
| Speculum | | | | |
| $Q_1$ | 400.0 (24.4) | 437.0 (26.3) | 498.3 (32.0) | 0.111 |
| $Q_2$ | 301.0 (15.7) | 335.2 (22.0) | 348.9 (22.6) | 0.414 |
| $Q_3$ | 491.9 (36.4) | 526.1 (37.8) | 514.7 (36.2) | 0.839 |
| $Q_4$ | 350.2 (31.3) | 387.5 (30.5)* | 467.5 (32.3)* | 0.081 |
| Blue tertial | | | | |
| $Q_1$ | 1920.3 (83.0) | 2024.0 (88.6) | 2144.0 (107.0) | 0.372 |
| $Q_2$ | 1223.8 (48.8) | 1302.3 (54.4) | 1375.9 (70.3) | 0.312 |
| $Q_3$ | 859.2 (35.8) | 913.3 (33.7) | 971.0 (45.1) | 0.215 |
| $Q_4$ | 912.8 (38.4) | 971.0 (31.3) | 1049.4 (48.1) | 0.098 |

[1] ANOVAs for subspecies effect. Means with same symbol within a row are different as determined using Bonferroni corrected *P*-values ($P_{adjusted} < 0.1$).

[2] $Q_1$ is receptor quantum catch of the violet sensitive cone (VS), $Q_2$ the short-wave sensitive cone (SWS), $Q_3$ the middle-wave sensitive cone (MWS), and $Q_4$ the long-wave sensitive cone (LWS).

of color within this perceptual space is limited by noise originating in the receptors, and no visual signal results when a stimulus and background differ only in intensity (Vorobyev *et al.* 1998). The model is supported from behavioral data for several bird species, bees, and humans (Vorobyev *et al.* 1998, Vorobyev *et al.* 2001, Goldsmith & Butler 2003).

To calculate $\Delta S$ (color divergence) for each subspecies comparison, we used methods described in detail by Eaton (2005), substituting spectral sensitivity and relative photoreceptor abundance data from the peacock for those of the blue tit. Spectral sensitivity data do not exist for *A. cyanoptera* or other ducks, so we used the peacock data as an approximation. These data provide a good estimate for *A. cyanoptera*, as the visual pigment characteristics of other Anseriformes are similar to those of the peacock, and thus, photoreceptor sensitivities are highly conserved between these taxa for much of the visual range (Hart 2001). The units of $\Delta S$ are jnd (just noticeable differences), where 1.0 jnd is the threshold value for discrimination of colors. Thus, $\Delta S$ values $< 1.0$ jnd indicate two colors are visually indistinguishable, while values $> 1.0$ jnd indicate the magnitude of discrimination above threshold (Vorobyev *et al.* 1998, Vorobyev 2003, Siddiqi *et al.* 2004). Thus, $\Delta S$ values represent the divergence of color between Cinnamon Teal subspecies in relation to anseriform visual capabilities. 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).

*Statistical analysis of spectral data.* Average receptor quantum catches for each feather patch were used in the color discrimination model, and thus, color differences among subspecies generated by the model might be misleading if the variance in coloration between subspecies is too large. Thus, a multivariate analysis of variance (MANOVA) was performed to evaluate the overall differences in receptor quantum catch of each cone ($Q_1$–$Q_4$) among subspecies for each sex. Analysis of variance (ANOVA) and pairwise comparisons for the average receptor quantum catch of each cone for each feather patch were performed using a general linear model with Bonferroni-correction for multiple comparisons.

## RESULTS

Color divergence was greatest for most plumage areas between *A. c. septentrionalium* and *A. c. cyanoptera* and *A. c. orinomus* (Table 1). For example, considering the crown and speculum of males, $\Delta S$ comparing North American to South American subspecies was ~2–5 times larger than $\Delta S$ comparing between South American subspecies. The same pattern was observed for both female plumage patches, as well. Color divergence between South American subspecies was relatively low for all plumage patches for males and females, with the exception of male cheek color. $\Delta S$ values for this plumage area were relatively large among all three subspecies (Table 1).

We observed statistical differences in overall color in males (MANOVA: Wilks' $\lambda = 0.0381$, $F_{(56, 26)} = 1.92$, $P = 0.036$) but not in females (MANOVA: Wilks' $\lambda = 0.2225$, $F_{(16, 14)} = 0.98$, $P = 0.52$). Significant differences for male plumage in average receptor quantum catches in each cone ($Q_1$–$Q_4$) were found only between *A. c. septentrionalium* and the two South American subspecies (Table 2). No significant differences were observed for quantum catches in any cone among any of the subspecies for female plumage (Table 3).

## DISCUSSION

There was striking plumage color divergence

TABLE 3. Average receptor quantum catches of each of the four cones for each feather patch on female Cinnamon Teal (*Anas cyanoptera*) subspecies.

| Feathers | *A. c. orinomus* (n = 7) Mean (SE) | *A. c. cyanoptera* (n = 8) Mean (SE) | *A. c. septentrionalium* (n = 3) Mean (SE) | $P^1$ |
|---|---|---|---|---|
| Blue wing patch | | | | |
| $Q_1^2$ | 1722.0 (149.0) | 1711.3 (97.3) | 1601.3 (61.7) | 0.844 |
| $Q_2$ | 1137.0 (80.7) | 1146.5 (55.4) | 1123.8 (35.8) | 0.981 |
| $Q_3$ | 899.8 (49.6) | 913.8 (37.3) | 932.0 (40.3) | 0.912 |
| $Q_4$ | 1058.1 (48.9) | 1102.1 (36.6) | 1177.6 (81.9) | 0.368 |
| Speculum | | | | |
| $Q_1$ | 370.5 (64.4) | 350.3 (47.4) | 510.0 (165.0) | 0.420 |
| $Q_2$ | 286.5 (45.3) | 275.5 (32.9) | 412.0 (141.0) | 0.331 |
| $Q_3$ | 268.0 (40.0) | 260.5 (28.6) | 402.0 (141.0) | 0.260 |
| $Q_4$ | 354.0 (55.2) | 361.3 (41.9) | 592.0 (225.0) | 0.190 |

[1] ANOVAs for subspecies effect.

[2] $Q_1$ is receptor quantum catch of the violet sensitive cone (VS), $Q_2$ the short-wave sensitive cone (SWS), $Q_3$ the middle-wave sensitive cone (MWS), and $Q_4$ the long-wave sensitive cone (LWS).

among Cinnamon Teal subspecies, when color differences were analyzed from an avian visual perspective. Some areas of the plumage (e.g., crown and speculum) differed to a degree that should be easily distinguishable to the ducks, thus representing novel plumage signals (e. g., $\Delta S > 2$). Additionally, some plumage areas have diverged to a lesser degree, but still above the threshold for visual discrimination (e. g., $\Delta S$ values between 1 and 2). These differences represent potentially biologically significant differences for birds (Siddiqi *et al.* 2004, Eaton 2005), and thus could function as visual signals to the ducks, although the large variances in coloration for many of these plumage patches raise questions about their utility as reliable subspecies visual indicators (Tables 2 and 3). Nonetheless, the variation in color shown herein provides the raw material for selection to operate on plumage colors in Cinnamon Teal populations, assuming that coloration is heritable for a plumage area.

Signaling systems and color patterns are subject to a variety of selection pressures influenced by all aspects of life (e.g., mating success and foraging; Burtt, Jr. 1981, Endler 1992, Saetre 2000), as well as stochastic processes (e.g., genetic drift). It is unclear if the observed color divergence in Cinnamon Teal is a result of (1) genetic drift, (2) local natural selection acting upon plumage patterns to maximize signal strength in the particular environment of each subspecies, or (3) sexual selection acting to promote assortative mating. However, our results reveal plumage color differences that, to date, were unknown for Cinnamon Teal, thus providing the contextual basis for testing evolutionary hypotheses as future behavioral and genetic data are collected. Furthermore, use of avian visual modeling for analyses of plumage color morphology offers a powerful tool for quantifying geographic variation, and even individual variation, of color patterns among birds.

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