

GEOGRAPHIC VARIATION IN THE YELLOW-BILLED CACIQUE, *AMBYLCERCUS HOLOSERICUS*, A PARTIAL BAMBOO SPECIALIST¹

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Abstract. Geographic variation in the Yellow-billed Cacique (*Amblycercus holosericeus*) was examined to determine whether bamboo-specialized populations in highland Costa Rica and the Andes are more phenetically similar to one another than to lowland populations not specialized on bamboo. Significant geographic variation was found for all mensural characters; in general, characters varied in accordance with Bergmann's rule. Specimens largely separated into two groups: (1) the Andes and (2) Middle America and the Chocó forests of northwestern South America. The bamboo-specialized population of highland Costa Rica grouped with the non-specialized lowland samples of group 2, not with specialists in the Andes. This suggests that bamboo specialization arose independently in these two populations. There is no convergence in morphology evident between the two populations specialized on bamboo; thus specialization on bamboo as a foraging site or habitat may not be associated with morphological specialization in this species.

Key words: *Geographic variation; Amblycercus holosericeus; bamboo; specialization; Neotropics; Icteridae.*

INTRODUCTION

In tropical bird communities, narrow resource specialization is exhibited by many taxa. The processes responsible for the evolution and maintenance of specialization are controversial and relate to the conflicting importances of historical (evolutionary) versus ecological factors in determining specialization (Sherry 1990). Specialization may either be an evolutionary complex character, capable of arising only once in a lineage, or certain ecological conditions, such as a high level of competition, may cause different populations or taxa to become convergently specialized. For instance, in the antwren genus *Myrmotherula* (Formicariidae), it was found that the group of species specialized for foraging in dead-leaf clusters formed a monophyletic group, separate from non-specialist antwrens in the genus (Rosenberg 1990, Hackett and Rosenberg 1990). Likewise, Richman and Price (1992) found that foraging method in the genus *Phylloscopus* (Sylviidae) arose early in the evolution of lineages; habitat choice, however, appeared to be much less evolutionarily constrained.

One of the resources upon which tropical bird species specialize is bamboo. The Neotropics

have a number of bamboo specialist species (Parker 1982; Pierpont and Fitzpatrick 1983; Remsen 1985; Fitzpatrick and Willard 1990; Parker et al., in press), including the Yellow-billed Cacique (*Amblycercus holosericeus*). Andean and highland Costa Rican populations of *A. holosericeus* are restricted to dense stands of bamboo, predominantly *Chusquea*, where they use their heavy bills to pry into bamboo stems for insects (Slud 1964; Wolf 1976; Orians 1985; Stiles and Skutch 1989; Ridgely and Tudor 1989; J. V. Remsen, pers. comm.; T. A. Parker, III, pers. comm.; pers. observ.). However, lowland populations, in the Chocó forests of northwestern South America (Peru, Ecuador, and Colombia) north through Middle America to San Luis Potosí in Mexico (Fig. 1), are not restricted to bamboo; these caciques also occur in a number of dense understory habitats lacking bamboo (Carraker 1910, Skutch 1954, Slud 1964, Orians 1985, Stiles and Skutch 1989). North of Costa Rica, *A. holosericeus* is restricted to forests below 1,680 m (Griscom 1932, Monroe 1968, Binford 1989), although *Chusquea*, an entirely montane genus in the tropics outside of southeast Brazil (Calderón and Soderstrom 1980), extends well into Mexico (Soderstrom et al. 1988).

A. holosericeus has three currently recognized subspecies (Fig. 1), based on univariate morphological measurements, plumage, and soft part

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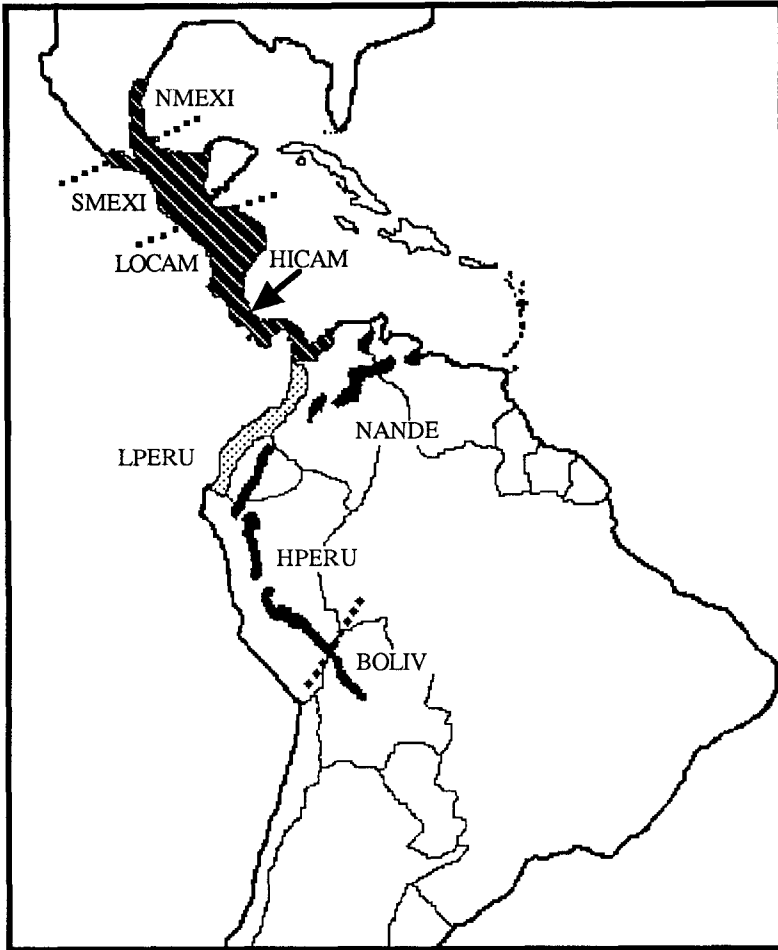


FIGURE 1. Distribution of *Amblycercus holosericeus* subspecies and location of sample areas. Dark hatched area is *A. h. holosericeus*; stippled area is *A. h. flavirostris*; solid area is *A. h. australis*. See Table 1 for area codes.

coloration (Chapman 1915, 1919): *A. h. holosericeus* from Mexico to Colombia, *A. h. flavirostris* in the lowlands from west Colombia to northwest Peru, and Andean *A. h. australis* from Venezuela to Bolivia (Blake 1968). Thus, the bamboo specialist population in highland Costa Rica is grouped with the otherwise non-specialized, nominate lowland form, whereas the highland specialists in the Andes are recognized as the subspecies *A. h. australis*, distinct from lowland forms.

The degree of overlap between lowland and highland forms in Costa Rica is unknown. Although most authors state that this species occurs from sea-level to timberline in Costa Rica (Car-

riker 1910, Skutch 1954, Slud 1964, Stiles and Skutch 1989), of 39 locales where caciques have been collected or seen in Costa Rica (Carriker 1910; Slud 1964; M. Marin, pers. comm.; pers. observ.; specimens from Louisiana State University Museum of Natural Science and museums in Acknowledgments), only one site, with uncertain elevation, was between 1,300 and 2,450 m (Achiote: "... probable altitude 6,000 to 7,000 feet [1,830–2,140 m]," p. 333, in Carriker 1910). Carriker (1910) alone mentioned over 170 collecting locales for the country, with many sites in the elevational gap where this species appears to be missing; thus, the cacique's absence at these elevations is not likely an artifact of poor cov-

erage. For example, *A. holosericeus* is absent from the well-studied site at Monteverde, at 1,300–1,500 m on the west slope of Cordillera Central in Costa Rica (Stiles 1983). It thus appears that the cacique is either absent or extremely uncommon in middle elevations of Costa Rica, and that bamboo-specialized populations in the highlands may have little contact with non-specialized lowland populations.

The Yellow-billed Cacique, therefore, provides an opportunity to test whether the two disjunct, specialized populations in the Andes and montane Costa Rica are more similar phenetically to one another than to the non-specialized populations of the lowlands. Similarity could result either from a sister-group relation among the bamboo-specialized populations or from ecological convergence if the populations are not sister taxa. Much of the montane avifauna of highland Costa Rica has its closest affinities with the Andes (e.g., *Bolborhynchus lineola*, *Glaucidium jardinii*, *Pseudocolaptes lawrencii*, *Margarornis rubiginosus*, *Scytalopus argentifrons*, *Pachyrhamphus versicolor*, *Diglossa plumbea*, *Haplospiza rustica*; Chapman 1917, Wolf 1976); a sister relationship between bamboo-specialized populations of *A. holosericeus* in the Andes and Costa Rica cannot be discounted. Although 450 km of lowland forest separate the highlands of Costa Rica from the northern Andes, the montane forests occur at similar elevation and latitude, and both areas share the same genus of bamboo (*Chusquea*); thus, morphological convergence may also be expected in the Cacique. Because bamboo provides a unique foraging substrate relative to other woody plants, morphological adaptations might be expected in bamboo specialists. Bamboo thickets have dense growths of homogeneous stems with slick, hard, nonhorizontal surfaces. Leisler and Winkler (1985) found that *Acrocephalus* warblers restricted to reed beds, which are superficially similar to bamboo thickets, had longer toes and slimmer pelvises relative to more arboreal genera of sylviid warblers.

I quantified geographic variation in morphological characters in *Amblycercus holosericeus*. Although a phenetic approach using unpolarized character states cannot be used to test directly whether the Andean and highland Central American forms are sister taxa, it may reveal: (1) if the bamboo-specialized populations in Costa Rica and the Andes are morphologically similar;

(2) if bamboo specialization requires specific morphological traits; and (3) which morphological features may be important in bamboo specialization.

METHODS

Small samples from many collecting localities precluded statistical analysis (less than five specimens for most), and so localities were pooled into general areas. Areas were chosen by biogeographical affinities, sample size, and political boundaries. The Mexico area was subdivided into northern and southern areas upon a *a posteriori* inspection of the mensural data. Results of *t*-tests confirmed this split, as 11 of 16 characters over both sexes were significant ($P < 0.05$), or nearly so ($0.05 < P < 0.10$). The lowland Costa Rica area was merged with the rest of lowland Central America, because only one character differed significantly between the two areas and because the lowland Costa Rican sample ($n = 5$) was small. Samples (with major political divisions) and sample sizes used were: northern Mexico (NMEXI-12: San Luis Potosí), southern Mexico (SMEXI-24: Veracruz, Tabasco, Oaxaca, Chiapas), lowland Central America (LOCAM-27: Belize, Honduras, Guatemala, El Salvador, lowland Costa Rica, and Panama), highland Central America (HICAM-8: all from the bamboo-specialized population in the Cordillera Talamanca, Costa Rica), northern Andes (NANDE-6: Colombia and Venezuela), lowland Peru (LPERU-3: Dpto. Tumbes), highland Peru (HPERU-34: dptos. Piura, Amazonas, San Martín, La Libertad, Huánuco, Piura, Pasco, Cuzco), and Bolivia (BOLIV-15: dptos. La Paz and Cochabamba) (Fig. 1).

Univariate measures. Eight quantitative characters (Baldwin et al. 1931) were measured on skin specimens: length of culmen (CULM), length of mandible along gonys (MAND), length of tarsus (TARS), wing chord (WING), tail length (TAIL), bill depth at base (BLLD), mandible width at base (BLLW), and length of hind claw (HDCL). Each measure was ln-transformed to provide equal variance. Geographic variation was analyzed using analysis of variance (ANOVA). *A posteriori* tests were restricted to Scheffe's *F*-tests, which use experiment-wide error and provide independent tests of area pairs within each of the 16 ANOVAs.

Measurement error. To determine whether

TABLE 1. Measurement error (%ME), sample sizes (n), means and standard deviations ($\bar{x} \pm SD$), and coefficients of variation (CV) for each area and sex.

Area	Sex	n	Culmen (CULM) %ME = 1.97		Mandible (MAND) %ME = 1.13		Wing (WING) %ME = 3.58	
			$\bar{x} \pm SD$	CV	$\bar{x} \pm SD$	CV	$\bar{x} \pm SD$	CV
Northern Mexico (NMEXI)	M	8	30.96 \pm 0.83	2.69	19.73 \pm 0.51	2.58	100.33 \pm 3.42	3.41
	F	3	30.08 \pm 1.14	3.78	19.31 \pm 0.50	2.43	94.48 \pm 3.58	3.79
Southern Mexico (SMEXI)	M	9	29.77 \pm 1.15*	3.88	18.68 \pm 1.02	5.44	99.48 \pm 3.58	3.60
	F	14	28.08 \pm 1.88	6.67	17.43 \pm 1.61	9.25	93.10 \pm 5.04	5.48
Lowland Central America (LOCAM)	M	13	30.14 \pm 1.48	4.92	18.42 \pm 1.25	6.81	100.61 \pm 6.75	6.71
	F	13	27.55 \pm 1.55	5.75	16.70 \pm 1.04	6.26	91.40 \pm 3.37	3.70
Highland Central America (HICAM)	M	5	30.75 \pm 1.48	4.82	19.97 \pm 1.42	7.09	101.64 \pm 2.38	2.34
	F	3	25.86 \pm 1.38	5.34	15.48 \pm 2.09	13.48	94.81 \pm 1.47	1.55
Northern Andes (NANDE)	M	4	27.95 \pm 0.61	2.19	18.21 \pm 0.20	1.08	93.80 \pm 5.50	5.86
	F	2	26.08 \pm 0.63	2.41	16.31 \pm 0.16	0.95	87.16 \pm 5.74	6.58
Lowland Peru (LPERU)	M	1	27.94		17.35		98.08	
	F	2	25.28 \pm 0.26	1.04	16.20 \pm 1.18	7.23	88.08 \pm 1.45	1.64
Highland Peru (HPERU)	M	16	28.42 \pm 1.07	3.75	17.75 \pm 0.80	4.54	93.39 \pm 0.98	2.12
	F	20	26.41 \pm 1.10	4.15	16.23 \pm 1.05	6.48	86.58 \pm 3.04	3.51
Bolivia (BOLIV)	M	7	28.29 \pm 0.67	2.35	17.48 \pm 0.68	3.89	98.55 \pm 2.53	2.57
	F	7	27.28 \pm 0.77	2.84	16.49 \pm 0.73	4.42	90.99 \pm 3.34	3.70

* Sample size = $n - 1$.

TABLE 1. Continued.

Area	Sex	Hind claw (HDCL) %ME = 9.13	
		$\bar{x} \pm SD$	CV
Northern Mexico (NMEXI)	M	11.50 \pm 0.57	4.97
	F	10.83 \pm 0.16	1.48
Southern Mexico (SMEXI)	M	10.66 \pm 0.72	6.73
	F	10.02 \pm 0.62	6.18
Lowland Central America (LOCAM)	M	11.06 \pm 0.83	7.49
	F	9.44 \pm 0.73	7.73
Highland Central America (HICAM)	M	11.49 \pm 0.70	6.13
	F	10.39 \pm 0.48	4.63
Northern Andes (NANDE)	M	11.87 \pm 0.59	4.98
	F	11.01 \pm 1.88	17.08
Lowland Peru (LPERU)	M	9.80	
	F	8.83 \pm 0.13	1.52
Highland Peru (HPERU)	M	11.63 \pm 0.62	5.37
	F	10.96 \pm 0.58	5.33
Bolivia (BOLIV)	M	11.04 \pm 1.33	12.01
	F	11.20 \pm 0.49	4.36

variation within a character could result from within-individual error in measuring the character, an analysis of measurement error was conducted following Bailey and Byrnes (1990). A random sample of 25 specimens was chosen to determine measurement error, and each character was measured three times for each specimen.

Latitudinal trends. Latitudinal gradients in size variation (Bergmann's Rule) were analyzed using unpooled samples. Latitudes were taken from distributional surveys (Russell 1964, Monroe 1968, Binford 1989), gazetteers (Paynter and

Traylor 1981; Paynter 1982, 1992; Stephens and Traylor 1983), and available maps. Principal component analyses (PCA) were used to reduce the eight character matrix to a few orthogonal axes that summarized character variance. PCA1 loadings for each individual from the correlation matrix and univariate characters were then regressed against degrees latitude from the equator. PCA1 scores are perhaps better indices of "size" than univariate characters (Zink and Remsen 1986).

Multivariate analyses. PCA factor scores were computed using character means from each sample area. Minimum spanning trees were used to describe phenetic relationships among samples.

Phenograms. A matrix of mean distances between populations was calculated from the morphological data for each sex (SAS 1985). Distance matrices were used to construct phenograms using the UPGMA algorithm.

RESULTS

Sexual dimorphism. Many icterid species show sexual dimorphism in size, the males generally being larger than the females (Orians 1985). In *A. holosericeus*, all eight characters showed significant ($P < 0.05$ in t -tests) sexual dimorphism in each of the four populations with sample sizes larger than five birds for each sex (SMEXI, LOCAM, HPERU, and BOLIV), except in four cases (TAIL in SMEXI, BLLW in HPERU, and TARS and HDCL in BOLIV). Because each population showed dimorphism in a majority of the char-

TABLE 1. Extended.

Tail (TAIL) %ME = 7.49		Tarsus (TARS) %ME = 6.96		Bill width (BLLW) %ME = 3.65		Bill depth (BLLD) %ME = 2.98	
$\bar{x} \pm SD$	CV	$\bar{x} \pm SD$	CV	$\bar{x} \pm SD$	CV	$\bar{x} \pm SD$	CV
111.22 ± 5.74	5.16	34.60 ± 1.20	3.48	10.38 ± 0.41	3.96	15.82 ± 0.27	1.73
100.51 ± 2.59	2.57	32.45 ± 1.68	5.16	9.64 ± 0.45	4.67	14.23 ± 0.19	1.36
101.76 ± 4.40	4.32	32.11 ± 1.38	4.31	9.80 ± 0.44	4.47	15.06 ± 0.71	4.72
99.78 ± 5.90	5.92	30.05 ± 1.24	4.12	9.22 ± 0.69	7.46	14.12 ± 0.87	6.14
102.11 ± 8.78	8.60	31.69 ± 2.08	6.57	9.76 ± 0.45	4.64	14.69 ± 0.60	4.06
95.63 ± 4.25	4.45	29.80 ± 0.56	1.87	9.21 ± 0.56*	6.13	13.56 ± 0.55*	4.08
106.84 ± 3.10	2.90	31.67 ± 1.25	3.96	9.39 ± 0.47	5.00	14.24 ± 0.48	3.38
101.42 ± 2.39	2.36	28.08 ± 0.82	2.93	8.48 ± 0.31	3.70	12.97 ± 0.37	2.88
105.04 ± 4.80	4.57	30.32 ± 2.11	6.96	8.68 ± 0.35	4.06	12.92 ± 0.38	2.93
101.26 ± 1.31	1.29	29.07 ± 1.61	5.55	8.91 ± 0.34	4.04	11.60 ± 0.19	1.64
98.74		28.04		9.30		14.47	
93.36 ± 9.66	10.35	28.48 ± 0.37	1.29	9.84 ± 0.93	9.41	12.96 ± 0.22	1.69
102.90 ± 4.49	4.36	29.77 ± 1.07	3.58	8.11 ± 0.37	4.52	12.45 ± 0.54	4.31
99.55 ± 4.95*	4.97	28.60 ± 1.78*	4.12	7.95 ± 0.27	3.35	11.81 ± 0.90*	7.60
113.75 ± 2.65	2.33	29.99 ± 0.89	2.98	8.59 ± 0.36	4.24	12.72 ± 0.36	2.84
110.01 ± 3.03	2.75	29.56 ± 1.56	5.27	8.13 ± 0.36	4.44	11.80 ± 0.44	3.74

acters across nearly the entire range of the species (see Table 1), the sexes were analyzed separately.

Measurement error. Measurement error (Table 1) varied from 1.13 (MAND) to 9.13% (HDCL). All characters were maintained in the analysis because the range of values among areas within a character was at least twice the variation within individuals as measured by %ME.

Univariate statistics. Means, standard deviations, and coefficients of variation for each character in each area are given in Table 1. All characters showed significant ($P < 0.05$) variation across the range of the species for both sexes (Table 2). For each character and sex, there were 28 possible area pairs, which totaled 448 pairwise *a posteriori* tests. Of these, 50 were significant at the $P < 0.05$ level (Table 2). Of these significant tests, 47 (94%) were between a group of Middle American/Chocó samples (NMEXI, SMEXI, LOCAM, HICAM, LPERU) and a group of Andean samples (NANDE, HPERU and BOLIV). The area combinations with the greatest number of significant tests were NMEXI-HPERU (8), LOCAM-HPERU and LOCAM-BOLIV (6), and SMEXI-HPERU (5). Males from the bamboo-specialist population in highland Costa Rica (HICAM) were significantly different from those in the Andes (HPERU: 3 tests and BOLIV: 1 test). There was only one significant test between HICAM and a Middle American sample (NMEXI for BLLD in males). Twelve combinations were significant for both sexes, all were between the Middle American region (NMEXI,

SMEXI, LOCAM) and the Andean region (HPERU and BOLIV). The characters with the greatest number of significant tests were BLLD (18) and BLLW (17); CULM and MAND each had only one significant test.

Latitudinal trends. Regression of latitude with PCA1 loadings for individuals showed a significant relationship for both females ($r = 0.573$, $P < 0.0001$) and males ($r = 0.673$, $P < 0.0001$) (Fig. 2); the relationship was significant on both sides of the equator for each sex, except females south of the equator ($r = 0.347$, $P = 0.0827$). Latitude accounted for 45.3% of variation in PCA1 for males and 32.8% in females. All 16 regressions (8 for each sex) of latitude with univariate characters (Table 3) were positive and significant ($P < 0.05$), except for TAIL for females ($P = 0.291$); however, only BLLW ($r = 0.671$) for males had an r -value greater than that for the regression of latitude with PCA1.

Multivariate analyses. In the PCAs, the sexes showed many incongruences in loadings on the characters (Table 3). In males, all characters except HDCL loaded positively on the first eigenvector (PCA1), indicating that this component was related to size (Johnston and Selander 1971). HDCL had a slight negative value on PCA1. In females, BLLW and HDCL loaded moderately high and negative on PCA1; the other characters had positive loadings. For PCA2 in males, TARS and HDCL (positive) and BLLD and BLLW (negative) had the highest loadings, indicating a shape relationship between foot and bill char-

TABLE 2. Analysis of variance results. See Table 1 for area and character codes.

Character	F-test	P	Significant Scheffe's Tests
(a) Males			
CULM	7.622	0.0001	NMEXI/HPERU
MAND	5.940	0.0001	NMEXI/HPERU
WING	5.086	0.0002	LOCAM/HPERU
TAIL	5.022	0.0002	
TARS	10.394	0.0001	NMEXI/NANDE HPERU BOLIV
BLLW	35.402	0.0001	NMEXI/NANDE HPERU BOLIV SMEXI/NANDE HPERU BOLIV LOCAM/NANDE HPERU BOLIV HICAM/HPERU
BLLD	46.863	0.0001	NMEXI/HICAM NANDE HPERU BOLIV SMEXI/NANDE HPERU BOLIV LOCAM/NANDE HPERU BOLIV HICAM/HPERU BOLIV
HDCL	2.489	0.0270	
(b) Females			
CULM	4.732	0.0003	
MAND	3.562	0.0032	
WING	5.779	0.0001	SMEXI/HPERU HICAM/HPERU
TAIL	6.166	0.0001	LOCAM/BOLIV HPERU/BOLIV
TARS	5.733	0.0001	NEMXI/HPERU
BLLW	16.841	0.0001	NMEXI/HPERU SMEXI/HPERU BOLIV LOCAM/HPERU BOLIV LPERU/HPERU HPERU/BOLIV
BLLD	17.747	0.0001	NMEXI/HPERU BOLIV SMEXI/HPERU BOLIV LOCAM/HPERU BOLIV
HDCL	11.500	0.0001	LOCAM/HPERU BOLIV LPERU/HPERU BOLIV

acters (Johnston and Selander 1971). In females the shape relationship was similar, but less clear. Like the males, HDCL had a high and positive loading and BLLW was negative, but BLLD had a positive loading in the females.

Minimum spanning trees plotted on scatterplots of PCA1 and PCA2 (Fig. 3), however, showed nearly identical patterns for males and females: an Andean group (NANDE, HPERU, BOLIV) was distinct from a Middle American group (LOCAM, SMEXI, NMEXI). In females, the highland Central American sample (HICAM) bridged the Andean and Middle American groups, whereas in males HICAM was within the Middle American group. The sample from the lowland Chocó forests of northwestern South America (LPERU) was linked with the Middle American group in both sexes, although quite

distinct on PCA2. Scatterplots of PCA1 and PCA3 showed largely similar groupings, mainly as a result of separation on PCA1. Scatterplots of PCA2 and PCA3 showed little pattern in both sexes.

Phenograms. Separate phenograms were generated for each sex (Fig. 4). Unlike the Principal Component Analysis, the phenograms showed little congruence between the sexes, especially for the more basal nodes. The only grouping common to both sexes was the Andean NANDE with HPERU. However, all groupings based on distances less than 0.7 are wholly composed of either the Middle American/Chocó group (NMEXI, SMEXI, LOCAM, HICAM, LPERU) or the Andean group (NANDE, HPERU, BOLIV). In the phenograms, the phenetic sister group to the bamboo specialists in highland Central America

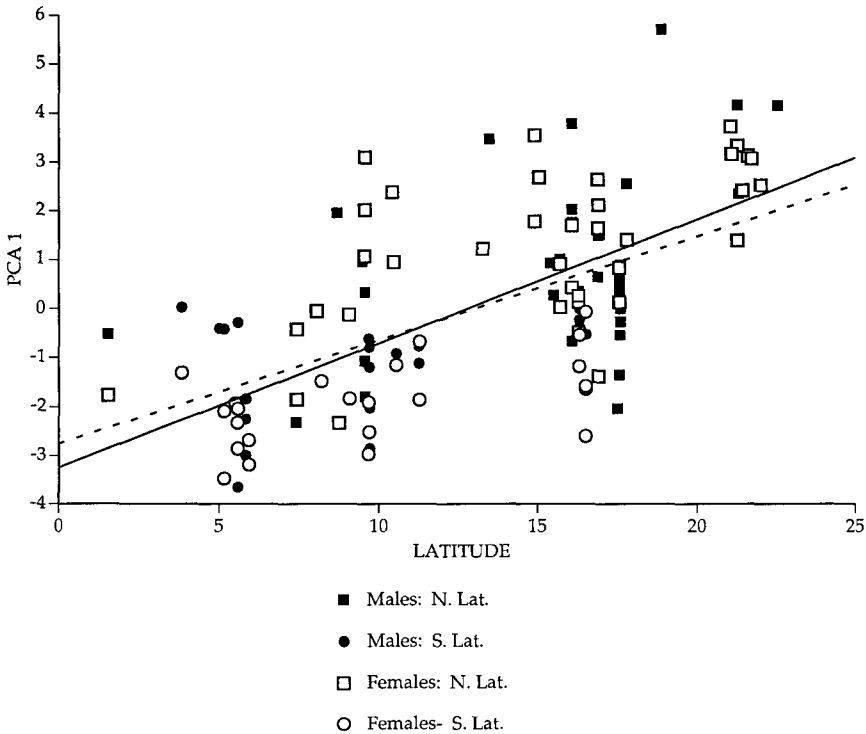


FIGURE 2. Regression of latitude with PCA1 for males (solid symbols, solid line: $y = 0.254x - 3.284$, $r = 0.673$, $F = 48.033$, $P < 0.001$) and females (open symbols, dashed line: $y = 0.212x - 2.779$, $r = 0.573$, $F = 27.867$, $P < 0.001$). Localities north of the equator are shown as squares, those south of the equator as circles.

(HICAM) in both sexes was Middle American (SMEXI and LOCAM in males and SMEXI in females).

DISCUSSION

In *Amblycercus holosericeus*, variation in body size generally follows the expectations of Bergmann's Rule: size, as measured here by PCA1 and univariate characters, decreases from more temperate locales toward the equator. This trend occurs both north (NMEXI to NANDE) and south (HPERU, LPERU to BOLIV) of the equator in *A. holosericeus*. The trend is strongest for males, which show a greater size component in its loadings on the first eigenvector (Table 3; Johnston and Selander 1971). J. V. Remsen (pers. comm.) found that only four of 48 Andean bird species sampled followed Bergmann's Rule; one of these four was *A. holosericeus*. In their broad review of latitudinal trends in size, Zink and Remsen (1986) did not present any published material that examined Bergmann's Rule in Neo-

tropical species that span the latitudinal range of *A. holosericeus*. Subsequently, Graves (1991) found that one Andean bird species follows Bergmann's Rule both north and south of the equator.

Nearly all data presented here confirm that *A. holosericeus* consists of at least two distinct groups: one in Middle America from Mexico to Panama and a bamboo-specialized population in the Andes from Venezuela to Bolivia. The univariate statistics, phenograms, and minimum spanning trees group the lowland Chocó population (LPERU) with the Middle American samples; PCA2, however, suggests that the LPERU populations in the Chocó (LPERU) may be distinct, although the sample size for this population is small. Although the phenograms do not show as distinct a dichotomy between Middle American and Andean populations as the rest of the results, the only consistent relationship in both sexes (HPERU and NANDE) is a subgroup of the Andean group, and the more terminal groupings support the Andean and Middle

TABLE 3. Principal components analysis eigenvalues, cumulative proportion, loadings on characters from the covariance matrix, and *r*- and *P*-values from regression with latitude (LAT). See Table 1 for character codes.

Character	PCA1	PCA2	PCA3	LAT	
				<i>r</i>	<i>P</i>
(a) Males					
CULM	0.269	0.170	-0.049	0.458	0.0002
MAND	0.289	0.311	-0.199	0.312	0.0129
WING	0.177	-0.055	0.298	0.448	0.0002
TAIL	0.028	0.386	0.848	0.329	0.0084
TARS	0.360	0.416	-0.013	0.537	0.0001
BLLW	0.567	-0.162	0.062	0.671	0.0001
BLLD	0.598	-0.274	-0.088	0.671	0.0001
HDCL	-0.045	0.668	-0.373	0.211	0.0970
Eigenvalue	0.01963	0.00727	0.00163		
Cumulative proportion	66.0	90.5	96.0		
(b) Females					
CULM	0.214	0.431	-0.007	0.499	0.0001
MAND	0.318	0.437	-0.433	0.365	0.0035
WING	0.133	0.134	0.575	0.457	0.0001
TAIL	-0.200	0.303	0.266	0.137	0.2913
TARS	0.202	0.314	-0.213	0.508	0.0001
BLLW	0.547	-0.150	-0.264	0.446	0.0003
BLLD	0.567	0.100	0.543	0.531	0.0001
HDCL	-0.364	0.619	-0.009	0.263	0.0359
Eigenvalue	0.01892	0.01151	0.00206		
Cumulative proportion	56.2	90.4	96.5		

American dichotomy. Furthermore, the more distant nodes in phenograms are not as reliable as the more apical nodes (Sneath and Sokal 1973).

The bamboo-specialized population in highland Costa Rica (HICAM) grouped with other Middle American samples in almost all analyses, not with the other bamboo-specialized populations of the Andes. The only exceptions were the minimum spanning trees for females (but not males), which placed the HICAM population intermediate between the Middle American and Andean groups, and BLLD for males, which showed a difference between HICAM and NMEXI, within the Middle American group. The latter exception may only be due to clinal variation in size with latitude (see above).

Clinal variation in size with latitude could obscure some of the findings here. By eliminating the size-dependent PCA1 and examining only PCA2 and PCA3, Bergmannian size variation could be controlled for. Plots of PCA2 and PCA3, however, showed little pattern in relation to either bamboo specialization or to geography. Latitude accounted for less than half the variation in PCA1 for either sex (individual, not pooled samples; see above); therefore, most variation in PCA1, which accounted for 53.1 and 46.8% of total variation in males and females from the

correlation matrix, respectively, would be lost if only PCA2 (15.6 and 22.8% of total) and PCA3 (12.4 and 10.7% of total) were used. PCA1 thus has importance outside of latitudinal variation in size, and was maintained in the analysis.

The results indicate that the two bamboo-specialized populations are not morphologically similar: the HICAM population is phenetically most similar to nearby Middle American populations that are not specialized. The most parsimonious phylogenetic explanation for this result is that the HICAM population is derived from nearby lowland populations, not from the other bamboo-specialized populations in the Andes. Under this scenario, bamboo specialization arose independently in the two populations. A sister-group relationship between the specialized populations would require additional steps: an ancestral cacique would have had to disperse between the Andes and Costa Rican highlands, and then secondarily diverge. The HICAM population then would have had to spread into the lowlands, including areas between HICAM and the Andes, without diverging significantly. Analysis of genetic characters not as subject to natural selection are needed to confirm the evolutionary relationships within this species.

If the two highland areas are considered en-

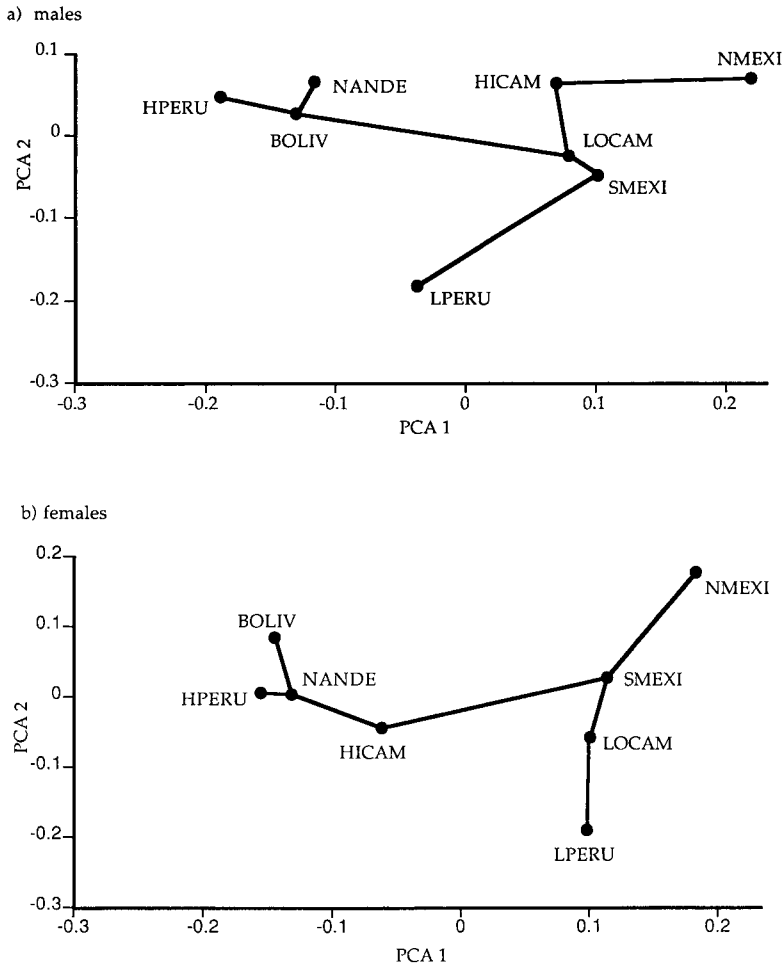


FIGURE 3. Scatterplots of PCA results for males (a) and females (b). Lines between samples represent minimum spanning trees. See Table 1 for explanation of area codes.

environmental equivalents (see above), then the morphological differences between the two specialized populations suggest that bamboo specialization does not require a strict morphology with regard to the characters used in this study; otherwise, the characters would be expected to show more convergence. However, unknown differences between the areas or the effects of non-selective drift in morphological characters could account for the differences.

If bamboo specialization is considered solely a matter of habitat choice, as opposed to substrate choice, then the scenario of independent evolution of specialization in the Yellow-billed Cacique is similar to Richman and Price's (1992) findings for *Phylloscopus* warblers: habitat choice appears to be a more evolutionarily labile char-

acter than morphology. The generality of this finding is unknown; the field of examining habitat choice and morphological adaptation in the context of evolutionary history is in its infancy. A few other Neotropical bird taxa also contain both bamboo specialists and non-specialists that do not differ conspicuously in morphology (e.g., the genera *Celeus*, *Automolus*, *Drymophila*, *Ramphotrigon*, *Hemitriccus*), and could provide additional tests of this generality.

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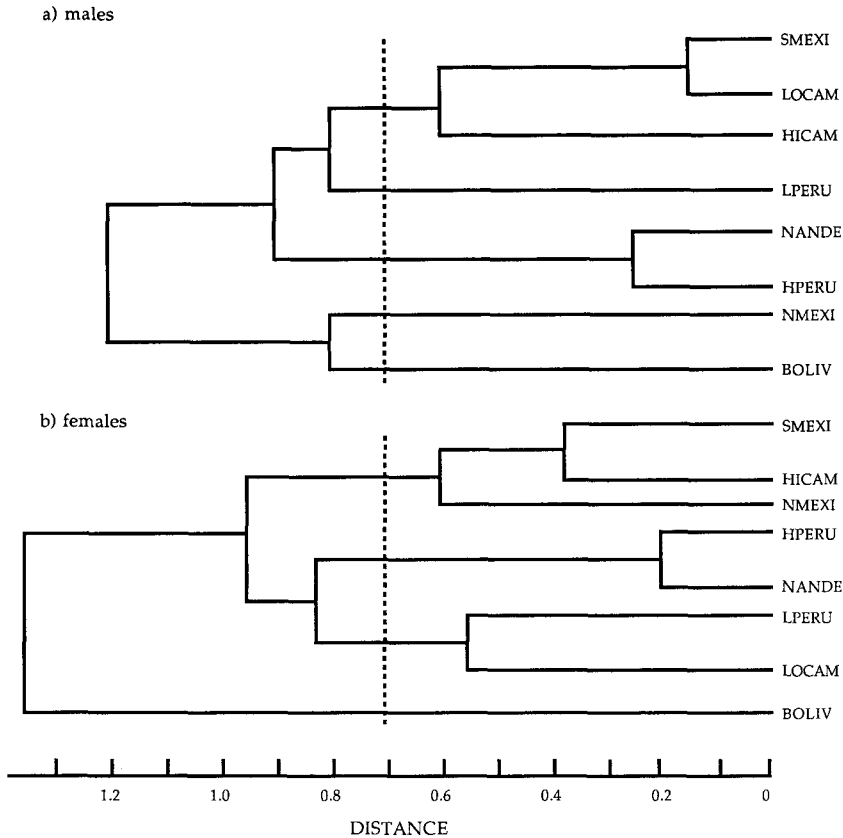


FIGURE 4. Phenograms for males (a) and females (b). Nodes to the right of the dotted line at 0.7 support the Andean and Middle American dichotomy (see text). For explanation of area codes, see Table 1.

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