

## ELEVATIONAL VARIATION IN BODY SIZE OF CRESTED DUCKS (*LOPHONETTA SPECULARIOIDES*) FROM THE CENTRAL HIGH ANDES, MENDOZA, AND PATAGONIA

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**Resumen.** – Variación altitudinal en tamaño corporal de Patos Crestones (*Lophonetta specularioides*) de los Andes centrales, Mendoza y Patagonia. – El Pato Crestón (*Lophonetta specularioides*) habita los Andes de Sudamérica desde Tierra del Fuego hasta el centro de Perú. Existen dos subespecies (*L. s. specularioides* y *L. s. alticola*) que ocupan ambientes con gran variación en elevación, desde el nivel del mar hasta los 5000 m de altura. Se evaluaron las diferencias en morfología entre las dos subespecies y se buscó evidencia a favor de las reglas de Bergmann y Allen, con el fin de comprender las fuerzas que actuaron para moldear la variación geográfica en morfología en las poblaciones de Pato Crestón de altura y del llano. Se encontraron diferencias en el tamaño corporal general entre las subespecies y entre los sexos. Machos y hembras de la subespecie *L. s. alticola*, colectados en los Andes centrales a elevaciones entre los 3338 y los 4611 m de altura, fueron mas grandes que los individuos de la subespecie *L. s. specularioides* colectados en Patagonia (< 934 m hasta el nivel del mar). Se hallaron individuos de la subespecie *L. s. alticola* de tamaño intermedio a una elevación intermedia (1522–2552 m) en la provincia de Mendoza, Argentina. Análisis discriminante clasificó correctamente el 96,1% de los machos de *L. s. alticola* y el 100% de los machos *L. s. specularioides*; el 100% de las hembras fueron correctamente clasificadas. Peso corporal, cuerda del ala, largo del tarso y largo del pico presentaron correlación positiva con elevación en machos *L. s. alticola*, mientras que en machos *L. s. specularioides* se observó una correlación negativa entre tarso total y elevación. El Pato Crestón conforma con la Regla de Bergmann. No se encontró evidencia a favor de la Regla de Allen. Patos Crestones de tamaño intermedio, tales como los que se encuentran en Mendoza, Argentina podrían resultar de introgresión entre *L. s. alticola* y *L. s. specularioides*, y/o selección natural en tamaño corporal de individuos localmente adaptados a hábitats de elevación intermedia.

**Abstract.** – The Crested Duck (*Lophonetta specularioides*) inhabits the Andes of South America from Tierra del Fuego to central Perú, with two subspecies (*L. s. specularioides* and *L. s. alticola*) inhabiting different elevational environments in the Andes from sea level to 5000 m. We evaluated morphological differences between the two subspecies of Crested Duck and evidence for Bergmann’s and Allen’s rules to gain a better understanding of the forces that have acted to shape geographic variation in morphology of highland

and lowland populations. Overall body size of Crested Ducks differed between subspecies and between sexes. Male and female *L. s. alticola* from the central high Andes sampled at 3338–4611 m were larger than *L. s. specularioides* from southern Patagonia (< 934 m to sea level). *L. s. alticola* individuals of intermediate body size were found at mid elevations (1522–2552 m) in Mendoza, Argentina. Stepwise discriminant analysis (DA) classified 96.1% of *L. s. alticola* and 100% of *L. s. specularioides* males correctly; 100% of females were classified correctly. Body mass, wing chord, tarsus length, and bill length were positively correlated with elevation in male *L. s. alticola*, whereas total tarsus was negatively correlated with elevation in male *L. s. specularioides*. Crested Ducks conform to Bergmann's Rule. No evidence was found for Allen's Rule. Intermediate size Crested Ducks, such as those found in Mendoza, Argentina, might result from introgression between *L. s. alticola* and *L. s. specularioides*, and/or natural selection on body size of individuals locally adapted to intermediate elevational habitats. Accepted 6 September 2007.

**Key words:** Andes, Crested Duck, elevation, geographic variation, *Lophonetta specularioides*, morphology, Patagonia.

## INTRODUCTION

Similar morphological adaptations among species that live in similar environments are often expressed in terms of ecological or ecogeographic principles. Two of the most important ecogeographic principles are Bergmann's rule and Allen's rule (e.g., Mayr 1942). Bergmann's rule predicts that smaller-sized individuals are found in warmer parts of a species' range, and that larger individuals occur in cooler regions (Bergmann 1847). Allen's rule predicts that protruding body parts (e.g., tail, ears, bill) are relatively shorter in colder environments (Allen 1877). The usual explanation for Bergmann's and Allen's rules is that large animals with smaller extremities expend less energy for thermoregulation because of their smaller surface-to-volume ratio. Snow (1954a, 1954b) found widespread support for Bergmann's rule, but further expressed the principle as a "latitudinal effect", size being greater at higher than lower latitudes; and an "elevational effect", individuals living at higher elevations tend to be larger than those in lowlands. However, there are contrasting points of view regarding the physiological and ecological significance of these rules (Ray 1960, McNab 1971, James 1991). Bergmann's rule was criticized by Scholander (1955), who argued that many

species do not conform to it, and those examples that show clinal increases in body mass are physiologically not significant because vascular control and fur insulation are more efficient at heat dissipation and conservation than are changes in body size. Furthermore, some poikilotherms show similar body size trends with latitude and temperature (Ray 1960, Lindsey 1966), a pattern that may not easily be explained by heat conservation. James (1970) reformulated Bergmann's rule to account for the combined effects of several climatic variables such as temperature and moisture, rather than temperature alone. McNab (1971) argued that food availability also might explain why most homeotherms are larger at higher latitudes. More recently, Ashton (2002) found strong support for Bergmann's rule in birds, and Millien *et al.* (2006) concluded that patterns underlying ecotypic variation are complex, involve a number of interrelated variables, and highly context-dependent.

Waterfowl inhabiting South America offer an excellent opportunity to evaluate evidence for Bergmann's and Allen's rules because they are distributed in the alpine wetlands and grasslands of the Andean Cordillera, which spans large elevational and latitudinal gradients. The Crested Duck (*Lophonetta specularioides*) is a partially migrant, sexually mono-



FIG. 1. Geographic distribution of Crested Duck specimens collected between 2002 and 2006. Black circles represent the highland subspecies *L. s. alticola* from the central high Andes, triangles represent *L. s. alticola* from Mendoza, and white circles represent the lowland subspecies *L. s. specularioides*.

morphic, dabbling duck that is endemic to the central Andean and Patagonian regions of South America, and comprises two subspecies: Patagonian Crested Duck (*L. s. specularioides*) and Andean Crested Duck (*L. s. alticola*; Phillips 1922–1926, Johnsgard 1978). The two subspecies inhabit different elevational environments ranging from 5000 m in the central

high Andes (*L. s. alticola*) to sea level in Patagonia and the Malvinas Islands (*L. s. specularioides*, Fig. 1). The subspecies are reported to intergrade in an elevational transition zone at the latitude of Mendoza, Argentina, and Talca, Chile, respectively (Navas & Bo 1998).

Subspecies designations have been based on morphological and plumage differences. *L.*

*s. specularioides* has red iris color, smaller body size, and more brownish or blackish mottled plumage, whereas *L. s. alticola* possesses yellow-orange iris color, larger body size, and more uniform washed out plumage with fewer breast spots (Phillips 1922-1926).

The objective of this study was to evaluate morphological differences between the two subspecies of Crested Duck and evaluate evidence for Bergmann's and Allen's rules to gain a better understanding of the forces that have acted to shape geographic variation in morphology of highland and lowland populations of Crested Ducks. We examined specimens collected throughout the geographic range of the species, with a much larger sample size and more extensive morphological measurement than previous studies.

## METHODS

*Specimen collecting and measurement.* We collected 67 Crested Ducks (40 males and 27 females) from Andean regions of Argentina (2003, 2005), Bolivia (2005) and Perú (2002, 2006) (Appendix 1, Fig. 1). Specimens are archived at the Univ. of Alaska Museum (Fairbanks, Alaska), Colección Boliviana de Fauna (La Paz, Bolivia), and Museo de Historia Natural de la Univ. de San Marcos (Lima, Perú).

Ten morphological measurements ( $\pm 0.1$  mm, unless otherwise specified) were taken from each bird: wing chord length (WC, carpal joint to longest primary feather unflattened), tail length (TL), total tarsus length (TS1, top of bent knee to bottom of foot), tarsus bone length (TS2), bill length (BL1, exposed culmen), bill length at nares (BL2), bill width at nares (BW), bill height (BH, height of upper mandible at posterior edge of nares), skull length (SK, back of the skull to tip of bill), and body mass (BM,  $\pm 50$  g). All measurements were taken the day the specimens were collected and before they were prepared. Sex was determined by dissecting

the gonads.

Specimens were classified as either *L. s. specularioides* or *L. s. alticola* based on previously published plumage differences (Johnsgard 1978, Young 2005). All individuals collected from the highlands of Catamarca, Argentina, north to Perú were classified as *L. s. alticola*, and all individuals collected from Patagonia (coastal and inland) were classified as *L. s. specularioides*. All but one individual female (KGM 1221) from Mendoza, Argentina, were classified as *L. s. alticola* because these specimens had more uniform washed out plumage with few or no breast spots. Iris color faded too rapidly after collection to be consistently useful for identification.

*Statistical analyses.* Statistical analyses were performed on untransformed measurements using Statistica 6.0 (StatSoft 1995). Normality and homogeneity of variances were tested prior to the analysis. Multivariate analysis of variance (MANOVA) was performed to evaluate overall differences between subspecies and each sex. Following a significant MANOVA, we used analysis of variance (ANOVA) to test whether individual measurements differed between subspecies; significance levels were corrected for multiple comparisons using Bonferroni methods. We also performed principal components analysis (PCA) of the same ten measurements. The first three principal components (PC1–3) possessed eigenvalues greater than one (Kaiser 1960) and were plotted separately for females and males. We used stepwise discriminant function analysis (DA) to determine the accuracy of subspecies identification (Sokal & Rohlf 1969, Sneath & Sokal 1973). DA was conducted separately for females and males. The final discriminant function included five measurements for males (WC, BL1, TS1, BW, BM) and six measurements (WC, BL1, BW, BH, SK, BM) for females.

TABLE 1. Measurements (mm) and body mass (g) of Crested Duck subspecies.

	<i>p</i> *	<i>L. s. alticola</i>			<i>L. s. specularioides</i>		
		Mean	SE	Range	Mean	SE	Range
MALE		(n = 26)			(n = 14)		
Body mass (BM)	0.66	1056.5	25.0	1004.9-1108.1	1040.0	21.7	993.1-1086.9
Wing cord (WC)	0.001	300.9	2.7	295.2-306.6	266.2	1.9	262.1-270.3
Tail (TL)	0.001	179.6	3.7	171.9-187.4	147.4	1.3	144.6-150.2
Total tarsus (TS1)	0.76	61.9	1.2	59.4-64.4	62.4	0.6	61.1-63.7
Tarsus bone (TS2)	0.001	50.0	0.7	48.4-51.6	43.2	0.4	42.3-44.1
Bill length at nares (BL1)	0.001	37.7	0.4	36.8-38.6	33.5	0.3	32.8-34.1
Bill length at culmen (BL2)	0.09	17.2	0.3	16.5-17.9	16.3	0.2	15.8-16.9
Bill height (BH)	0.98	19.6	0.2	19.1-20.0	19.5	0.2	19.2-19.9
Bill width at nares (BW)	0.001	110.6	1.4	107.7-113.5	103.1	0.8	101.2-104.9
Skull length (SK)							
FEMALE		(n = 20)			(n = 7)		
Body mass	0.42	966.0	24.7	914.2-1017.7	926.4	42.9	821.4-1031.4
Wing cord	0.001	285.6	2.0	281.3-289.8	252.5	4.9	240.4-264.7
Tail	0.005	151.6	3.6	144.0-159.2	130.1	5.6	116.2-144.0
Total tarsus	0.31	60.6	1.3	58.0-63.4	58.4	1.1	55.7-60.9
Tarsus bone	0.001	48.3	0.6	47.1-49.5	41.5	1.2	38.5-44.5
Bill length at nares	0.001	34.9	0.5	34.0-36.0	31.8	0.6	30.1-33.4
Bill length culmen	0.006	46.4	0.7	45.0-47.9	42.7	0.8	40.7-44.7
Bill height	0.78	15.5	0.3	14.9-16.2	15.7	0.6	14.3-17.1
Bill width at nares	0.32	18.3	0.1	18.1-18.6	18.7	0.4	17.6-19.8
Skull length	0.001	104.7	0.9	102.7-106.8	96.7	1.6	92.6-100.7

\*ANOVA *P*-value for subspecies effect.

Finally, we used partial correlation analysis of elevation and latitude with ten morphological measurements and PC1–3 to examine the joint relationship between elevation and latitude and morphological measurements, and to evaluate the partial correlation coefficients of each measurement and environmental variable (Sokal 1965). Analyses were performed separately for males and females within each subspecies. Significance levels were corrected for multiple comparisons using Bonferroni methods.

## RESULTS

Overall body size of Crested Ducks differed between subspecies (Wilks'  $\lambda = 0.25$ ,  $F_{10, 54} =$

15.5,  $P < 0.001$ ) and between sexes (Wilks'  $\lambda = 0.51$ ,  $F_{10, 54} = 5.1$ ,  $P < 0.001$ , Table 1). No significant interaction between subspecies and sex was observed ( $P > 0.90$ ). Male and female *L. s. alticola* were significantly larger than male and female *L. s. specularioides*, respectively, for WC, TL, TS2, BL1, BL2, and SK (Table 1).

Three principal components with eigenvalues  $> 1$  were retained in the principal components analysis and accounted for 78.4% of the total variance observed between subspecies in males and 81.1% in females, respectively. PC1 represented an overall difference in body size (male eigenvalue = 4.83, female eigenvalue = 5.00) and accounted for 48.3% and 50.0% of the variance for males and

TABLE 2. Principal components (PC1–3) for 10 body size measurements of male and female Crested Ducks. Bold text indicates variables with a strong association ( $|r| > 0.7$ ) with the principal component.

	Male			Female		
	PC1	PC2	PC3	PC1	PC2	PC3
Body mass	0.34	0.23	<b>0.73</b>	0.40	0.30	<b>0.72</b>
Wing chord	<b>0.90</b>	-0.05	0.09	<b>0.90</b>	0.11	0.00
Tail	<b>0.81</b>	-0.38	-0.05	<b>0.74</b>	0.42	-0.22
Total tarsus	0.21	<b>0.82</b>	0.38	0.12	-0.35	<b>0.82</b>
Tarsus bone	<b>0.89</b>	0.10	0.20	<b>0.83</b>	-0.13	0.21
Bill length at nares	<b>0.91</b>	0.00	0.09	<b>0.88</b>	-0.03	0.34
Bill length at culmen	<b>0.87</b>	0.15	0.09	<b>0.77</b>	-0.09	0.49
Bill height	0.26	<b>-0.77</b>	0.39	0.19	<b>0.79</b>	-0.22
Bill width	-0.02	-0.12	<b>0.88</b>	-0.13	<b>0.87</b>	0.11
Skull length	0.63	-0.03	0.28	<b>0.84</b>	0.11	0.37
Eigenvalue	4.83	1.65	1.34	5.00	2.05	1.04
% of variance	48.3	16.5	13.4	50.0	20.5	10.4
Cumulative %	48.3	64.9	78.4	50.0	70.6	81.1

females, respectively. PC2 accounted for 16.5% of the variance in males (eigenvalue = 1.65) and corresponded to variations in TS1 and BH, whereas it accounted for 20.5% of the variance in females (eigenvalue = 2.05), and represented bill shape because BH and BW were the most highly correlated variables. PC3 (male eigenvalue = 1.34, female eigenvalue = 1.04) accounted for 13.5% and 10.4% of the variance for males and females, respectively, and represented a bill shape and body size difference between subspecies, as BW and BM were the most highly correlated variables in males. In females, TS1 and BM were the most influential variables (Table 2, Fig. 2). Plots of PC1 versus PC2 grouped all male *L. s. specularioides* and one *L. s. alticola* specimen (REW 130) together. It is possible that this individual is a subadult, as its measurements are smaller than the rest of the *L. s. alticola* specimens we sampled. Male *L. s. alticola* were more loosely scattered than *L. s. specularioides* in this plot, with specimens from Mendoza showing intermediate PC1 values. Plots of PC1 versus PC2 for females,

grouped one *L. s. specularioides* (KGM 1221) together with *L. s. alticola*; this female was from Mendoza (Fig. 2). Plots of PC1 versus PC3 showed similar differences between subspecies for both males and females.

Stepwise DA classified 96.1% of *L. s. alticola* and 100% of *L. s. specularioides* males correctly. The only male that was misclassified was a small body-sized Andean Crested Duck (REW 130; see above) from Perú that grouped with Patagonian Crested Ducks. Female *L. s. alticola* and *L. s. specularioides* were correctly classified 100% of the time. Clear separation of subspecies within each sex resulted from larger measures of WC, BL2, BW, and BM in *L. s. alticola*. BH and SK also contributed to differences between subspecies in females, as did TS1 in males.

Partial correlations coefficients for elevation and latitude regressed on all measurements are shown in Table 3. Most of the morphological measurements show a positive association with elevation in male *L. s. alticola*. In contrast, TS1 was negatively corre-

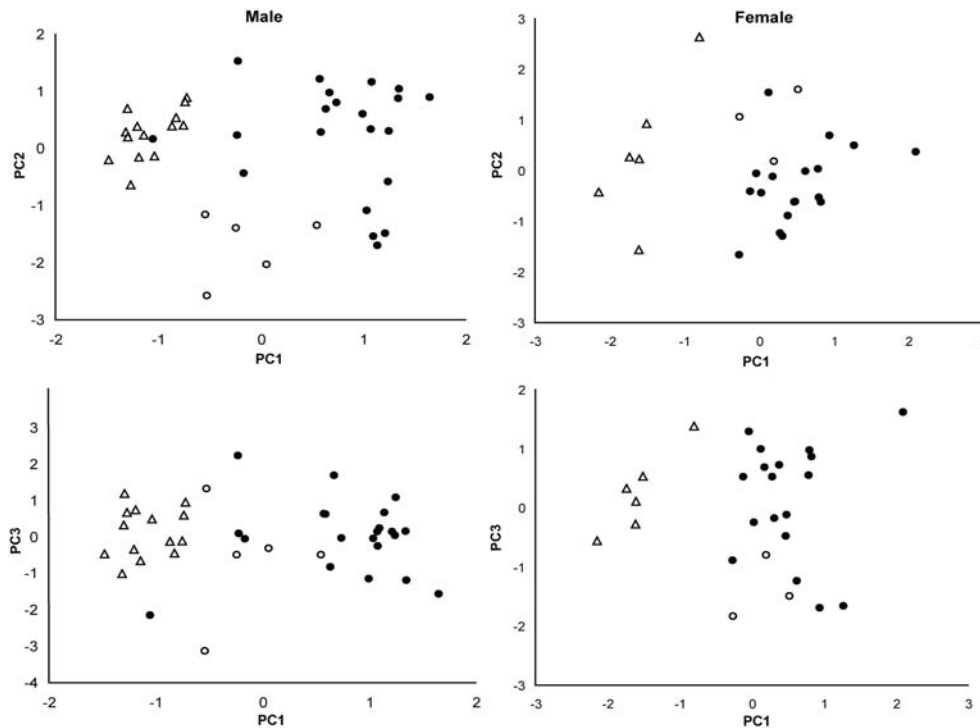


FIG. 2. Principal components (PC1 vs PC2 and PC1 vs PC3) analysis of 10 body size measurements for female and male Crested Ducks (*Lophonetta specularioides*). Black circles represent *L. s. alticola* from the central high Andes, white circles represent *L. s. alticola* from Mendoza, and triangles represent *L. s. specularioides* from Patagonia.

lated with elevation for male and female *L. s. specularioides*, whereas in both sexes of *L. s. alticola*, TS1 was positively correlated with elevation ( $P < 0.05$ ). In female *L. s. alticola*, PC3 was strongly correlated with elevation. After adjusting the significance level with Bonferroni corrections, only WC, TS1, TS2, PC1 and PC2 were positively correlated with elevation in male *L. s. alticola* ( $P < 0.002$ ) (Table 3, Fig. 3).

*L. s. alticola* individuals collected from intermediate elevations in Mendoza (1522–2552 m) exhibited smaller body size than individuals collected from the Altiplano for all variables and showed strongly positive correlations with elevation (Fig. 3). For example, the  $r^2$  values for TS1 and TS2 vs elevation

were  $> 0.90$  in male *L. s. alticola* from Mendoza, with an increase in TS1 from 48 mm at 1522 m to 60 mm at 2552 m, an overall increase in elevation of only  $\sim 1000$  m (Fig. 3). *L. s. alticola* males inhabiting higher elevations in the Altiplano ( $> 3500$  m) showed a significant increase of WC with elevation ( $r^2 = 0.22$ ,  $P < 0.05$ ) in an elevational gradient of 700 m, from an altitude of 3900 m to 4600 m (Fig. 3).

No measurements showed significant correlations with latitude for females (Table 3). For males, PC2 was negatively correlated with latitude in *L. s. alticola*, and TS2 was positively correlated with latitude for *L. s. specularioides*, but after Bonferroni correction, neither was significant.

TABLE 3. Partial correlation coefficients of body size measurements, PC1, PC2, and PC3 versus elevation and latitude for Crested Ducks. Significant correlations ( $P < 0.05$ ) indicated in bold text. Correlations significant after Bonferroni correction are indicated by asterisks.

	Male		Female	
	<i>L. s. alticola</i>	<i>L. s. specularioides</i>	<i>L. s. alticola</i>	<i>L. s. specularioides</i>
ELEVATION				
Body mass (BM)	<b>0.47</b>	-0.38	0.31	-0.12
Wing chord (WC)	<b>0.64*</b>	-0.14	-0.29	-0.23
Tail (TL)	-0.01	0.10	-0.12	-0.41
Total tarsus (TS1)	<b>0.71*</b>	<b>-0.56</b>	<b>0.56</b>	<b>-0.91</b>
Tarsus bone (TS2)	<b>0.71*</b>	-0.50	0.34	-0.34
Bill length at nares (BL1)	<b>0.43</b>	-0.32	0.22	-0.07
Bill length at culmen (BL2)	<b>0.53</b>	-0.38	0.28	-0.11
Bill height (BH)	-0.32	-0.20	-0.42	-0.65
Bill width (BW)	0.01	-0.30	-0.36	-0.73
Skull length (SK)	0.21	-0.43	0.23	-0.19
PC1	<b>0.58*</b>	-0.41	-0.01	0.11
PC2	<b>0.67*</b>	-0.22	-0.41	-0.71
PC3	0.23	-0.45	<b>0.50</b>	-0.61
LATITUDE				
Body mass	0.15	0.03	0.28	-0.18
Wing chord	0.32	0.12	-0.29	-0.52
Tail	0.35	-0.15	0.11	-0.64
Total tarsus	-0.28	0.31	0.42	-0.69
Tarsus bone	0.05	<b>0.58</b>	-0.07	-0.71
Bill length at nares	-0.11	0.20	-0.13	-0.51
Bill length at culmen	-0.02	0.23	-0.07	-0.55
Bill height	0.35	0.12	-0.23	-0.74
Bill width	0.09	0.22	0.14	-0.72
Skull length	0.17	0.40	0.12	-0.42
PC1	0.13	0.34	-0.25	-0.50
PC2	-0.43	0.08	0.04	-0.73
PC3	0.14	0.25	0.38	-0.43

## DISCUSSION

Explanations for the evolution of geographic variation within species state that populations inhabiting different localities are subject to different ecological and climatic pressures, thus giving rise to phenotypic distinctions (e.g., Mayr 1963). Phenotypic differences are maintained in part by the reduction of gene flow among populations separated by large distances and/or physical-ecological barriers

(Gould & Johnston 1972). Empirical support relating morphometric variation and regional climates in birds is provided by a number of studies (e.g., Rand 1936, James 1970, Power 1970, Niles 1973). On the other hand, Remsen (1984) pointed out the influence of random processes in the differentiation of polytypic bird species in the Andes; the appearance of phenotypic changes, at different times and rates, at random with respect to geography.



BODY SIZE OF CRESTED DUCKS FROM CENTRAL HIGH ANDES

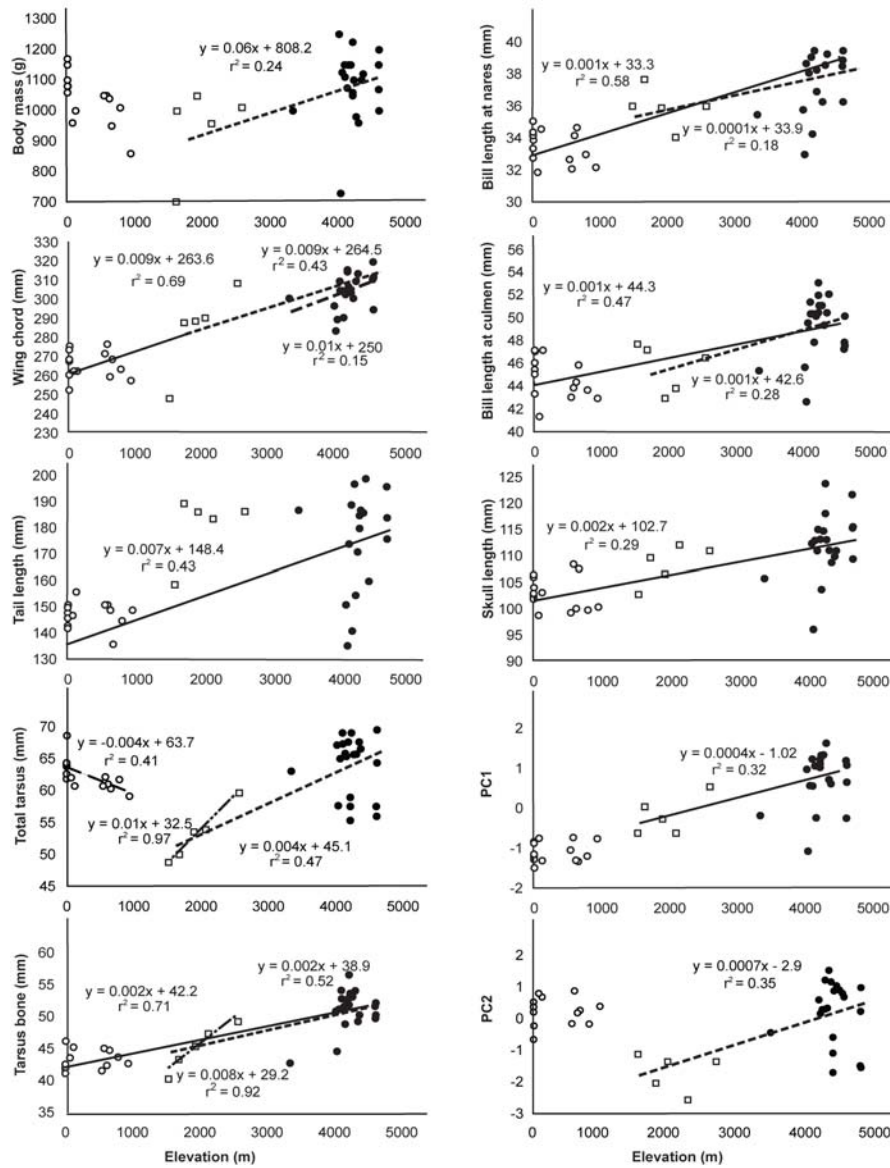


FIG. 3. Linear regressions of body size measurements and elevation for male Crested Ducks. Black circles represent *L. s. alticola* from the central high Andes, white squares represent *L. s. alticola* from Mendoza, and white circles represent *L. s. specularioides* from Patagonia. The regression lines for *L. s. alticola* and *L. s. alticola* & *L. s. specularioides* (combined) are overlaid in the wing chord graph.

It has long been recognized that an increase in body size frequently correlates with an increase in latitude and elevation

(Bergmann 1847, Rand 1936, Traylor 1950, Snow 1954b). This trend is most often explained by thermoregulatory advantages of

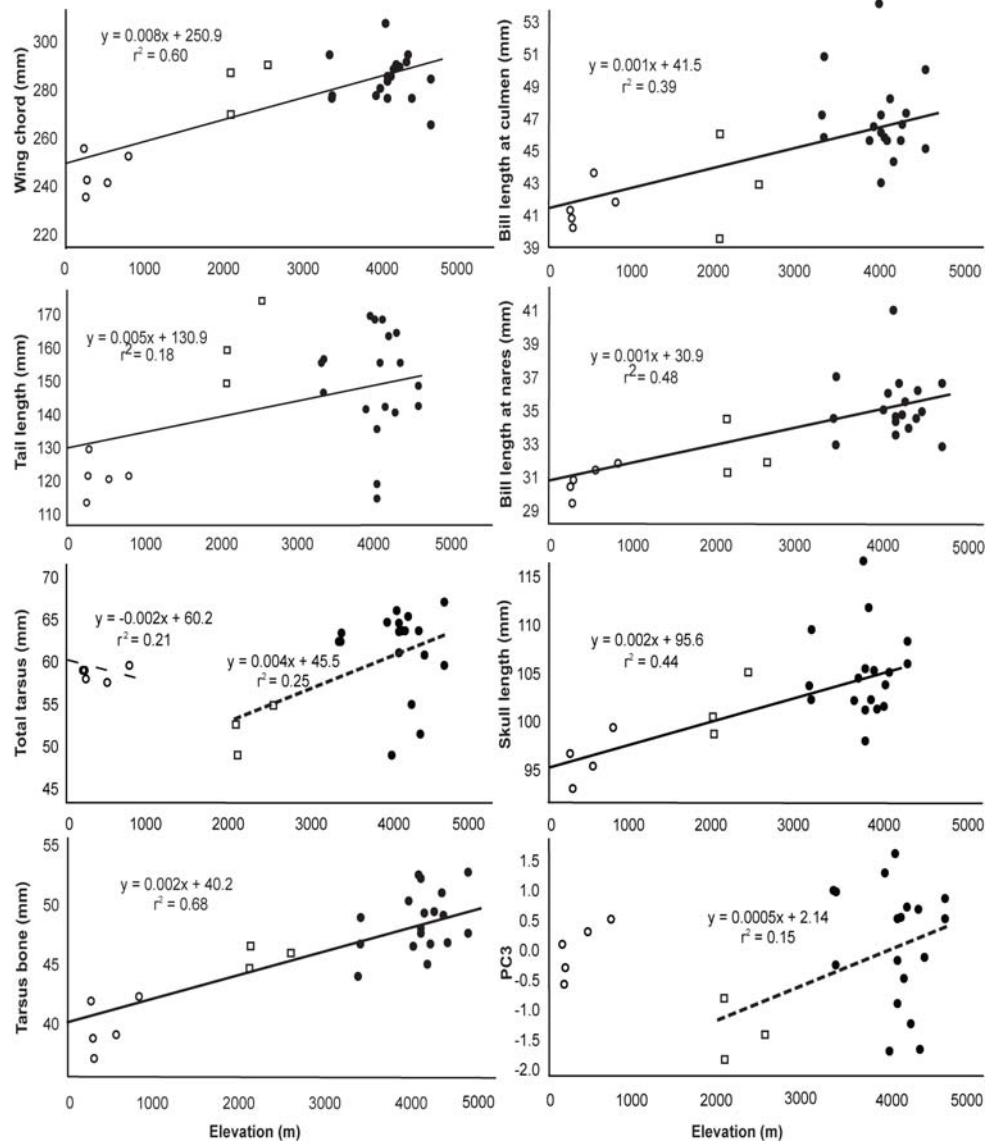


FIG. 4. Linear regressions of body size measurements and elevation for female Crested Ducks. Black circles represent *L. s. alticola* from the central high Andes, white squares represent *L. s. alticola* from Mendoza, and white circles represent *L. s. specularioides* from Patagonia.

being larger in colder environments; larger animals face smaller heat losses in cold climates because of their proportionally smaller surface areas (Randall *et al.* 2002). Millien *et al.*

(2006), however, argued that the patterns underlying geographic variation are complex and highly context-dependent, reducing the ‘predictive-power’ of ecogeographical rules.

Geographic variation in size of Crested Ducks can be explained as a combination of processes leading to the observed overall trend of larger bodied individuals at higher elevations in the Andes (3000–5000 m), with the coastal and inland specimens from Patagonia being smaller, and Mendoza specimens being intermediate in size between the two populations.

Patagonia and the central high Andes have similar cold, semi-arid climates, associated with strong winds year-round, with elevation and air density being the main differences. Northern Patagonia is semiarid, with minimum mean temperatures from  $-11$  to  $-5^{\circ}\text{C}$ , and prevailing cold, dry and strong southwest winds. Southern Patagonia becomes increasingly peninsular with higher latitude, with minimum temperatures between  $-9$  and  $-33^{\circ}\text{C}$ . The climate is cold and dry, with strong west winds. Frosts can occur throughout the year; spring and autumn provide only short transitions between summer and winter (Encyclopedia Britannica 2006). The Altiplano climate is semiarid, with reported mean minimum temperatures of  $5^{\circ}\text{C}$  at Cusco, Perú (3248 m),  $1^{\circ}\text{C}$  at La Paz, Bolivia (4012 m) and  $-8^{\circ}\text{C}$  at La Quiaca, Argentina (3461 m; Weatherbase 2007).

In our study, the low air density and oxygen supply ( $\sim 60\%$  of sea level at 4000 m) associated with high elevation, may be part of the explanation of why the Andean subspecies is larger. Aldrich & James (1991) and James (1991) described a negative relationship between size in birds and either wet-bulb temperature, vapor pressure, or absolute humidity (all measurements sensitive to both temperature and moisture). Their model, thus, accounts for the fact that size tends to increase in arid regions, independently of latitude and altitude, and that widespread species tend to be largest in areas that are high, cool, and dry, such as the high Andes. James' modification better supported Bergmann's rule in other studies including birds and mammals

(Wigginton & Dobson 1999, Meiri & Dayan 2003). Snow (1954b) stated that wings of montane bird species are longer not only because they have larger overall body size, but also because the thinner air at high altitudes necessitates a relatively larger wing for efficient flight. Moreover, Hopkins & Powell (2001) found a relationship between body size and  $P_{50}$  (the oxygen partial pressure at which hemoglobin is half saturated), with small animals generally having lower affinity hemoglobin than larger animals. Smaller animals have a higher mass specific metabolic rate and may be selected to favor oxygen unloading to the tissues (Hopkins & Powell 2001). Therefore, even when there are no thermal gradients among populations, Crested Ducks conform to Bergmann's rule.

According to Allen's rule, heat will be conserved most efficiently in colder climates if protruding parts, from which heat loss is most rapid, are reduced (Snow 1954b). *L. s. specularioides* and *L. s. alticola* showed conflicting relationships between tarsus length and elevation. Specifically, male and female *L. s. alticola* increased TS1 with increasing elevation, whereas both sexes of *L. s. specularioides* showed decreased TS1 with increasing elevation. Bill length also increased with elevation for male *L. s. alticola*. No other consistent pattern of appendage variation with elevation or latitude was observed; therefore, Crested Ducks do not seem to conform to Allen's rule.

Little is known about the elevational movements of the different populations of Crested Ducks. This information is vital when analyzing trends within and between subspecies. Patagonian Crested Ducks are mostly sedentary, even in the southern parts of their range. Farther north Andean Crested Ducks from the Bolivian and Peruvian Andean lakes, breed in the Cordilleras and descend in winter (Delacour 1954); they may migrate as low as to 2000 m (Young 2005). Evidence also shows

that Crested Ducks are encountered in both extremes of the range in the very same season (Phillips 1922-1926). Little snow accumulates in the central high Andean plateau, so many Crested Ducks remain high in the Altiplano year-round. In contrast, the Andes in Mendoza are narrower and snow-covered much of the year, however, no information is available about how regional variation in vertical movement influences the biology and morphology of this species.

Morphologically intermediate populations of Crested Ducks, such as those found in Mendoza, Argentina, might be interpreted as evidence for introgression between the two populations, i.e., Andean Crested Ducks in the north and Patagonian Crested Duck populations in the south (Navas & Bo 1998). Intermediate morphology might also be maintained by natural selection on body size of individuals locally adapted for inhabiting intermediate or a range of different elevational environments.

Finally, did Crested Ducks diverge from other duck species in the lowlands and then colonize the highlands spreading north through Mendoza, thus increasing in body size as they adapted to a new highland environment? Or did Crested Ducks originate in the central high Andes and disperse south and to the lowlands? Additional genetic and physiological analyses will be necessary to determine historical directions of colonization of the Andes and identify factors related to body size that may be of selective advantage to Crested Ducks inhabiting different elevational environments.

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#### REFERENCES

- Aldrich, J. W., & F. C. James. 1991. Ecogeographic variation in the American Robin (*Turdus migratorius*). *Auk* 108: 230–249.
- Allen, J. A. 1877. The influence of physical conditions in the genesis of species. *Rad. Rev.* 1: 108–140.
- Ashton, K. G. 2002. Patterns of within-species body size variation of birds: strong evidence for Bergmann's rule. *Glob. Ecol. Biogeogr.* 11: 505–523.
- Bergmann, C. 1847. Über die verhältnisse der Wärmeökonomie der thiere zu ihrer grosse. *Gött. Studien* 1: 595–708.
- Delacour, J. 1954. *The waterfowl of the world*. Arco Publishing Company, Inc. New York,

- New York.
- Encyclopedia Britannica 2006. Patagonia. Encyclopedia Britannica online. 1 Sept. 2006. <http://www.britannica.com/eb/article-41675>.
- Gould, S. J., & R. F. Johnston. 1972. Geographic variation. *Ann. Rev. Ecol. Syst.* 3: 457–498.
- Hopkins, S. R., & F. L. Powell. 2001. Common themes of adaptation to hypoxia. Insights from comparative physiology. *Adv. Exp. Med. Biol.* 502: 153–167.
- James, F. C. 1970. Geographic size variation in birds and its relationship to climate. *Ecology* 51: 365–390.
- James, F. C. 1991. Complementary descriptive and experimental studies of clinal variation on birds. *Am. Zool.* 31: 694–706.
- Johnsgard, P. A. 1978. Ducks, geese, and swans of the world. Univ. of Nebraska Press, Lincoln, Nebraska.
- Kaiser, H. F. 1960. The application of electronic computers to factor analysis. *Educ. Psych. Measurement* 20: 141–151.
- Lindsey, C. D. 1966. Body sizes of poikilotherm vertebrates at different latitudes. *Evolution* 20: 456–465.
- Mayr, E. 1942. Systematics and the origin of species. Columbia, New York, New York.
- Mayr, E. 1963. Animal species and evolution. Belknap Press, Cambridge, Massachusetts.
- Meiri, S., & T. Dayan. 2003. On the validity of Bergmann's rule. *J. Biogeogr.* 30: 331–351.
- Millien, V., S. K. Lyons, L. Olson, F. A. Smith, A. B. Wilson, & Y. Yom-Tov. 2006. Ecotypic variation in the context of global climate change: revisiting the rules. *Ecol. Lett.* 9: 853–869.
- McNab, B. K. 1971. On the ecological significance of Bergmann's rule. *Ecology* 52: 845–854.
- Navas, J. R., & N. A. Bo. 1998. The geographical distribution of the subspecies of *Lophonetta specularioides* and *Merganetta armata* (Anatidae) in the provinces of Mendoza and San Juan, Argentina. *Hornero* 15: 57–59.
- Niles, D. M. 1973. Adaptive variation in body size and skeletal proportions of Horned Larks of the southwestern United States. *Evolution* 27: 405–426.
- Phillips, J. C. 1922–1926. A natural history of the ducks. Houghton Mifflin, Boston, Massachusetts.
- Power, D. M. 1970. Geographic variation in the surface/volume ratio of the bill of Red-winged Blackbirds in relation to certain geographic and climatic factors. *Condor* 72: 299–304.
- Rand, A. L. 1936. Results of the Archbold expeditions No. 12. Altitudinal variation in New Guinea birds. *Am. Mus. Nov.* 890: 1–14.
- Randall, D., W. Burggren, & K. French. 2002. Ecker animal physiology. Mechanisms and adaptations. Freeman & Co., New York, New York.
- Ray, C. 1960. The application of Bergmann and Allen's rules to the poikilotherms. *J. Morphol.* 106: 85–108.
- Remsen, J. V., Jr. 1984. High incidence of “leap-frog” pattern of geographic variation in Andean birds: Implications for the speciation process. *Science* 24: 171–173.
- Scholander, P. F. 1955. Evolution of climatic adaptation in homeotherms. *Evolution* 9: 15–26.
- Sneath, P. H. R. A., & R. R. Sokal. 1973. Numerical taxonomy; the principles and practice of numerical classification. 2<sup>nd</sup> ed. Freeman and Co., San Francisco, California.
- Snow, D. W. 1954a. Trends in geographical variation in palearctic members of the genus *Parus*. *Evolution* 8: 19–28.
- Snow, D. W. 1954b. Climate and geographical variation in birds. *New Biol.* 25: 56–84.
- Sokal, R. R. 1965. Statistical methods in systematics. *Biol. Rev.* 40: 337–391.
- Sokal, R. R., & J. F. J. Rohlf. 1969. Biometry. Freeman and Co., San Francisco, California.
- StatSoft. 1995. Statistica 6.0 for Windows. StatSoft, Tulsa, Oklahoma.
- Traylor, M. A. 1950. Altitudinal variation in Bolivian birds. *Condor* 52: 123–126.
- Weatherbase. 2007. Weatherbase online: [www.weatherbase.com](http://www.weatherbase.com). Accessed 28 January 2007.
- Wigginton, J. D., & F. S. Dobson 1999. Environmental influences on geographic variation in body size of western bobcats. *Can. J. Zool.* 77: 802–813.
- Young, G. 2005. Crested Duck *Lophonetta specularioides*. Pp. 484–486 in Kear J. (ed.). Ducks, geese and swans. Volume 2. Oxford Univ. Press, New York, New York.

## APPENDIX 1. Locality and specimen information for Crested Ducks included in this study.

UAM no.	Field catalog no.	Date	Country	Prov./ Depart.	Locality	Longitude	Latitude	Elevation (m)	Subspecies	Sex
22741	REW-094	11 Aug 2002	Perú	Junín	S Junín, Carretera Central, km 218	-75.94180	-11.23270	4177	<i>alticola</i>	F
	REW-104	12 Aug 2002	Perú	Pasco	c. Cerro de Pasco	-76.89150	-11.20410	4234	<i>alticola</i>	M
20829	REW-107	12 Aug 2002	Perú	Pasco	c. Cerro de Pasco	-76.22320	-10.69380	4188	<i>alticola</i>	M
	REW-130	23 Aug 2002	Perú	Ancash	Laguna Conococha	-77.28350	-10.11970	4039	<i>alticola</i>	M
	REW-131	23 Aug 2002	Perú	Ancash	Laguna Conococha	-77.28350	-10.11970	4039	<i>alticola</i>	F
	REW-139	25 Aug 2002	Perú	Ancash	Laguna Tapara, SE Pachacoto	-77.36490	-9.90790	4065	<i>alticola</i>	F
	REW-140	25 Aug 2002	Perú	Ancash	Laguna Tapara, SE Pachacoto	-77.36490	-9.90790	4065	<i>alticola</i>	M
	REW-160	30 Aug 2002	Perú	Ancash	Laguna Canrash	-77.05580	-9.68520	4270	<i>alticola</i>	M
20793	REW-213	5 Oct 2002	Perú	Ayacucho	Razuhuilca, c. Huanta	-74.17310	-12.87980	4100	<i>alticola</i>	M
	REW-214	6 Oct 2002	Perú	Ayacucho	Razuhuilca	-74.15460	-12.91380	4065	<i>alticola</i>	F
	REW-215	6 Oct 2002	Perú	Ayacucho	Razuhuilca	-74.15460	-12.91380	4065	<i>alticola</i>	F
20784	REW-289	21 Oct 2002	Perú	Puno	Laguna Lagunillas	-70.81310	-15.69090	4157	<i>alticola</i>	M
20789	REW-290	23 Oct 2002	Perú	Arequipa	c. Imata	-71.24380	-15.97340	4349	<i>alticola</i>	M
19628	KGM-719	20 Oct 2003	Argentina	Chubut	RP 17, W Tecka	-71.06760	-43.60620	804	<i>specularioides</i>	F
19632	KGM-720	20 Oct 2003	Argentina	Chubut	RN 40, S Tecka	-70.87550	-43.71010	934	<i>specularioides</i>	M
19626	KGM-726	22 Oct 2003	Argentina	Chubut	RN 40, W Shaman	-70.67430	-44.38960	655	<i>specularioides</i>	M
19629	KGM-732	23 Oct 2003	Argentina	Chubut	RN 40, N Río Mayo	-70.43980	-45.42210	578	<i>specularioides</i>	M
22747	KGM-746	26 Oct 2003	Argentina	Santa Cruz	RP 41, Estancia La Frontera	-71.86200	-46.84210	783	<i>specularioides</i>	M
19636	KGM-749	26 Oct 2003	Argentina	Santa Cruz	RN 40, c. Estancias Telken & La Paloma	-70.74550	-46.87610	618	<i>specularioides</i>	M
20781	KGM-753	28 Oct 2003	Argentina	Santa Cruz	RN 40, N Las Horquetas	-70.97490	-48.30230	540	<i>specularioides</i>	F
19627	KGM-754	28 Oct 2003	Argentina	Santa Cruz	RN 40, N Las Horquetas	-70.97490	-48.30230	540	<i>specularioides</i>	M
19630	KGM-774	31 Oct 2003	Argentina	Santa Cruz	Estancia Santa Margarita, c. Lago Viedma	-72.41400	-49.55810	246	<i>specularioides</i>	F
19625	KGM-794	3 Nov 2003	Argentina	Santa Cruz	RN 40, c. El Zurdo	-71.22580	-51.99600	122	<i>specularioides</i>	M
19640	KGM-795	5 Nov 2003	Argentina	Santa Cruz	RN 40, c. Estancia Monte Dinero	-68.66560	-52.26760	72	<i>specularioides</i>	M
19631	KGM-802	6 Nov 2003	Argentina	Santa Cruz	RN 3, c. Paraje Lemarchand	-69.48180	-50.75020	281	<i>specularioides</i>	F
19633	KGM-803	6 Nov 2003	Argentina	Santa Cruz	RP 288, c. Puerto Punta Quilla	-68.48800	-50.08890	3	<i>specularioides</i>	M
19635	KGM-806	8 Nov 2003	Argentina	Santa Cruz	Bahía Río Deseado	-65.97270	-47.74210	0	<i>specularioides</i>	M

APPENDIX 1. Continued.

UAM no.	Field catalog no.	Date	Country	Prov./ Depart.	Locality	Longitude	Latitude	Elevation (m)	Subspecies	Sex
19747	KGM-809	10 Nov 2003	Argentina	Chubut	S Lago Colhué Huapí	-68.94000	-45.65240	267	<i>specularioides</i>	F
19637	KGM-820	11 Nov 2003	Argentina	Chubut	Bahía Bustamante	-66.53500	-45.13480	0	<i>specularioides</i>	F
19634	KGM-821	11 Nov 2003	Argentina	Chubut	Bahía Bustamante	-66.52120	-45.14930	0	<i>specularioides</i>	M
19639	KGM-824	12 Nov 2003	Argentina	Chubut	S Camarones	-65.71630	-44.80330	0	<i>specularioides</i>	M
19624	KGM-827	13 Nov 2003	Argentina	Chubut	Cabo Raso	-65.23010	-44.33410	0	<i>specularioides</i>	M
19638	KGM-828	13 Nov 2003	Argentina	Chubut	Playa Bonita, S Rawson	-65.04820	-43.36090	0	<i>specularioides</i>	M
22749	KGM-1073	4 Nov 2005	Argentina	Catamarca	Laguna Antofagasta, Antofagasta de la Sierra	-67.42409	-26.11280	3338	<i>alticola</i>	M
22744	KGM-1074	4 Nov 2005	Argentina	Catamarca	Laguna Antofagasta, Antofagasta de la Sierra	-67.42409	-26.11280	3338	<i>alticola</i>	F
22739	KGM-1087	7 Nov 2005	Argentina	Catamarca	Río Punilla, 35 km N Antofagasta de la Sierra	-67.28391	-25.82775	4140	<i>alticola</i>	F
22738	KGM-1088	7 Nov 2005	Argentina	Catamarca	Río Punilla, 35 km N Antofagasta de la Sierra	-67.28391	-25.82775	4140	<i>alticola</i>	M
22743	KGM-1122	12 Nov 2005	Argentina	Catamarca	Río Chaschuil, S La Gruta	-68.06677	-27.02894	3923	<i>alticola</i>	F
22745	KGM-1139	13 Nov 2005	Argentina	Catamarca	Río Chaschuil, c. Embalse Cortaderas	-68.14524	-27.56000	3363	<i>alticola</i>	F
22748	KGM-1140	14 Nov 2005	Argentina	Catamarca	Río Chaschuil, c. Embalse Cortaderas	-68.14498	-27.55590	3369	<i>alticola</i>	F
22735	KGM-1159	15 Nov 2005	Argentina	Catamarca	Laguna de los Aparejos	-68.54215	-27.64755	4106	<i>alticola</i>	M
22751	KGM-1160	15 Nov 2005	Argentina	Catamarca	Laguna de los Aparejos	-68.54215	-27.64755	4106	<i>alticola</i>	F
22737	KGM-1184	17 Nov 2005	Argentina	Catamarca	La Gruta	-68.14566	-26.92542	4020	<i>alticola</i>	M
22742	KGM-1211	29 Nov 2005	Argentina	Mendoza	E Los Penitentes	-69.80995	-32.85187	2552	<i>alticola</i>	F
22746	KGM-1212	29 Nov 2005	Argentina	Mendoza	E Los Penitentes	-69.80995	-32.85187	2552	<i>alticola</i>	M
22734	KGM-1218	2 Dec 2005	Argentina	Mendoza	NW El Sosneado	-69.63432	-35.01203	1670	<i>alticola</i>	M
22740	KGM-1220	2 Dec 2005	Argentina	Mendoza	Laguna El Sosneado	-69.91977	-34.84570	2093	<i>alticola</i>	F
23413	KGM-1221	2 Dec 2005	Argentina	Mendoza	Laguna El Sosneado	-69.91977	-34.84570	2093	<i>specularioides</i>	F
22733	KGM-1224	2 Dec 2005	Argentina	Mendoza	Laguna El Sosneado	-69.91977	-34.84570	2093	<i>alticola</i>	M
22736	KGM-1228	3 Dec 2005	Argentina	Mendoza	Pampa del Rodeo, 45 km SW Malargüe, RN 40	-69.62811	-36.76321	1891	<i>alticola</i>	M
22750	KGM-1232	4 Dec 2005	Argentina	Mendoza	Río Grande	-70.06362	-35.81625	1522	<i>alticola</i>	M

BODY SIZE OF CRESTED DUCKS FROM CENTRAL HIGH ANDIES

UAM no.	Field catalog no.	Date	Country	Prov./ Depart.	Locality	Longitude	Latitude	Elevation (m)	Subspecies	Sex
23412	REW-709	27 Nov 2005	Bolivia	La Paz	Laguna Khara Kkota	-68.38254	-16.18806	4307	<i>alticola</i>	M
23415	REW-710	27 Nov 2005	Bolivia	La Paz	Laguna Khara Kkota	-68.38254	-16.18806	4307	<i>alticola</i>	F
23411	REW-714	27 Nov 2005	Bolivia	La Paz	Laguna Kkota	-68.35228	-16.12941	4374	<i>alticola</i>	M
23416	REW-715	27 Nov 2005	Bolivia	La Paz	Laguna Kkota	-68.35228	-16.12941	4374	<i>alticola</i>	F
23419	REW-721	27 Nov 2005	Bolivia	La Paz	Laguna Janyuo Kkota	-68.31933	-16.08057	4611	<i>alticola</i>	F
23418	REW-723	27 Nov 2005	Bolivia	La Paz	Laguna Janyuo Kkota	-68.31933	-16.08057	4611	<i>alticola</i>	M
23417	REW-724	27 Nov 2005	Bolivia	La Paz	Laguna Janyuo Kkota	-68.31933	-16.08057	4611	<i>alticola</i>	F
23414	REW-727	27 Nov 2005	Bolivia	La Paz	Laguna Janyuo Kkota	-68.31933	-16.08057	4611	<i>alticola</i>	M
	KGM-1278	14 Jun 2006	Perú	Junín	35 km SE Huaros	-76.26123	-11.20559	4602	<i>alticola</i>	M
	KGM-1290	15 Jun 2006	Perú	Junín	c. Marcapomacocha	-76.17382	-11.24202	4218	<i>alticola</i>	M
	KGM-1292	15 Jun 2006	Perú	Junín	c. Marcapomacocha	-76.17382	-11.24202	4218	<i>alticola</i>	F
	KGM-1293	15 Jun 2006	Perú	Junín	c. Marcapomacocha	-76.17382	-11.24202	4218	<i>alticola</i>	M
22755	KGM-1301	16 Jun 2006	Perú	Junín	c. Marcapomacocha	-76.17382	-11.24202	4218	<i>alticola</i>	M
22753	KGM-1310	19 Jun 2006	Perú	Junín	Huarimarcán	-76.23129	-11.05242	4605	<i>alticola</i>	M
22754	KGM-1319	21 Jun 2006	Perú	Pasco	24 km NE Paucartambo	-75.56150	-10.52204	4325	<i>alticola</i>	F
22752	KGM-1359	3 Jul 2006	Perú	Ancash	Laguna Pelagato	-77.81005	-8.17287	3976	<i>alticola</i>	F