



CHAPTER 12

ECO GEOGRAPHIC VARIATION IN CINNAMON TEAL (*ANAS CYANOPTERA*) ALONG ELEVATIONAL AND LATITUDINAL GRADIENTS

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ABSTRACT.—The Cinnamon Teal (*Anas cyanoptera*) comprises five subspecies that inhabit a variety of habitats along an elevational gradient at temperate and tropical latitudes. North American and South American subspecies differ in their migratory behavior, which may have contributed to differences in body size. We measured body size of the five recognized subspecies (*A. c. cyanoptera*, *A. c. orinomus*, *A. c. borroeroi*, *A. c. tropica*, and *A. c. septentrionalium*) throughout their ranges and evaluated morphometric differentiation in relation to Bergmann's rule. Subspecies and geographic regions differed significantly, with the largest subspecies and the largest individuals found at high elevations in the central Andes (*A. c. orinomus*) and at high latitudes in southern Patagonia (*A. c. cyanoptera*). Smaller-bodied individuals (*A. c. cyanoptera*) were found at the northern and southern limits of the Altiplano, where intermixing between subspecies with different body sizes might occur. However, there is no direct evidence of *A. c. cyanoptera* breeding at high elevations (>3,500 m). In contrast to patterns within South America, the migratory subspecies in North America (*A. c. septentrionalium*) showed few significant correlations with elevation and no relationship between latitude and body size. Morphological diversity within Cinnamon Teal appears to have arisen from spatial and temporal heterogeneity in selection pressures resulting in adaptations to their local environments.

Key words: Andes, Bergmann's rule, body size, geographic variation, high altitude, morphology.

Variación Ecológica en *Anas cyanoptera* en Gradientes de Altitud y Latitud

RESUMEN.—*Anas cyanoptera* comprende cinco subespecies que se encuentran en una variedad de hábitats a lo largo de un gradiente altitudinal en latitudes templadas y tropicales. Las subespecies norteamericanas y suramericanas difieren en su comportamiento migratorio, lo que puede haber conducido a diferencias en su tamaño. Medimos el tamaño corporal de cinco subespecies reconocidas (*A. c. cyanoptera*, *A. c. orinomus*, *A. c. borroeroi*, *A. c. tropica* y *A. c. septentrionalium*) a través de sus áreas de distribución y evaluamos su diferenciación morfológica con relación a la regla de Bergmann. Las subespecies y las regiones geográficas se diferenciaron significativamente de manera que las subespecies e individuos de mayor tamaño corporal se encontraron a altitudes mayores en los Andes centrales (*A. c. orinomus*) y a altas latitudes en el sur de la Patagonia (*A. c. cyanoptera*). Individuos de *A. c. cyanoptera* de menor tamaño se encontraron en los límites norte y sur del altiplano, donde podrían mezclarse subespecies con diferentes tamaños corporales. Sin embargo, no existe evidencia directa de que *A. c. cyanoptera* se reproduzca a altitudes mayores que 3500 m. En contraste con los patrones observados en Suramérica, la subespecie migratoria de Norteamérica *A. c. septentrionalium* mostró pocas correlaciones significativas con la altitud y

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ninguna relación entre la latitud y el tamaño corporal. La diversidad morfológica en *A. cyanoptera* parece haber surgido debido a adaptaciones a los ambientes locales impulsadas por la heterogeneidad espacial y temporal de las presiones selectivas.

GEOGRAPHIC VARIATION IN morphology is common, and widespread patterns are often explained within an adaptive framework (Price 2008). One of the best-known ecogeographical patterns of variation in body size among vertebrates is Bergmann's rule, which states that individuals from populations in colder climates tend to be larger than those from populations in warmer climates (Bergmann 1847; Mayr 1956, 1963). Modifications to Bergmann's rule showed that larger body size would also be expected at higher latitudes and elevations, or in cooler or drier climates (Snow 1954; James 1968, 1970, 1991). Even though birds show a strong tendency to conform to modified definitions of Bergmann's rule (Ashton 2002, Meiri and Dayan 2003), the adaptive mechanisms responsible for this pattern have been debated. Various mechanisms have been proposed, such as heat conservation, fasting endurance, and competition for resources (Bergmann 1847; McNab 1971; Calder 1974, 1984; James 1991). Thus, ecotypic variation may result from complex underlying processes involving various interrelated variables (Millien et al. 2006).

South American ducks (Anseriformes: Anatidae) are particularly good candidates for a study of ecogeographic variation. Unlike their Northern Hemisphere relatives, which are migratory and show little morphological variation, ducks in South America tend to be less migratory, more restricted in geographic range, and well differentiated into two or more subspecies that differ in plumage and other morphological characters (Phillips 1923, Johnsgard 1978, Williams 1991, Bulgarella et al. 2007). For example, the ducks that inhabit the puna grasslands and wetlands of the high Andes (3,000–5,000 m) tend to have overall larger body size and differ in conspicuous traits, such as plumage, bill color, or eye color, from those in southern Patagonia, where most breeding habitat occurs below 1,500 m (Fjeldså and Krabbe 1990). Most Andean waterfowl thus comprise one or more predominantly lowland subspecies (or species) and one or more highland subspecies (Phillips 1923).

Cinnamon Teal (*Anas cyanoptera*) are widespread throughout the Western Hemisphere, and five subspecies that inhabit distinct geographic and ecological zones are currently recognized: *A. c. cyanoptera*, *A. c. orinomus*, *A. c. borroroi*, *A. c. tropica*, and *A. c. septentrionalium* (Snyder and Lumsden

1951, Delacour 1956, American Ornithologists' Union 1957, Gammonley 1996). *Anas c. septentrionalium* breeds throughout western North America (Bellrose 1980, Madge and Burn 1988, Gammonley 1996), whereas the other four subspecies breed in South America. In South America, *A. c. borroroi* is endemic to the Colombian Andes and is replaced by *A. c. tropica* in the adjacent tropical lowlands; intermediate elevational habitat is unsuitable for either subspecies (Snyder and Lumsden 1951, Delacour 1956). *Anas c. orinomus* is endemic to the Altiplano and adjacent puna region of Argentina, Bolivia, Chile, and Peru. *Anas c. cyanoptera* occurs throughout the Andean lowlands of Peru, Bolivia, Chile, Paraguay, Brazil, Uruguay, and Argentina and is occasionally found sympatrically with *A. c. orinomus* in the high Andes (Evarts 2005). Each Cinnamon Teal subspecies thus has a distinct geographic distribution with little or no overlap, with the exception of *A. c. cyanoptera* and *A. c. orinomus* where they co-occur in the central high Andes.

We collected Cinnamon Teal throughout their range in North America and South America and compared differences in body size among geographic regions. Evidence for Bergmann's rule was evaluated to gain insight into factors shaping morphological divergence over elevational and latitudinal gradients.

METHODS

Specimen collection and subspecies classification.— We collected 153 Cinnamon Teal (39 females and 114 males) from Argentina (2001, 2003), Bolivia (2001), Peru (2002), and the western United States (2002–2003) during the breeding season (Fig. 1 and Appendix 1). Voucher specimens are archived at the University of Alaska Museum (Fairbanks), Museo de Historia Natural de la Universidad de San Marcos (Lima), and Colección Boliviana de Fauna (La Paz). Measurements from Colombian vouchered specimens from the Royal Ontario Museum and Smithsonian Institution National Museum of Natural History were obtained for *A. c. borroroi* (5 females and 13 males) and *A. c. tropica* (2 females and 2 males); new specimens could not be obtained because these subspecies are endangered.

We used a combination of geography and wing chord length to classify each specimen (Snyder and Lumsden 1951, Blake 1977). Despite differences in

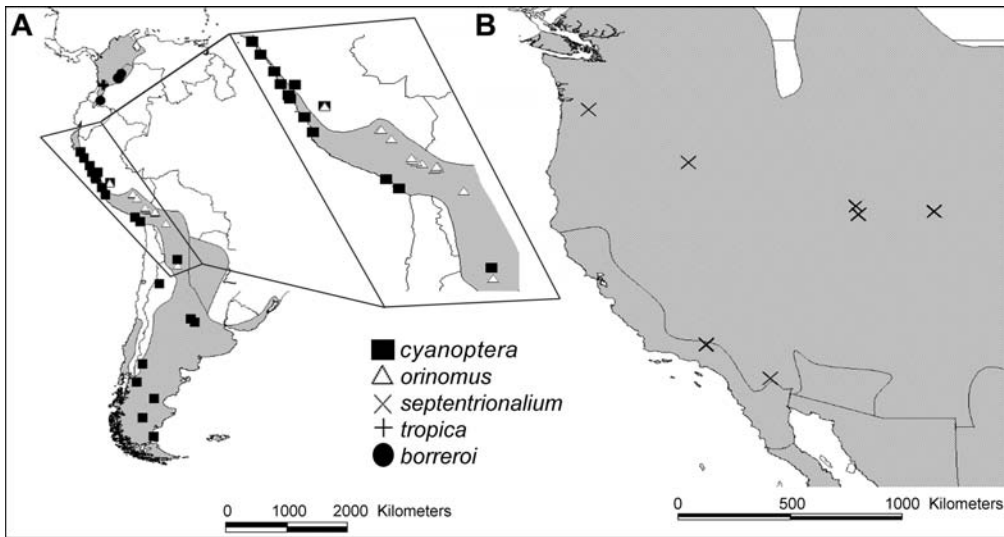


FIG. 1. Sampling localities and geographic ranges for Cinnamon Teal (Ridgely et al. 2003).

plumage (e.g., Blake 1977), coloration is variable, and *A. c. cyanoptera*, *A. c. orinomus*, and *A. c. septentrionalium* were difficult to classify to subspecies on the basis of plumage color alone (Wilson et al. 2008). We classified all individuals from North America as *A. c. septentrionalium* because it is the only subspecies known to occur there. The Colombian specimens we used were the basis of the original subspecies descriptions (Snyder and Lumsden 1951), and we followed them in classifying highland specimens as *A. c. borreroi* and lowland specimens as *A. c. tropica*. *Anas c. orinomus* is the most distinct of all the subspecies, which led some early researchers to consider it a separate species (Oberholser 1906). *Anas c. orinomus* was easily differentiated from *A. c. cyanoptera* by overall body size. To check the accuracy of classifications of *A. c. cyanoptera* and *A. c. orinomus* in areas of sympatry, we compared wing chord length to individuals of known classification. All initial classifications were confirmed.

Body measurements.—We took nine body-size measurements (± 0.1 mm) 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 (posterior edge of nares to tip of nail), tarsus bone length (tarsometatarsus), bill height (height of upper mandible at posterior edge of nares), bill width (width of upper mandible at posterior edge of nares), and body mass (g). Body mass was not

available from the Colombian subspecies and, therefore, was used only as a secondary character in subspecies identification. Measurements for all but 45 recently collected specimens were taken the day of collection and prior to preparation as museum specimens (wet measurements), and again several months or years after preparation (dry measurements; Appendix 2) by R.E.W. For 52 individuals from Argentina, Bolivia, and Colombia, only measurements from museum specimens were available (dry measurements). Specimen shrinkage during drying is a universal phenomenon and can cause analytical problems if not properly accounted for in studies that combine live or freshly killed birds and museum specimens (e.g., Winker 1996). Fresh and dry measurements taken by the first author differed significantly (Wilson and McCracken 2008). Therefore, dry measurements of those 52 individuals could not be directly substituted for wet measurements.

We chose to analyze wet measurements, and to use individuals missing these data we used a multiple imputation (MI) procedure implemented in the program NORM (Schafer 1999) to estimate wet measurements for the 52 individuals with only dry measurements, because we had both wet and dry measurements for most of the data set. An expectation-maximization algorithm (EM) was used to obtain starting values for the multiple imputation procedure, followed by data augmentation using Markov-chain Monte Carlo to produce multiple imputations of the missing data. We used

a random number seed and 10,000 iterations, with imputation every 1,000 iterations. The resulting 10 data sets were combined following Rubin's (1987) rules for scalar estimates to provide a single set of estimates for each specimen with missing data. The combined data composed of original wet measurements obtained from 123 specimens and estimated wet measurements from 52 specimens were used for all statistical analyses.

Statistical analysis of measurements.—Statistical analyses were performed with MINITAB Statistical Software (Minitab, State College, Pennsylvania). All traits were tested for normality with Kolmogorov-Smirnov tests and were normally distributed ($P_s > 0.05$). A multivariate analysis of variance (MANOVA) was performed to evaluate overall differences among subspecies and geographic regions for each sex. Geographic regions were defined as follows (with the corresponding subspecies inhabiting each area): (1) North America (*A. c. septentrionalium*); (2) Colombian highlands (*A. c. borreiroi*); (3) Colombian lowlands (*A. c. tropica*); (4) Peruvian coast (*A. c. cyanoptera*); (5) central high Andes of Argentina, Bolivia, and Peru (*A. c. orinomus* and *A. c. cyanoptera*); and (6) lowland Argentina (includes Patagonia and lowland areas of Cordoba; *A. c. cyanoptera*). Collection locations in North America (California, Oregon, and Utah) were treated as a single geographic unit, which is consistent with low levels of male breeding-site fidelity in North America (Anderson et al. 1992). Analysis of variance (ANOVA) and pairwise comparisons for each individual measurement were performed using a general linear model with Bonferroni correction for multiple comparisons. Pairwise comparisons were not made with *A. c. tropica* (lowland Colombia) because of low sample size. We used a principal component analysis to illustrate overall differences in body size among subspecies. Only those principal components with eigenvalues >1 were used for partial correlation and subspecies classification analyses.

Finally, the joint relationships between elevation and latitude and morphological variables were examined using partial correlation analysis for the following areas: all populations pooled, North America, South America, and southern South America (Altiplano and associated lowlands and Patagonia). In addition, correlations between latitude and body size were examined for *A. c. cyanoptera* (lowland and highland) separately, because it is the only subspecies with populations distributed over a large latitudinal gradient. Analyses were conducted separately for each sex, and

significance levels were corrected for multiple comparisons using Bonferroni methods.

Subspecies classification.—We used two methods to evaluate subspecies identifications. We first used linear discriminant analysis to evaluate whether the Cinnamon Teal subspecies conformed, on the basis of body-size measurements, to the 75% rule (Amadon 1949, Mayr 1969), which states that 75% of the individuals of one subspecies must be distinguishable from all other subspecies. Measurements found to be significantly different between at least two subspecies (classified based on overall body size) from the MANOVA and ANOVAs were included in this analysis. The reliability of the discriminant analysis was assessed using a cross-validation (jackknife) procedure, in which each observation was omitted one at a time and then reclassified using a classification function derived from the remaining observations (Manly 2000). Cross-validation gives a less biased error rate in classification, because it does not include observations that are used to create the classification function. We performed a discriminant analysis for each sex and locality of collection and did not include *A. c. tropica* because of low sample size.

We also tested the diagnosability of subspecies using the method of Patten and Unitt (2002), which focuses on the extent of overlap rather than detecting mean differences. Diagnosability of subspecies was determined for each measurement separately and for overall body size (PC1). An index value (D_{ij}) ≥ 0 indicates that subspecies i is diagnosable from subspecies j . Reciprocal tests were performed to determine whether subspecies i is diagnosable from subspecies j and whether subspecies j is diagnosable from subspecies i .

RESULTS

Subspecies differed significantly in overall body size (Wilks's $\lambda = 0.05$, $F = 25.38$, $df = 28$ and 574 , $P < 0.001$), as did the sexes (Wilks's $\lambda = 0.74$, $F = 7.16$, $df = 7$ and 159 , $P < 0.001$; Table 1). There was no significant interaction between subspecies and sex (Wilks's $\lambda = 0.78$, $F = 1.46$, $df = 28$ and 574 , $P = 0.061$). *Anas c. orinomus* was significantly larger than *A. c. tropica* (e.g., wing chord: 32.50 mm difference; tarsus: 4.01 mm difference) and *A. c. septentrionalium* (e.g., wing chord: 31.50 mm difference; tarsus: 4.83 mm difference) in most measurements, with *A. c. borreiroi* and *A. c. cyanoptera* intermediate in body size (Tables 1 and 2). In addition, when individuals were grouped on the basis of collection locality instead of

TABLE 1. Wet measurements (mm) and body mass (g) for male *Anas cyanoptera cyanoptera*, *A. c. orinomus*, and *A. c. septentrionalium* and dry measurements for *A. c. borroroi* and *A. c. tropica*. Letters after mean value correspond to subspecies (o = *orinomus*, c = *cyanoptera*, b = *borroroi*, and s = *septentrionalium*) and indicate significant pairwise differences determined using Bonferroni corrected *P* values ($P_{\text{adjusted}} < 0.05$). Pairwise comparisons were not performed for *A. c. tropica* because of the small sample size.

| | | Mass | Wing chord | Tarsus | Tail | Nare | Culmen | Bill height | Bill width |
|-------------------------------------|-------|---------|------------|-----------|-----------|-----------|-----------|-------------|------------|
| <i>orinomus</i> (n = 13) | Mean | 498.8 | 223.4 cbs | 35.52 cbs | 93.28 cbs | 37.28 cbs | 47.85 cbs | 14.67 cs | 17.41 cs |
| | SE | 10.7 | 2.20 | 0.37 | 1.14 | 0.38 | 0.57 | 0.19 | 0.18 |
| | Range | 425–550 | 211–237 | 33.8–37.6 | 86.7–99.9 | 35.6–40.4 | 44.9–52.1 | 13.7–15.9 | 16.1–18.3 |
| <i>cyanoptera</i> (n = 28) | Mean | 414.5 | 191.9 ob | 32.95 os | 81.95 ob | 33.96 o | 44.55 o | 14.02 obs | 16.92 o |
| | SE | 7.60 | 1.20 | 0.32 | 1.33 | 0.35 | 0.41 | 0.19 | 0.19 |
| | Range | 340–515 | 181–205 | 29.1–35.9 | 69.5–97.6 | 30.6–37.6 | 40.5–48.7 | 12.4–16.3 | 15.2–19.2 |
| <i>septentrionalium</i> (n = 50) | Mean | 361.8 | 188.8 ob | 31.01 ocb | 80.47 ob | 35.00 ob | 45.63 o | 13.39 ocs | 16.76 ob |
| | SE | 3.30 | 0.90 | 0.15 | 0.58 | 0.17 | 0.20 | 0.08 | 0.07 |
| | Range | 310–420 | 168–201 | 28.1–33.4 | 66.0–87.0 | 32.4–37.1 | 42.5–47.9 | 12.3–15.1 | 15.7–17.8 |
| <i>borroroi</i> (n = 13) | Mean | — | 196.0 ocs | 31.93 os | 99.54 ocs | 32.91 os | 43.65 o | 14.39 cs | 16.57 s |
| | SE | — | 1.86 | 0.43 | 2.77 | 0.88 | 0.73 | 0.21 | 0.25 |
| | Range | — | 179–205 | 28.7–35.2 | 82–115 | 28.3–40.2 | 38.9–46.7 | 13.1–15.9 | 15.2–18.2 |
| <i>tropica</i> (n = 2) | Mean | — | 184.0 | 30.93 | 105 | 29.68 | 40.99 | 14.13 | 16.54 |
| | SE | — | 2.50 | 0.59 | 6.00 | 0.36 | 0.03 | 0.17 | 0.62 |
| | Range | — | 182–187 | 30.2–31.4 | 99–111 | 29.3–30.0 | 40.9–41.0 | 13.9–14.3 | 15.9–17.2 |
| <i>P</i> ^a | | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 |

^a ANOVAs for subspecies effect based on pooled data (wet measurements and transformed dry measurements). Sample sizes: *orinomus*, n = 30; *cyanoptera*, n = 34; *septentrionalium*, n = 50; *borroroi*, n = 13; and *tropica*, n = 2.

TABLE 2. Wet measurements (mm) and body mass (g) for female *Anas cyanoptera cyanoptera*, *A. c. orinomus*, and *A. c. septentrionalium* and dry measurements for *A. c. borroroi* and *A. c. tropica*. Letters after mean values correspond to subspecies (o = *orinomus*, c = *cyanoptera*, b = *borroroi*, and s = *septentrionalium*) and indicate significant pairwise differences determined using Bonferroni corrected *P* values ($P_{\text{adjusted}} < 0.05$). Pairwise comparisons were not performed for *A. c. tropica* because of the small sample size.

| | | Mass | Wing chord | Tarsus | Tail | Nare | Culmen | Bill height | Bill width |
|-------------------------------------|-------|---------|------------|-----------|-----------|-----------|-----------|-------------|------------|
| <i>orinomus</i> (n = 9) | Mean | 450.6 | 209.9 cbs | 34.59 cbs | 88.96 s | 33.94 c | 44.34 c | 13.81 s | 17.26 cs |
| | SE | 11.30 | 1.32 | 0.24 | 1.62 | 0.24 | 0.51 | 0.26 | 0.22 |
| | Range | 390–495 | 204–217 | 33.7–36.1 | 77.9–95.7 | 33.1–35.1 | 41.7–46.2 | 12.6–14.8 | 16.1–18.3 |
| <i>cyanoptera</i> (n = 13) | Mean | 394.2 | 180.5 bo | 31.14 o | 77.85 b | 31.85 o | 42.15 o | 12.29 b | 16.01 o |
| | SE | 10.60 | 1.10 | 0.37 | 1.97 | 0.26 | 0.41 | 0.22 | 0.22 |
| | Range | 340–470 | 172–185 | 29.2–33.1 | 63.1–90.0 | 30.1–33.6 | 38.8–44.6 | 12.1–14.9 | 15.1–17.6 |
| <i>septentrionalium</i> (n = 10) | Mean | 363.5 | 180.7 b | 30.69 o | 76.30 ob | 32.74 | 43.10 | 12.59 ob | 16.13 o |
| | SE | 14.20 | 1.60 | 0.55 | 2.02 | 0.48 | 0.61 | 0.23 | 0.25 |
| | Range | 315–430 | 171–187 | 29.2–34.9 | 67.0–86.0 | 30.5–35.1 | 40.1–46.0 | 11.1–13.8 | 15.0–17.4 |
| <i>borroroi</i> (n = 5) | Mean | — | 190.6 ocs | 31.22 o | 104.8 cs | 33.81 | 41.58 | 14.06 cs | 15.92 |
| | SE | — | 2.68 | 0.99 | 10.4 | 1.19 | 1.01 | 0.46 | 0.50 |
| | Range | — | 182–198 | 30.1–35.2 | 86–145 | 29.6–36.9 | 38.1–43.8 | 12.6–14.9 | 14.9–17.6 |
| <i>tropica</i> (n = 2) | Mean | — | 171.5 | 28.94 | 104.00 | 24.82 | 37.84 | 14.28 | 15.39 |
| | SE | — | 4.50 | 0.78 | 5.00 | 0.21 | 0.52 | 0.82 | 0.40 |
| | Range | — | 167–176 | 28.2–29.7 | 99–109 | 24.6–25.0 | 37.3–38.4 | 13.5–15.1 | 14.9–15.8 |
| <i>P</i> ^a | | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | 0.003 |

^a ANOVAs for subspecies effect based on pooled data (wet measurements and transformed dry measurements). Sample sizes: *orinomus*, n = 15; *cyanoptera*, n = 14; *septentrionalium*, n = 10; *borroroi*, n = 5; *tropica*, n = 2.

TABLE 3. Measurements (mm) and body mass (g) for populations of *Anas cyanoptera cyanoptera* in lowland Argentina, the Peruvian coast, and the central high Andes.

| Sex | | Mass | Wing chord | Tarsus | Tail | Nare | Culmen | Bill height | Bill width |
|----------------------------|-------|---------|------------|-----------|-----------|-----------|-----------|-------------|------------|
| Male | | | | | | | | | |
| Argentina (n = 10) | Mean | 429.2 | 194.96 | 32.50 | 85.53 | 35.64 | 46.02 | 14.56 | 17.68 |
| | SE | 9.67 | 1.20 | 0.55 | 1.08 | 0.46 | 0.54 | 0.26 | 0.28 |
| | Range | 450–540 | 190–200 | 29.6–34.8 | 80.9–91.0 | 33.0–37.6 | 43.3–48.7 | 13.5–15.9 | 16.7–19.2 |
| Peruvian coast (n = 18) | Mean | 394.4 | 190.5 | 33.06 | 80.39 | 33.21 | 43.98 | 13.74 | 16.51 |
| | SE | 4.88 | 1.61 | 0.37 | 1.52 | 0.36 | 0.43 | 0.16 | 0.14 |
| | Range | 340–430 | 181–205 | 29.1–35.4 | 69.5–97.6 | 30.6–36.1 | 40.5–47.6 | 12.7–15.1 | 15.2–17.6 |
| Andes (n = 6) | Mean | 429.2 | 195.68 | 34.07 | 82.45 | 34.71 | 44.45 | 13.79 | 17.13 |
| | SE | 14.4 | 3.18 | 0.48 | 2.61 | 0.38 | 0.89 | 0.60 | 0.38 |
| | Range | 380–470 | 186–204 | 32.5–35.9 | 75.7–92.6 | 33.4–35.9 | 42.6–47.3 | 12.4–16.3 | 15.5–18.3 |
| Female | | | | | | | | | |
| Argentina (n = 4) | Mean | 418.8 | 182.23 | 30.75 | 81 | 32.24 | 42.09 | 14.14 | 16.73 |
| | SE | 21.4 | 0.65 | 0.87 | 3.32 | 0.53 | 0.84 | 0.34 | 0.34 |
| | Range | 365–470 | 181–184 | 29.3–32.3 | 76.0–90.0 | 31.2–33.6 | 40.3–43.6 | 13.3–14.9 | 15.9–16.9 |
| Peruvian coast (n = 10) | Mean | 387.0 | 179.8 | 31.5 | 76.4 | 31.68 | 41.98 | 12.95 | 15.71 |
| | SE | 10.4 | 1.37 | 0.40 | 2.15 | 0.26 | 0.48 | 0.16 | 0.18 |
| | Range | 340–430 | 172–185 | 29.2–33.1 | 63.1–86.7 | 30.1–32.8 | 38.8–44.6 | 12.1–13.9 | 15.1–16.9 |

subspecies identification, geographic regions differed significantly in body size (Wilks's $\lambda = 0.06$, $F = 17.54$, $df = 35$ and 662 , $P < 0.001$), as did the sexes (Wilks's $\lambda = 0.75$, $F = 7.57$, $df = 7$ and 157 , $P < 0.001$). There was no significant interaction between geographic region and sex (Wilks's $\lambda = 0.78$, $F = 1.16$, $df = 35$ and 662 , $P = 0.244$). The same basic overall pattern was observed, regardless of whether individuals were grouped by subspecies or by geographic region. Highland individuals were significantly larger and intermediate body sizes were found in Patagonia (*A. c. cyanoptera*) and the Colombian highlands (*A. c. borroroi*), except for some notable exceptions. Among females, the lowland Argentine population (*A. c. cyanoptera*) was not significantly different from the central high Andean population (*A. c. orinomus*) in either bill length measurements (bill length at nares: 2.04 mm difference; culmen length: 2.59 mm difference) or bill width (0.39 mm difference). In males, the lowland Argentine population was similar to the Andean populations (*A. c. cyanoptera* and *A. c. orinomus* combined) in tail length, bill length at nares, bill height, and bill width and was significantly larger than the Peruvian coastal population in most measurements (Table 3). Specimens of *A. c. cyanoptera* collected at high elevation in the Andes were significantly smaller than *A. c. orinomus* only in wing chord (27.7 mm difference) and tail length (10.83 mm difference). The North American and Argentine lowland populations

of *A. c. cyanoptera* had similar bill lengths, but the Argentine population had significantly greater bill height (1.17 mm difference) and bill width (0.91 mm difference). North American populations had significantly larger bill length at nares (1.78 mm difference) and culmen length (1.65 mm difference) than Peruvian coastal populations of *A. c. cyanoptera*.

Principal component analysis.—The first principal component (PC1; female eigenvalue = 3.54, male eigenvalue = 3.33) accounted for 50.5% and 47.6% of the variance for females and males, respectively,

TABLE 4. Principal components (PC1 and PC2), eigenvectors, eigenvalues, and percent of variance calculated from male and female Cinnamon Teal (*Anas cyanoptera*).

| | Males | | Females | |
|------------------|-------|-------|---------|-------|
| | PC1 | PC2 | PC1 | PC2 |
| Wing chord | 0.48 | 0.01 | 0.48 | -0.06 |
| Tarsus bone | 0.41 | -0.09 | 0.42 | 0.05 |
| Tail | 0.32 | -0.48 | 0.14 | -0.66 |
| Bill length-nare | 0.33 | 0.56 | 0.39 | 0.41 |
| Culmen length | 0.33 | 0.54 | 0.40 | 0.36 |
| Bill height | 0.36 | -0.39 | 0.30 | -0.51 |
| Bill width | 0.39 | -0.09 | 0.42 | -0.12 |
| Eigenvalue | 3.33 | 1.63 | 3.54 | 1.57 |
| Variance (%) | 47.6 | 23.2 | 50.5 | 22.5 |
| Cumulative (%) | 47.6 | 70.9 | 50.5 | 73.0 |

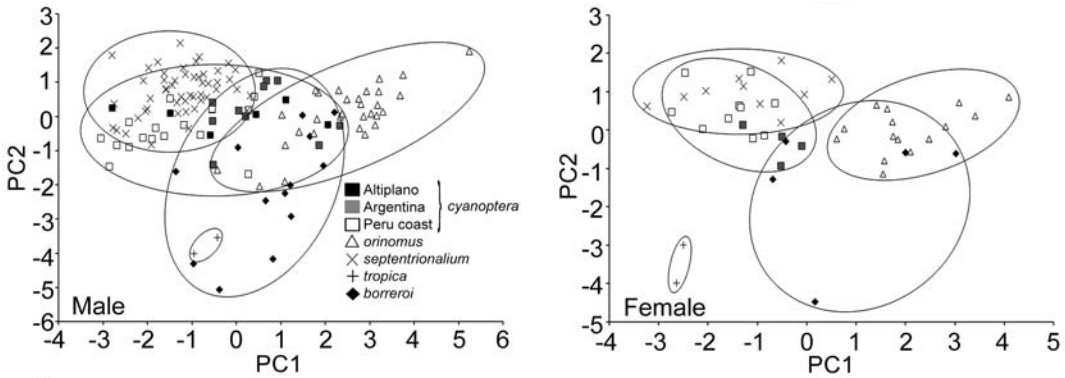


FIG. 2. Principal component analysis (PC1 vs. PC2) of nine body-size measurements for male (left) and female (right) Cinnamon Teal.

and represented an overall body-size difference (Table 4). The second principal component (PC2; female eigenvalue = 1.57, male eigenvalue = 1.63) accounted for 23.2% and 22.5% of the variance for females and males, respectively, and represented a bill-shape difference among the subspecies, as bill measurements were the most influential variables. A longer, thinner bill corresponded with a higher score. Even though plots of PC1 versus PC2 showed some overlap among subspecies, only *A. c. septentrionalium* and *A. c. cyanoptera* did not differ in PC1, and *A. c. orinomus* and *A. c. cyanoptera* did not differ in PC2 (Fig. 2). When subsets of *A. c. cyanoptera* were analyzed geographically (Argentina, Peruvian coast, and Andes), the Argentine population was significantly larger in overall body size

(PC1), whereas the Peruvian coastal population was more similar to *A. c. septentrionalium* (North America). *Anas c. orinomus* had the largest overall body size, with *A. c. borreroi* and the lowland Argentine population and individual *A. c. cyanoptera* collected in northwest Argentina showing intermediate body size. *Anas c. septentrionalium* had the longest bill (PC2) after controlling for variation in body size (Fig. 2).

Partial correlation analysis.—Several significant patterns were found after Bonferroni correction in relation to latitude and elevation (Tables 5 and 6 and Figs. 3–10). Most measurements showed a significant increase with elevation for males and females among all individuals and within South America only (elevation increase of ~4,000 m). In

TABLE 5. Partial correlation coefficients between latitude ^a and body measurements and principal components for Cinnamon Teal (*Anas cyanoptera*). Significant values determined using Bonferroni corrected *P* values (*P*_{adjusted} < 0.05) are in bold.

| | Male | | | | Female | | | |
|------------------|---------------|-------------------------|------------------------|---------------|-------------|-------------------------|------------------------|---------------|
| | Pooled data | <i>A. c. cyanoptera</i> | Southern South America | North America | Pooled data | <i>A. c. cyanoptera</i> | Southern South America | North America |
| Wing chord | -0.096 | 0.381 | 0.097 | 0.145 | -0.092 | 0.044 | -0.061 | 0.329 |
| Tarsus bone | -0.343 | -0.280 | -0.213 | 0.029 | -0.178 | -0.219 | -0.290 | -0.371 |
| Tail | -0.425 | 0.319 | 0.184 | 0.039 | -0.362 | -0.321 | 0.041 | 0.449 |
| Bill length-nare | 0.476 | 0.619 | 0.382 | 0.088 | 0.223 | 0.081 | 0.113 | -0.101 |
| Culmen | 0.358 | 0.544 | 0.294 | -0.155 | 0.291 | 0.081 | 0.052 | -0.173 |
| Bill height | -0.278 | 0.557 | 0.434 | 0.197 | -0.236 | 0.681 | 0.569 | -0.334 |
| Bill width | -0.005 | 0.662 | 0.560 | -0.33 | 0.022 | 0.407 | 0.438 | -0.589 |
| PC1 | -0.065 | 0.629 | 0.383 | -0.013 | 0.007 | 0.320 | 0.271 | -0.340 |
| PC2 | 0.582 | 0.259 | 0.133 | -0.111 | 0.398 | -0.240 | -0.366 | -0.261 |

^aLatitude is calculated in degrees as the absolute value of distance from the equator.

TABLE 6. Partial correlation coefficients between elevation and body measurements and principal components for Cinnamon Teal (*Anas cyanoptera*). Significant values determined using Bonferroni corrected *P* values ($P_{\text{adjusted}} < 0.05$) are in bold.

| Elevation | Male | | | Female | | |
|------------------|---------------|---------------|---------------|--------------|---------------|---------------|
| | Pooled data | South America | North America | Pooled data | South America | North America |
| Wing chord | 0.724 | 0.782 | -0.038 | 0.905 | 0.928 | -0.122 |
| Tarsus bone | 0.603 | 0.619 | -0.018 | 0.705 | 0.754 | 0.018 |
| Tail | 0.417 | 0.354 | -0.265 | 0.388 | 0.333 | -0.529 |
| Bill length-nare | 0.381 | 0.547 | 0.270 | 0.454 | 0.575 | -0.356 |
| Culmen | 0.262 | 0.426 | 0.312 | 0.458 | 0.611 | -0.167 |
| Bill height | 0.292 | 0.275 | -0.243 | 0.357 | 0.373 | -0.590 |
| Bill width | 0.265 | 0.356 | -0.188 | 0.497 | 0.605 | -0.461 |
| PC1 | 0.649 | 0.710 | -0.040 | 0.784 | 0.861 | -0.419 |
| PC2 | -0.018 | 0.214 | 0.494 | -0.118 | 0.007 | 0.584 |

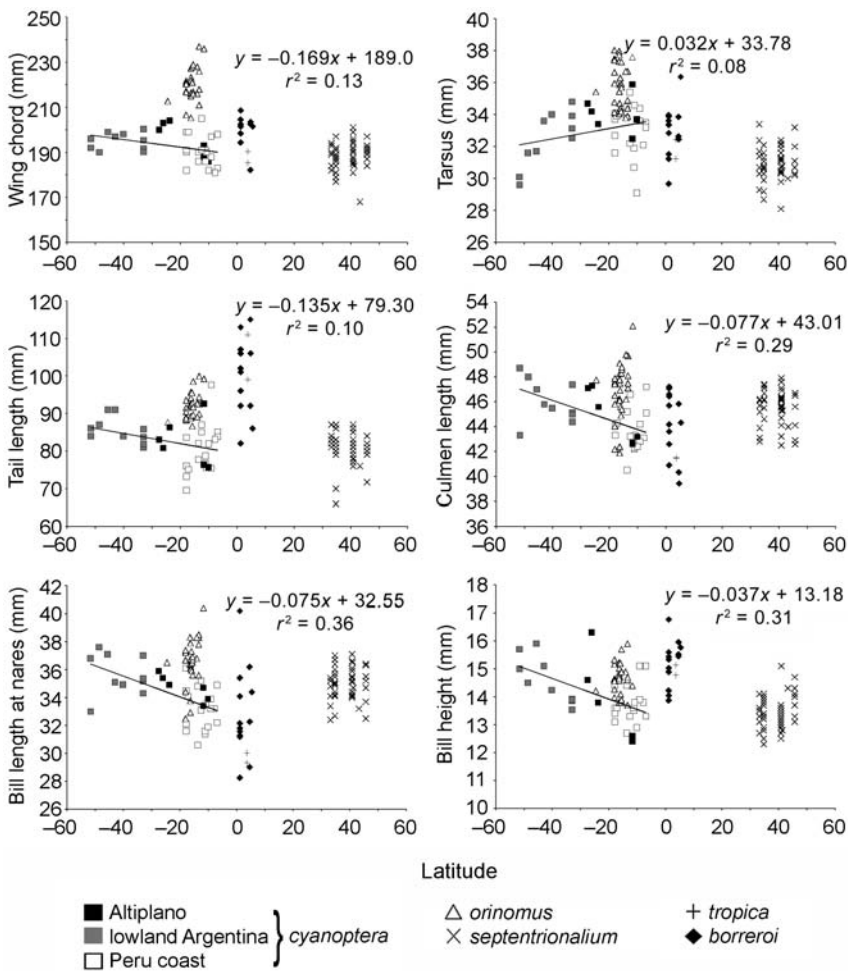


FIG. 3. Relationships between latitude and body-size measurements for male Cinnamon Teal. Regression line is for populations of *Anas cyanoptera cyanoptera* only.

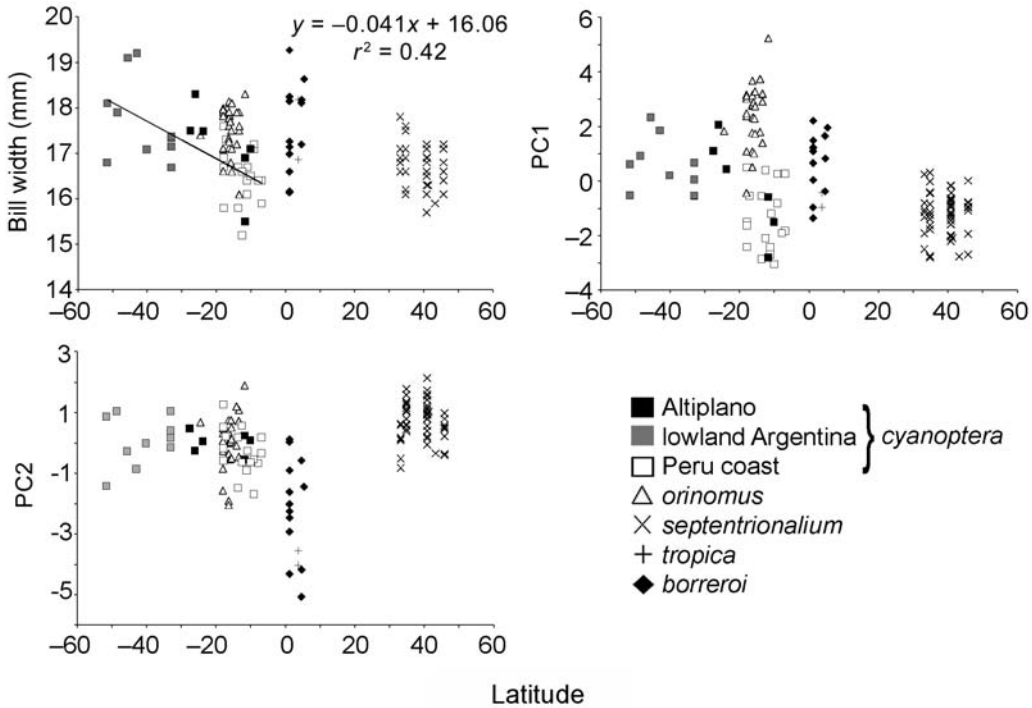


FIG. 4. Relationships between latitude and body-size measurements for male Cinnamon Teal. Regression line is for populations of *Anas cyanoptera cyanoptera* only.

males, PC2 (bill shape) decreased when all individuals were pooled and increased within North America over an elevational increase of ~1,600 m.

Significant correlations with latitude were primarily restricted to males. In females, only bill height showed a positive correlation with latitude within southern populations in South America (*A. c. cyanoptera* and *A. c. orinomus*). In males, tarsus, tail length, and bill height showed a negative correlation, and bill length at nares, culmen length, and PC2 were positively correlated with increasing distance from the equator. Within southern South America, only bill height and bill width were positively correlated with increasing latitude. When only *A. c. cyanoptera* (lowland subspecies) was considered, there was a strong positive correlation between latitude and bill length at nares, culmen length, bill height, bill width, and PC1 from the Peruvian coast to southern Patagonia.

Subspecies classification.—Discriminant analysis with cross-validation correctly classified males to originally assigned subspecies with 69–100% and females with 40–100% accuracy (Table 7).

Discriminant analysis correctly assigned 53.8–86.0% of males and 40.0–100.0% of females to their area of origin (Table 8). Six misclassified male individuals from the central high Andes were assigned to the nearest lowland population adjacent to the area where they were collected, Argentina ($n = 3$) or the Peruvian coast ($n = 3$). All of these individuals were assigned correctly as *A. c. cyanoptera* in the subspecies discriminant analysis.

Male *A. c. orinomus* were diagnosable from *A. c. cyanoptera* using wing chord, tarsus, tail length, and PC1; from *A. c. septentrionalium* using wing chord, tarsus, tail length, bill height, and PC1; and from *A. c. borreroi* using wing chord, tarsus, and bill length at nares (Table 9). The same pattern was found in female *A. c. orinomus*, except that females could not be distinguished from *A. c. borreroi* using bill length at nares (Table 10). *Anas c. septentrionalium* and *A. c. borreroi* were diagnosable using bill length at nares ($D_{sb} = 9.74$, $D_{bs} = 1.50$), culmen length ($D_{sb} = 7.63$, $D_{bs} = 0.01$), bill height ($D_{sb} = 0.02$, $D_{bs} = 2.60$), and PC1 ($D_{sb} = 4.40$, $D_{bs} = 0.91$) for males. When all three subpopulations of *A. c. cyanoptera* were pooled, *A. c.*

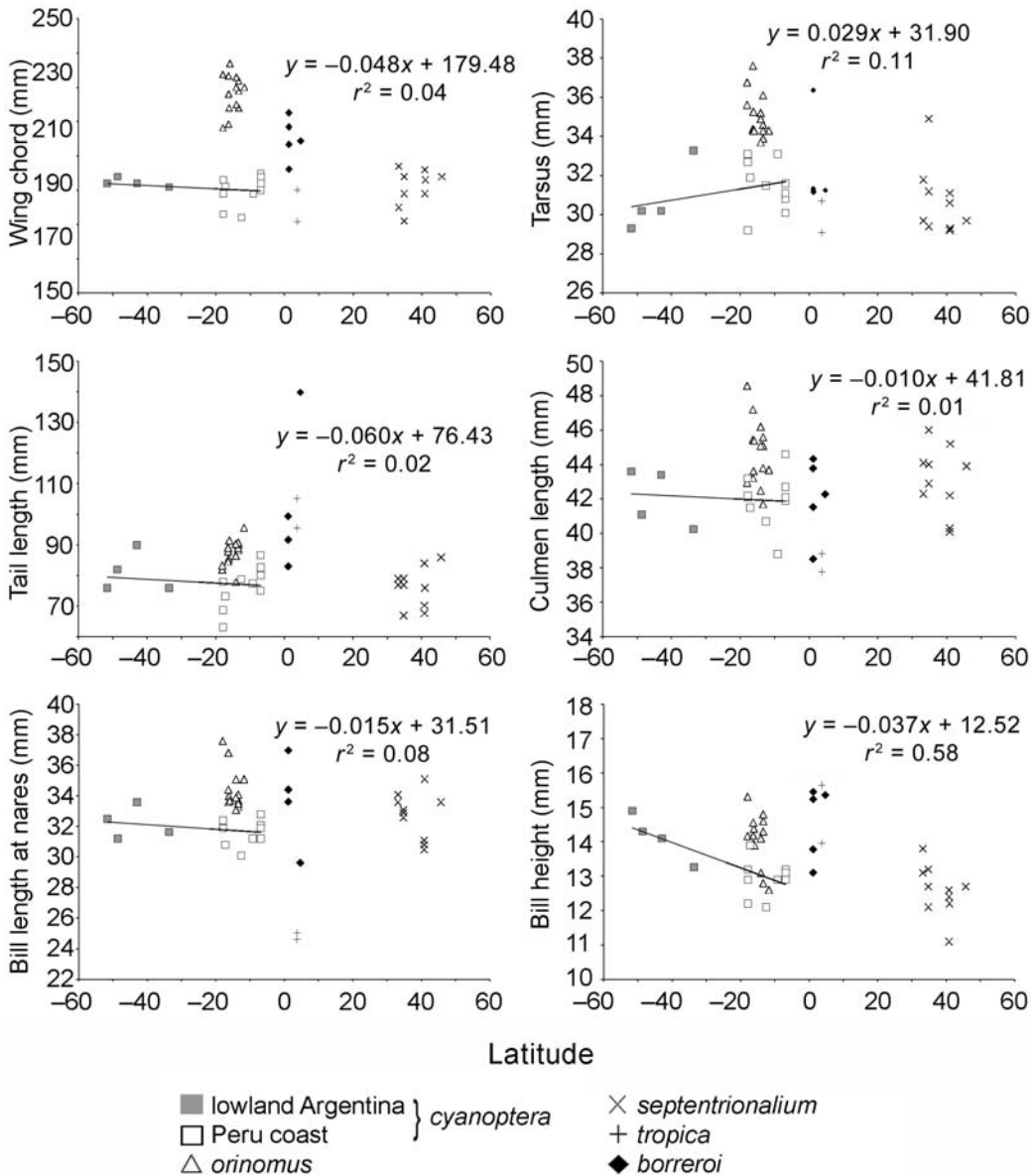


FIG. 5. Relationships between latitude and body-size measurements for female Cinnamon Teal. Regression line is for populations of *Anas cyanoptera cyanoptera* only.

cyanoptera was not diagnosable from *A. c. septentrionalium* or *A. c. borreroi* for any single measurement or PC1. However, at the individual population level, lowland Argentina (*A. c. cyanoptera*) was diagnosable from North America (*A. c. septentrionalium*) using tarsus ($D_{sa} = 5.24$, $D_{as} = 0.90$) and PC1 ($D_{sa} = 4.01$, $D_{as} = 0.61$) and from males in the Colombian highlands (*A. c. borreroi*)

using bill length at nares ($D_{ba} = 10.16$, $D_{ab} = 0.80$). The Peruvian coastal population (*A. c. cyanoptera*) was diagnosable from *A. c. septentrionalium* using bill length at nares ($D_{sp} = 4.91$, $D_{ps} = 0.06$). Female *A. c. borreroi* were diagnosable from both the Peruvian coast ($D_{pb} = 7.94$, $D_{bp} = 1.60$) and lowland Argentina ($D_{ab} = 7.12$, $D_{ba} = 0.37$) populations of *A. c. cyanoptera* using PC1.

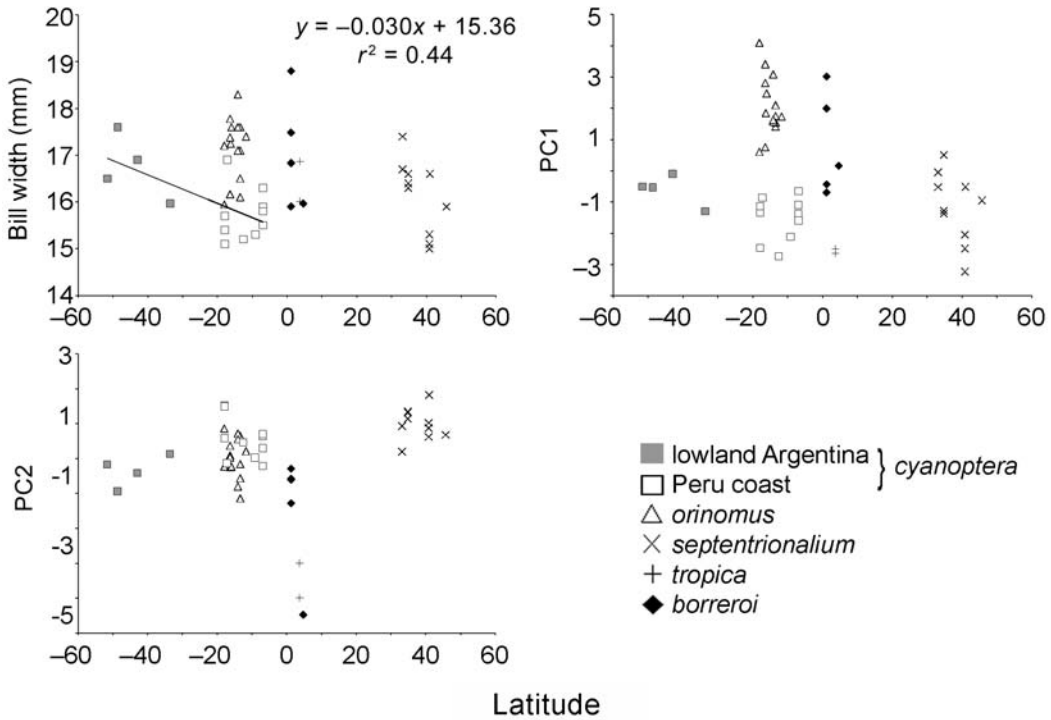


FIG. 6. Relationships between latitude and body-size measurements for female Cinnamon Teal. Regression line is for populations of *Anas cyanoptera cyanoptera* only.

DISCUSSION

Cinnamon Teal are distributed along elevational and latitudinal gradients, and within these gradients climatic and habitat variables change abruptly, placing different selection pressures on different populations (e.g., subspecies). Variances in morphological characteristics appear to conform to ecogeographic regions, given that larger individuals occupied higher elevations in the Andes (*A. c. orinomus* and *A. c. borreiroi*) and occur at higher latitudes in Patagonia (*A. c. cyanoptera*), whereas smaller conspecifics resided at lower elevations in temperate regions (*A. c. cyanoptera*, *A. c. septentrionalium*, and *A. c. tropica*). Environmental variables as a function of temperature and humidity have been related to body size, and modifications of Bergmann’s rule have been made to take into account factors associated with high latitudes and elevations as well as arid habitats (e.g., “latitude effect,” Snow 1954; “aridity effect,” Hamilton 1961). However, other factors, such as hypoxia, fasting endurance, and life-history traits (resource competition and migration),

are also known to facilitate variation in body size (Calder 1974, 1984; Hopkins and Powell 2001; Millien et al. 2006).

The climate of the Andes changes dramatically from the warm, wet temperate zone of the Colombian Andes to the colder, arid climates characteristic of the Altiplano and Patagonia. Patagonia is cool, dry, and windy, with substantial seasonal and diurnal temperature fluctuations. Birds that inhabit southern Patagonia experience average low temperatures ranging from 3°C (Esquel, Chubut) to 8°C (Rio Gallegos, Santa Cruz). The Andean Altiplano is also semi-arid, with most precipitation falling during the austral summer (December to February; Garreaud et al. 2003), leaving the rest of the year cool, dry, and windy. The average low temperatures at Cusco, Peru (3,248 m), and La Paz (4,012 m) have been reported as 5°C and 1°C, respectively (Canty and Associates 2005). Separated by an average of 115 km from the puna zone of the Andes, the lowlands of the Peruvian coast consist of scattered river valleys and associated wetlands that are also classified as semi-arid (Pearson and Plenge 1974).

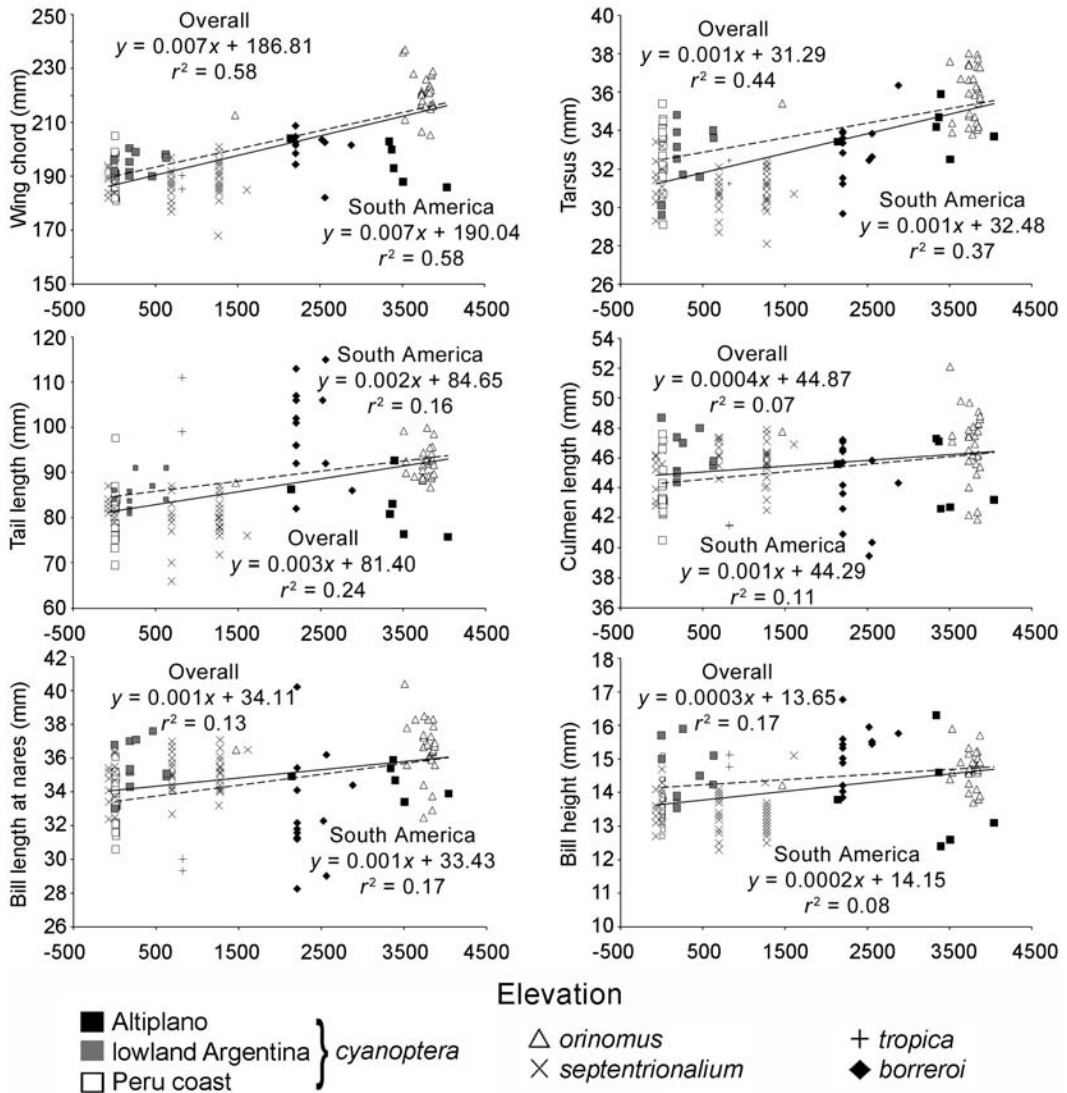


FIG. 7. Relationships between elevation and body-size measurements for male Cinnamon Teal. Dashed regression lines are for South American individuals only.

However, in contrast to the climates of the Altiplano and Patagonia, the Peruvian coast is, on average, 10°C warmer, with temperatures ranging from 15 to 18°C (Canty and Associates 2005). We found that individuals in the warmer, wetter climates of North America (*A. c. septentrionalium*), the Colombian lowlands (*A. c. tropica*), and the Peruvian coast (*A. c. cyanoptera*) had smaller body sizes than those in the central high Andes (*A. c. orinomus* and *A. c. cyanoptera*) and Patagonia (*A. c. cyanoptera*).

Individuals in high-altitude populations of Cinnamon Teal are significantly larger than their closest lowland relatives. The largest subspecies, *A. c. orinomus*, is found exclusively in the central high Andes, with no records of dispersal to adjacent lowland habitats. Individuals collected at mid-elevations (~2,500 m; *A. c. borreiroi* and *A. c. cyanoptera* in northwest Argentina) tended to have intermediate body size (Figs. 7–10). High-altitude habitats exert selection pressures that arise from multiple factors (Monge and León-Velarde 1991).

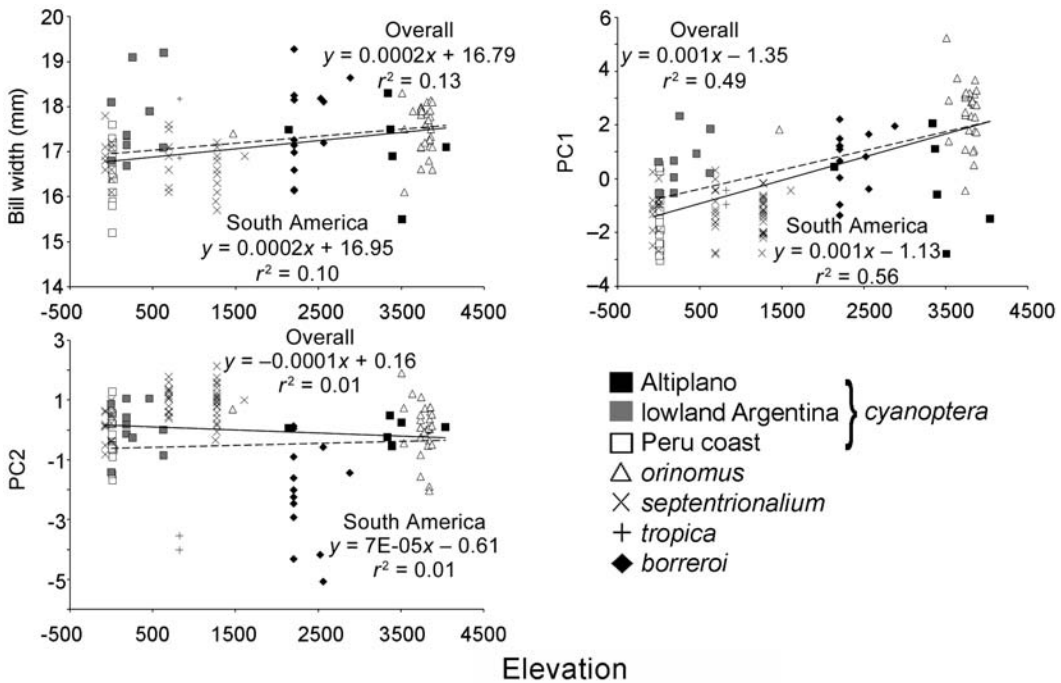


FIG. 8. Relationships between elevation and body-size measurements for male Cinnamon Teal. Dashed regression lines are for South American individuals only.

Besides having a cold, arid climate, these habitats have low air density and the partial pressure of oxygen at 4,000 m is ~60% that at sea level, which may also explain, in part, why high Andean resident populations have larger body size than individuals in populations at lower elevations in the Andes with similar climatic factors (Colombia and Patagonia). Hemoglobin oxygen affinity and body size, for example, have been found to be correlated, such that larger animals tend to have higher affinity (Schmidt-Nielsen and Larimer 1958, Hopkins and Powell 2001). By contrast, smaller-bodied animals tend to have higher metabolic requirements for oxygen, which may favor a higher venous oxygen tension (Schmidt-Nielsen and Larimer 1958, Hopkins and Powell 2001). Other waterfowl species that inhabit similar elevational gradients in the Andes also show a strong correlation between body size and elevation (Blake 1977, Bulgarella et al. 2007). Each highland population also possesses amino acid polymorphisms in the major hemoglobin genes that are likely adaptive (McCracken et al. 2009a, b). Thus, there is an overall trend among South American waterfowl. Larger individuals are found at higher elevations,

whereas the adjacent lowlands are inhabited by smaller conspecifics that also differ in other important traits.

Additionally, there is a general trend for sedentary species to comply more often with Bergmann's rule than migratory species, possibly because nonmigratory species are more affected than migratory species by climatic and other factors such as food availability, in that resident populations are exposed to the same local selection pressures throughout all seasons (Meiri and Dayan 2003). Cinnamon Teal comprise both sedentary and migratory subspecies, with the migratory small-bodied *A. c. septentrionalium* showing few significant correlations with either latitude or elevation. There was a correlation with bill shape (PC2) and elevation among males, which was attributable to a decrease of <0.6 mm in bill width or bill height between Utah (1,275 m) and either Oregon or California (<700 m). However, male breeding-site philopatry is typically very low in dabbling ducks (Anderson et al. 1992). Conversely, South American subspecies, with the exception of the southernmost populations in Argentina, may be predominantly nonmigratory

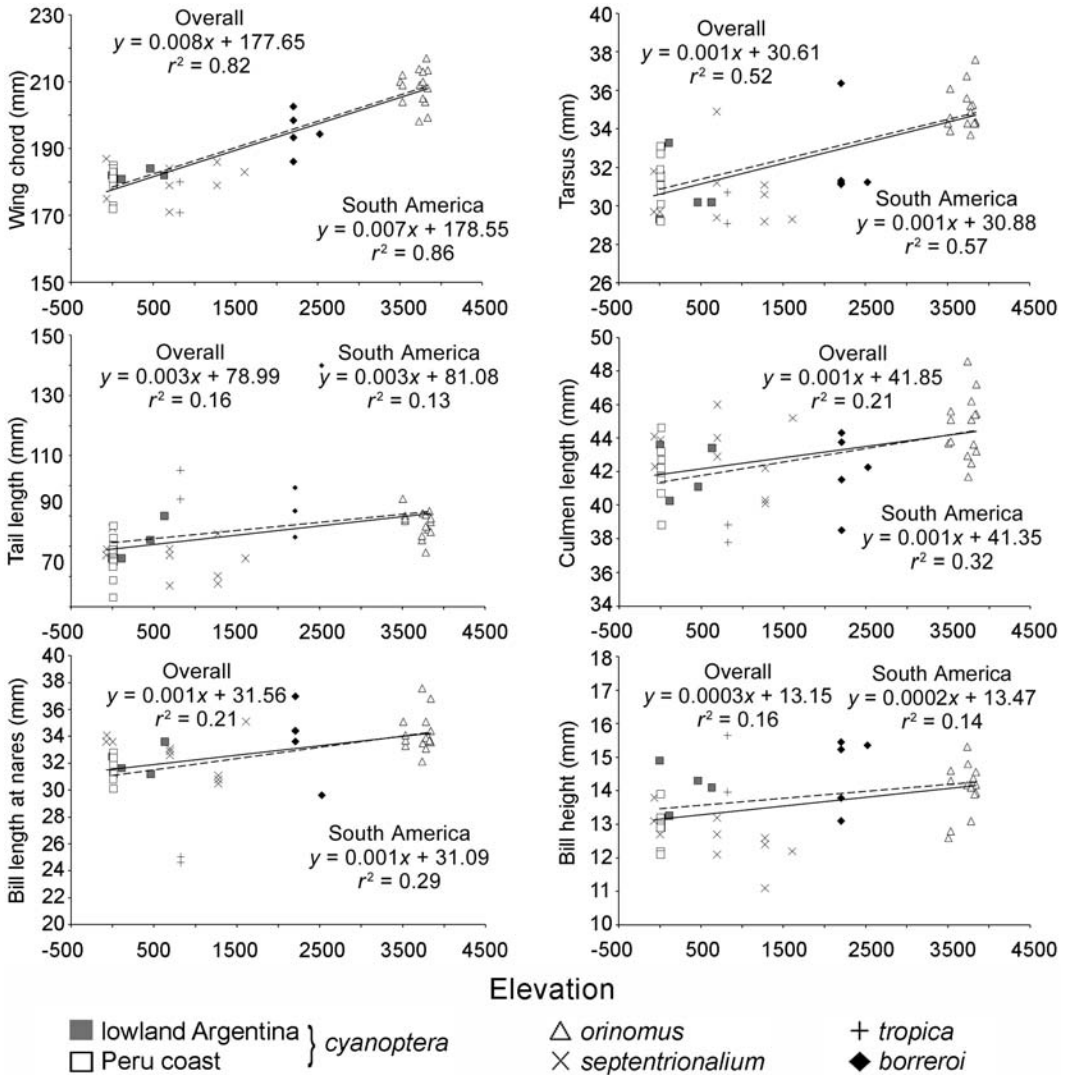


FIG. 9. Relationships between elevation and body-size measurements for female Cinnamon Teal. Dashed regression lines are for South American individuals only.

and show significant correlations between morphological and geographic variables, especially *A. c. cyanoptera*, which occupies a wide range of habitats from coastal Peru to southern Patagonia.

Little information is available on the movements of individual teal between the lowlands and highlands of South America. The lowland subspecies, *A. c. cyanoptera*, occurs in the highlands in small numbers, but the extent of its distribution in the Andes is unknown. We sampled individual *A. c. cyanoptera* in the highlands at only the northern and southern edges of the Altiplano.

Six individuals of this subspecies were collected at 2,141–3,369 m in northwestern Argentina (KGM 442, KGM 1110, KGM 1142) and at 3,393–4,039 m in Peru (REW 118, REW 122, REW 164). There are no records of *A. c. cyanoptera* breeding in the high Andes, and only one individual we collected was in breeding condition (KGM 1142), judging by gonad size (left testis: 30 × 10 mm), even though all individuals were in complete breeding plumage. Two individuals (REW 118, REW 122) from Jauja, Peru (3,506 m), were part of a large group that contained both highland and lowland subspecies.

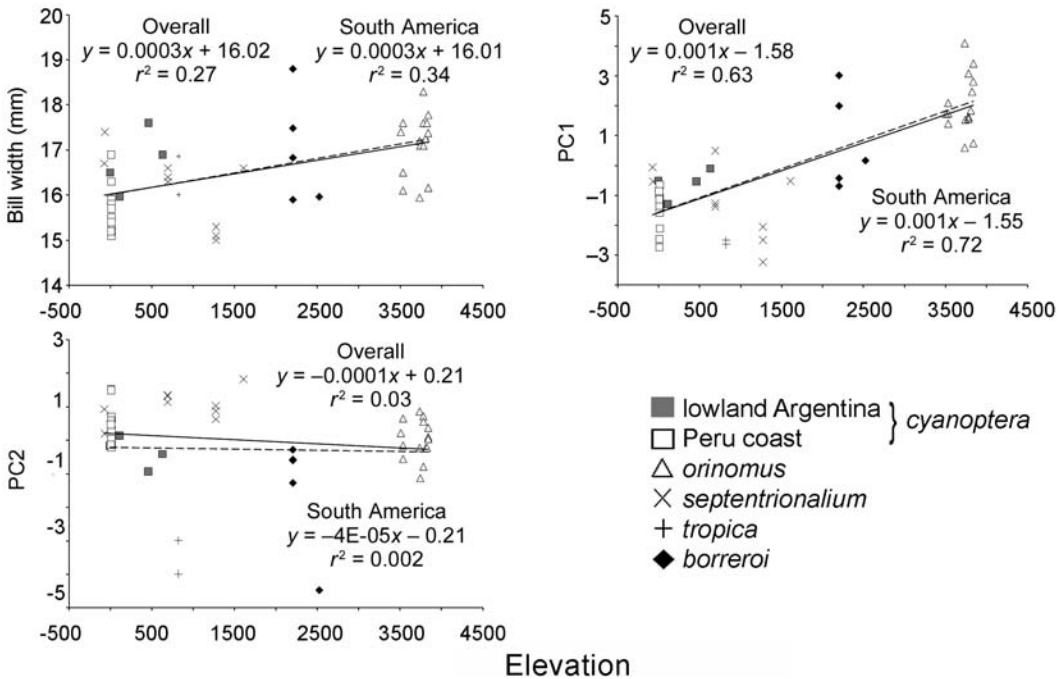


FIG. 10. Relationships between elevation and body-size measurements for female Cinnamon Teal. Dashed regression lines are for South American individuals only.

All other individuals were either solitary or accompanied by one or two other individuals, and no other Cinnamon Teal were found in the surrounding areas. This suggests that these individuals may have been migrants or, more likely, vagrants to these areas rather than permanent residents, as each individual was assigned to the nearest lowland population. In addition, there are no records of *A. c. orinomus* descending to coastal habitats. One *A. c. orinomus* (KGM 441) was collected at 1,468 m in Salta, Argentina, which, to our knowledge, is the lowest elevation reported for this subspecies. Pearson and Plenge (1974) recorded occasional sightings of other Andean waterfowl species (e.g., *A. puna* and *A. flavirostris*) on the coast of Peru, which they attributed to decreased food availability at high elevations during the dry season or competition with seasonal migrants from the south. Water temperature of high Andean lakes (>4,000 m) shows little seasonal variation within the Andean tropical regions, and only the shallow ponds and lakes will freeze or dry up (R. E. Wilson pers. obs.). Cinnamon Teal populations thus face a variety of environmental factors, and phenotypic diversity appears to have arisen from spatial and temporal heterogeneity in

selection pressures resulting in adaptations to the local environment.

Subspecies classification.—Morphological (plumage and body size) distinctiveness of individuals in adjacent geographic areas of North America and South America led to the naming of five Cinnamon Teal subspecies (Snyder and Lumsden 1951). However, this classification had not previously been tested. Our analyses (MANOVA and ANOVA) differentiated all subspecies for males, and female *A. c. orinomus* differed from all other subspecies. Discriminant analysis showed high accuracy of subspecies prediction for males of all subspecies and female *A. c. orinomus* and *A. c. cyanoptera*. However, diagnosability of individuals to subspecific groups using the 75% rule (Amadon 1949) showed that few characters reliably distinguished subspecies, excluding *A. c. orinomus*. Low diagnosability among subspecies for females may be attributable, in part, to low sample sizes. The most reliable characters that enabled diagnosis between *A. c. orinomus* and the other subspecies were wing chord, tarsus, and PC1 (overall body-size variable). Low diagnosability of *A. c. cyanoptera* with respect to North American and Colombian subspecies could be attributable to

Table 7. Classification of predicted subspecies of Cinnamon Teal (*Anas cyanoptera*) based on body-size measurements and discriminant analysis with (inside parentheses) and without (outside parentheses) cross-validation. The percentages of individuals that were assigned to their initial subspecific classification are in bold text.

| Initially classified as: | Predicted | | | |
|--------------------------|--------------------|------------------|-------------------------|--------------------|
| | <i>cyanoptera</i> | <i>orinomus</i> | <i>septentrionalium</i> | <i>borreroi</i> |
| Male (<i>n</i> = 127) | | | | |
| <i>cyanoptera</i> | 76.5 (76.5) | 0.0 (0.0) | 14.7 (14.7) | 8.8 (8.8) |
| <i>orinomus</i> | 0.0 (0.0) | 100 (100) | 0.0 (0.0) | 0.0 (0.0) |
| <i>septentrionalium</i> | 8.0 (10.0) | 0.0 (0.0) | 92.0 (90.0) | 0.0 (0.0) |
| <i>borreroi</i> | 7.7 (30.8) | 0.0 (0.0) | 0.0 (0.0) | 92.3 (69.2) |
| Total correct: | 89.8 (86.6) | | | |
| Female (<i>n</i> = 44) | | | | |
| <i>cyanoptera</i> | 85.7 (71.4) | 0.0 (0.0) | 0.0 (28.6) | 0.0 (0.0) |
| <i>orinomus</i> | 0.0 (0.0) | 100 (100) | 0.0 (0.0) | 0.0 (0.0) |
| <i>septentrionalium</i> | 30.0 (50.0) | 0.0 (0.0) | 70.0 (50.0) | 0.0 (0.0) |
| <i>borreroi</i> | 0.0 (20.0) | 0.0 (40.0) | 0.0 (0.0) | 100 (40.0) |
| Total correct: | 88.6 (72.7) | | | |

within-subspecies variation, given that there were significant mean differences between populations of *A. c. cyanoptera*. When analyzed at the population level, the Argentine and Peruvian coastal populations were diagnosable from *A. c. borreroi* and *A. c. septentrionalium* using bill length measurements or PC1. Upon examination of measurements originally used to define these subspecies, the results are not surprising, because there is considerable overlap in body-size measurements, which indicates

that measurements alone may not be sufficient to distinguish subspecies. Other characters, such as plumage coloration and patterns, have been proposed to differentiate subspecies (Snyder and Lumsden 1951). Although the coloration of males within and among subspecies is variable, plumage divergence in color patches that appear identical to the human eye has been reported between *A. c. septentrionalium* and South American subspecies (*A. c. orinomus* and *A. c. cyanoptera*; Wilson et

TABLE 8. Classification of predicted area of origin of individual Cinnamon Teal (*Anas cyanoptera*) based on body-size measurements and discriminant analysis with (inside parentheses) and without (outside parentheses) cross-validation. The percentages of individuals that were assigned to their collection locality are in bold text.

| Initially classified as: | Predicted | | | | |
|--------------------------|--------------------|--------------------|--------------------|--------------------|--------------------|
| | Central high Andes | Argentina | Peruvian Coast | North America | Colombia highlands |
| Male (<i>n</i> = 127) | | | | | |
| Central high Andes | 83.3 (83.3) | 8.3 (8.3) | 8.3 (8.3) | 0.0 (0.0) | 0.0 (0.0) |
| Argentina | 0.0 (0.0) | 80.0 (40.0) | 20.0 (30.0) | 0.0 (20.0) | 0.0 (10.0) |
| Peruvian Coast | 5.6 (5.6) | 0.0 (0.0) | 77.8 (77.8) | 11.1 (11.1) | 5.6 (5.6) |
| North America | 0.0 (0.0) | 6.0 (8.0) | 4.0 (6.0) | 90.0 (86.0) | 0.0 (0.0) |
| Colombian highlands | 7.7 (7.7) | 23.1 (23.1) | 0.0 (15.4) | 0.0 (0.0) | 69.2 (53.8) |
| Total correct: | 83.5 (77.2) | | | | |
| Female (<i>n</i> = 44) | | | | | |
| Central high Andes | 100 (100) | 0.0 (0.0) | 0.0 (0.0) | 0.0 (0.0) | 0.0 (0.0) |
| Argentina | 0.0 (0.0) | 75.0 (75.0) | 25.0 (25.0) | 0.0 (0.0) | 0.0 (0.0) |
| Peruvian Coast | 0.0 (0.0) | 20.0 (20.0) | 60.0 (60.0) | 20.0 (20.0) | 0.0 (0.0) |
| North America | 0.0 (0.0) | 10.0 (10.0) | 20.0 (40.0) | 70.0 (50.0) | 0.0 (0.0) |
| Colombian highlands | 0.0 (20.0) | 0.0 (20.0) | 0.0 (0.0) | 0.0 (0.0) | 100 (40.0) |
| Total correct: | 81.8 (70.5) | | | | |

TABLE 9. Pairwise diagnosability index values (D_{ij}/D_{ij}) for males of subspecies of Cinnamon Teal (*Anas cyanoptera*). D_{ij} values greater than zero indicate that population i is diagnosable from population j and are in bold.

| | Wing chord | Tarsus | Tail | Nare | Culmen | Bill height | Bill width | PCI |
|-----------------------------|--------------------|-------------------|--------------------|-------------------|-------------------|-------------------|-------------------|-------------------|
| <i>orinomus</i> | | | | | | | | |
| and <i>cyanoptera</i> | 37.91/14.22 | 5.57/0.46 | 21.27/5.30 | 5.41/-0.45 | 5.35/-2.04 | 2.50/-0.02 | 2.27/-0.15 | 0.37/4.79 |
| and <i>borroei</i> | 34.13/7.73 | 6.23/0.58 | -16.81/9.06 | 11.02/1.82 | 8.30/-1.03 | -1.27/1.31 | -2.25/0.65 | -0.50/3.68 |
| and <i>septentrionalium</i> | 40.98/17.92 | 6.34/2.15 | 18.65/5.85 | 3.25/-1.64 | 3.02/-3.37 | 2.25/0.33 | 1.48/-0.24 | 2.60/5.89 |
| and <i>cyanoptera</i> | | | | | | | | |
| and <i>borroei</i> | -7.06/17.32 | 3.33/-2.52 | -5.47/24.28 | 8.55/-0.66 | 6.30/-2.33 | -0.33/2.85 | -1.47/1.99 | 3.31/-1.32 |
| and <i>septentrionalium</i> | 13.92/-7.18 | 3.43/-0.96 | 7.30/-9.40 | -0.77/4.13 | -1.01/4.67 | 1.31/-1.21 | 0.69/-1.57 | -0.20/3.53 |
| and <i>septentrionalium</i> | | | | | | | | |
| and <i>borroei</i> | -3.40/20.39 | -1.64/3.30 | -4.94/21.66 | 9.74/1.50 | 7.63/0.01 | 0.02/2.60 | -1.55/1.19 | 4.40/0.91 |

TABLE 10. Pairwise diagnosability index values (D_{ij}/D_{ij}) for females of subspecies of Cinnamon Teal (*Anas cyanoptera*). D_{ij} values greater than zero indicate that population i is diagnosable from population j and are in bold.

| | Wing chord | Tarsus | Tail | Nare | Culmen | Bill height | Bill width | PCI |
|-----------------------------|--------------------|-------------------|---------------------|-------------------|-------------------|-------------------|-------------------|-------------------|
| <i>orinomus</i> | | | | | | | | |
| and <i>cyanoptera</i> | 34.35/16.45 | 6.67/1.80 | 24.91/3.07 | 3.84/-0.64 | 5.37/-1.14 | 2.31/-0.62 | 2.63/-0.13 | 0.64/0.27 |
| and <i>borroei</i> | 32.65/3.85 | 10.63/1.58 | -67.43/9.29 | 9.47/-1.25 | 9.91/-0.54 | -3.02/1.69 | 4.18/-0.74 | -4.18/2.62 |
| and <i>septentrionalium</i> | 38.24/17.13 | 8.46/2.65 | 26.19/4.21 | 4.82/-1.10 | 5.74/-1.91 | 3.01/0.05 | 2.75/-0.22 | 0.69/4.96 |
| <i>cyanoptera</i> | | | | | | | | |
| and <i>borroei</i> | -5.80/20.13 | -6.70/2.96 | -55.88/24.89 | -7.38/2.38 | -7.48/2.35 | -2.22/2.54 | -2.99/2.07 | 1.27/-4.51 |
| and <i>septentrionalium</i> | -11.40/6.83 | 4.53/-1.89 | 14.64/-12.21 | -2.73/2.22 | -3.32/3.71 | 2.22/-0.84 | -1.58/1.55 | -1.14/2.77 |
| <i>septentrionalium</i> | | | | | | | | |
| and <i>borroei</i> | -5.11/24.01 | -5.84/4.75 | -54.72/26.17 | -7.84/3.36 | 8.24/-2.73 | -1.54/3.24 | -3.09/2.19 | 7.28/-0.01 |

al. 2008). The Colombian subspecies (*A. c. borreiroi* and *A. c. tropica*) are typically darker in coloration, with spotting occurring at higher frequency (100% in *A. c. tropica*) than in the other three subspecies, but spotting also can be variable, with substantial overlap among other subspecies (Snyder and Lumsden 1951). The tone of the cinnamon color in males ranges from dark (Colombian subspecies) to pale (*A. c. orinomus*). Females are more difficult to differentiate with plumage, but in general, as with males, Colombian subspecies are darker in color. Thus, we suggest that the current subspecies classification is valid on the basis of body-size measurements (present study) and plumage coloration and as described by Snyder and Lumsden (1951) and Wilson et al. (2008).

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APPENDIX 1. Specimens of *Anas cyanoptera* examined, with collection locality. KGM, JT, and REW specimens are catalogued at University of Alaska Museum, Fairbanks.

A. c. borreiroi

COLOMBIA: Dept. Putumayo, Sibundoy

ROM 79230, ROM 79231, ROM 79232, ROM 79233, ROM 79234, ROM 91946, ROM 91947, ROM 91948, ROM 91949, ROM 91950, ROM 91954, SM437473, SM437474

COLOMBIA: Dept. Cundinamarca, La Herrera

ROM 91943, ROM 91953

COLOMBIA: Dept. Cundinamarca, Laguna Fuquene

SM 437475

COLOMBIA: Dept. Cundinamarca, Sabana de Bogota

ROM 91944, SM437472

A. c. tropica

COLOMBIA: Dpto. Valle del Cauca, Vijes

ROM 91957, ROM 91958, ROM 91959, ROM 91960

A. c. septentrionalium

USA: Utah, Weber Co., 41° 14' 59.7" N, 112° 07' 55.8" W, 1,275 m

REW 075

USA: Utah, Salt Lake Co., 40° 50' 50.7" N, 112° 01' 50.9" W, 1,275 m

REW 077, REW 078, REW 079

USA: Oregon, Columbia Co., 45° 45' 18.1" N, 122° 50' 51.4" W, 1 m

(continued)

APPENDIX 1. (Continued)

REW 797, REW 398, REW 399, REW 400, REW 401, REW 402, REW 403, REW 404, REW 406
 USA: California, Imperial Co., 33° 11' 24.0" N, 115° 35' 18.5" W, -68 m
 REW 411, REW 412, REW 414, REW 416, REW 418, REW 419, REW 421
 USA: California, Imperial Co., 33° 11' 39.0" N, 115° 34' 46.2" W, -73 m
 REW 415, REW 420
 USA: California, Kerns Co., 34° 47' 43.5" N, 118° 07' 11.3" W, 693 m
 REW 422, REW 423, REW 424, REW 425, REW 426, REW 427, REW 428, REW 429, REW 430, REW 431, REW 432,
 REW 433, REW 434, REW 435, REW 436, REW 437
 USA: Utah, Salt Lake Co., 40° 50' 45.1" N, 112° 01' 41.7" W, 1,275 m
 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
 USA: Colorado, Moffat Co., 40° 59' 10.7" N, 108° 59' 10.5" W, 1,609 m
 REW 457, REW 458
 USA: Oregon, Harney Co., 48° 43' 53.7" N, 118° 50' 25.3" W, 1,260 m
 REW 464

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, KGM 313, KGM 311, KGM 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, 2,141 m
 KGM 442
 PERU: Dpto. Lima, S. Huacho, 11° 10' 12.9" S, 77° 35' 31.4" W, 15 m
 REW 081, REW 082
 PERU: Dpto. Junin, Jauja, Laguna de Paca, 11° 44' 14.5" S, 75° 29' 32.7" W, 3,506 m
 REW 118, REW 122
 PERU: Dpto. Ancash, Laguna Conococha, 10° 07' 10.8" S, 77° 17' 00.7" W, 4,039 m
 REW 164
 PERU: Dpto. Lambayeque, ca. Puerto Eten, 06° 54' 51.9" S, 79° 52' 22.4" W, 13 m
 REW 193, REW 194, REW 195, REW 196
 PERU: Dpto. Lambayeque, Playa Monsefu, 06° 54' 03.7" S, 79° 53' 42.4" W, 12 m
 REW 198, REW 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, REW 204, REW 205
 PERU: Dpto. Ancash, Puerto Huarney, 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, REW 299, REW 300, REW 301, REW 302, REW 303, REW 304
 PERU: Dpto. Arequipa, Punta de Bombon-Islay, 17° 11' 31.9" S, 71° 46' 19.4" W, 8 m
 REW 305, REW 306
 PERU: Dpto. Lima, 2 km N. La Laguna, 12° 33' 13.0" S, 76° 42' 42.1" W, 9 m
 REW 315, REW 316, REW 317

(continued)

APPENDIX 1. (Continued)

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- ARGENTINA: Chubut, Laguna Terraplen, 42° 59' 50.7" S, 71° 30' 55.1" W, 630 m
KGM 712, KGM 713
- ARGENTINA: Santa Cruz, Estancia La Angostura, 48° 38' 33.9" S, 70° 38' 37.3" W, 460 m
KGM 766, KGM 767
- ARGENTINA: Santa Cruz, ca. Punta Loyola, 51° 37' 35.7" S, 69° 00' 59.4" W, -3 m
KGM 797, KGM 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 Alumbreira, 26° 06' 46.4" S 67° 25' 26.7" W, 3,338 m
KGM 1110
- ARGENTINA: Catamarca, Embalse Las Cortaderas, 27° 33' 21.2" S, 68° 08' 41.9" , 3,369 m
KGM 1142
- A. c. orinomus*
- ARGENTINA: Salta, NE La Caldera, 24° 33' 01" S, 65° 22' 15" W, 1,468 m
KGM 441
- BOLIVIA: Dpto. La Paz, Lago Titicaca, 16° 11' 45" S, 68° 37' 28" W, 3,808 m
KGM 485, KGM 486, KGM 487
- BOLIVIA: Dpto. La Paz, Lago Titicaca, 16° 20' 13" S, 68° 41' 20" W, 3,854 m
KGM 499
- BOLIVIA: Dpto. Oruro, Lago Uru Uru, 18° 02' 03" S, 67° 08' 46" W, 3,735 m
KGM 527, KGM 528, KGM 529, KGM 530, KGM 531, KGM 532, KGM 533, KGM 534, KGM 535
- BOLIVIA: Dpto. La Paz, Lago Titicaca, 16° 25' 28" S, 68° 51' 43" W, 3,850 m
KGM 557
- BOLIVIA: Dpto. La Paz, Lago Titicaca, Cohani, 16° 21' 03" S, 68° 37' 40" W, 3,839 m
KGM 559, KGM 560
- BOLIVIA: Dpto. La Paz, Lago Titicaca, Cohani, 16° 21' 02" S, 68° 37' 48" W, 3,840 m
KGM 561, KGM 562
- BOLIVIA: Dpto. La Paz, Lago Titicaca, Cohani, 16° 21' 07" S, 68° 38' 06" W, 3,845 m
KGM 563, KGM 564, KGM 565, KGM 566
- PERU: Dpto. Junin, Jauja, Laguna de Paca, 11° 44' 14.5" S, 75° 29' 32.7" W, 3,506 m
REW 125, REW 126
- PERU: Dpto. Cusco, Laguna Chacan, 13° 26' 02.6" S, 72° 07' 49.6" W, 3,533 m
REW 238, REW 239, REW 240, REW 241, REW 242
- PERU: Dpto. Cusco, ca. Chinchero, 13° 25' 49.3" S, 72° 03' 41.7" W, 3,789 m
REW 248
- PERU: Dpto. Cusco, Urubamba Valley, 13° 25' 22.9" S, 72° 02' 38.2" W, 3,743 m
REW 253, REW 254
- PERU: Dpto. Cusco, ca. Laguna Pomacanchi, 14° 06' 51.9" S, 71° 27' 56.6" W, 3,781 m
REW 255, REW 256, REW 257, REW 258, REW 259
- PERU: Dpto. Puno, Lago Titicaca, Jaru Jaru, 15° 59' 05.6" S, 69° 36' 24.3" W, 3,824 m
REW 268, REW 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
REW 284, REW 285, REW 286
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^aThese elevation values are interpolated from the U.S. Geological Survey's GTOPO30 digital elevation model (available at eros.usgs.gov/); all other elevations were measured with a GPS receiver.

APPENDIX 2. Dry body-size measurements (mm) for three subspecies of Cinnamon Teal (*A. cyanoptera cyanoptera*).

| | <i>A. c. orinimus</i> ^a | | | <i>A. c. cyanoptera</i> ^a | | | <i>A. c. septentrionalium</i> ^a | | |
|------------------|------------------------------------|------|------------|--------------------------------------|------|------------|--|------|-----------|
| | Mean | SE | Range | Mean | SE | Range | Mean | SE | Range |
| Male | | | | | | | | | |
| Wing chord | 215.4 | 1.05 | 200–229 | 186.8 | 1.39 | 176–201 | 185.5 | 1.0 | 163–199 |
| Tarsus bone | 34.75 | 0.30 | 32.2–37.3 | 32.31 | 0.21 | 30.1–34.1 | 30.32 | 0.14 | 27.7–32.1 |
| Tail | 96.07 | 1.08 | 82.0–108.0 | 86.52 | 1.22 | 75–102 | 78.75 | 0.53 | 66.0–85.0 |
| Bill length–nare | 36.61 | 0.32 | 32.4–39.6 | 34.32 | 0.37 | 30.9–37.6 | 35.05 | 0.16 | 32.0–36.8 |
| Culmen | 47.19 | 0.44 | 42.0–52.4 | 44.36 | 0.49 | 40.1–49.3 | 44.70 | 0.20 | 41.7–47.1 |
| Bill height | 14.36 | 0.23 | 12.5–17.6 | 13.34 | 0.14 | 11.5–15.2 | 12.58 | 0.10 | 11.0–14.4 |
| Bill width | 16.49 | 0.13 | 14.9–17.4 | 16.05 | 0.18 | 14.1–17.7 | 15.58 | 0.15 | 12.6–17.4 |
| Female | | | | | | | | | |
| Wing chord | 202.4 | 1.7 | 193–217 | 177.9 | 2.0 | 167–191 | 178.5 | 1.8 | 169–186 |
| Tarsus bone | 33.59 | 0.54 | 30.6–37.2 | 31.29 | 0.45 | 29.3–33.5 | 30.29 | 0.43 | 28.8–32.8 |
| Tail | 91.87 | 1.48 | 84.0–102.0 | 83.94 | 2.85 | 71.3–102.0 | 77.10 | 1.86 | 69.0–88.0 |
| Bill length–nare | 34.16 | 0.44 | 32.2–37.9 | 31.83 | 0.34 | 29.9–33.1 | 32.83 | 0.49 | 30.5–35.4 |
| Culmen | 44.57 | 0.55 | 41.7–49.8 | 41.41 | 0.62 | 38.6–43.8 | 42.37 | 0.54 | 39.7–44.9 |
| Bill height | 13.82 | 0.24 | 12.5–15.5 | 12.80 | 0.29 | 11.1–14.1 | 11.83 | 0.28 | 10.2–13.1 |
| Bill width | 15.70 | 0.28 | 13.6–17.2 | 15.04 | 0.16 | 14.2–16.2 | 15.07 | 0.39 | 13.1–17.3 |

^aSample sizes: *A. c. orinimus*, 29 males and 14 females; *A. c. cyanoptera*, 27 males and 10 females; *A. c. septentrionalium*, 47 males and 10 females.