Female and male (top) of *Cercomacra parkeri* sp. nov. and females of *C. tyrannina crepera* (Panama, lower left) and *C. t. tyrannina* (northern Colombia, lower right). From a painting by Larry McQueen.

COLORIMETRIC AND MORPHOMETRIC GRADIENTS IN COLOMBIAN POPULATIONS OF DUSKY ANTBIRDS (*CERCOMACRA TYRANNINA*), WITH A DESCRIPTION OF A NEW SPECIES, *CERCOMACRA PARKERI*

GARY R. GRAVES

*Department of Vertebrate Zoology, National Museum of Natural History,
Smithsonian Institution, Washington, D.C. 20560, USA*

ABSTRACT.—Two morphologically similar antbirds, *Cercomacra tyrannina* and *C. parkeri* sp. nov., are sympatric in the foothills of the Cordillera Occidental and Cordillera Central of the Colombian Andes. The two taxa appear to replace each other elevationally: *C. tyrannina*—sea level to ca. 730 m; *C. parkeri*—ca. 1,130 to 1,830 m. Colombian populations of *C. tyrannina* exhibit significant clines in plumage color and size that are consistent with the predictions of Gloger's and Bergmann's ecogeographic rules.

RESUMEN.—Dos hormigueros morfológicamente similares, *Cercomacra tyrannina* y *C. parkeri* sp. nov. son sympatrica en las lomas de las Cordilleras Occidentales y Central de las Andes Colombianas. Las dos taxa probablemente se reemplazan a diferentes niveles: *C. tyrannina*—nivel de mar ca 730 m; *C. parkeri*—ca. 1,130 to 1,830 m. La población de *C. tyrannina* Colombiana demuestra significante clines en el color de plumaje y tamaño que es consistente con las reglas ecogeográficas de Gloger y Bergmann.

The Dusky Antbird (*Cercomacra tyrannina*) is a polytypic species that ranges from southern Mexico through Central America to eastern Brazil (Peters 1951). Recently I discovered that the series of *Cercomacra tyrannina* from Colombia examined by Chapman (1917), Meyer de Schauensee (1950), and Wetmore (1972) were actually composed of two regionally sympatric taxa, the widespread *C. tyrannina* (including *C. t. tyrannina* and *C. t. rufiventris*) of the lowlands and a distinctive, undescribed highland taxon.

This paper focuses on the geographic variation, taxonomy, and systematics of *C. tyrannina* species complex in Colombia west of the Andes. First, I present a formal description of the new taxon based on female plumage and morphology. A second objective is to analyze patterns of geographic and elevational variation in plumage color and morphology in the trans-Andean populations of *Cercomacra tyrannina.*

MATERIALS AND METHODS

I quantitatively evaluated the external morphology and plumage color of museum specimens of adults of the *Cercomacra tyrannina* species complex from trans-Andean populations in Colombia. Measurements of wing chord, tail length (from point of insertion of central rectrices to tip of longest rectrix), tarsus length, bill length (from anterior edge of nostril), and bill width (at anterior edge of nostril) were made with digital calipers to the nearest 0.1 mm.

Color of the plumage of the crown, upper breast, and center of back was determined with a reflectance spectrophotometer (Colorscan, Hunter Laboratories) equipped with a 12-mm sample port. Each color measurement was independently replicated three times and averaged for analysis. Specimens with ruffled or worn body plumage were omitted. Geographic variation in plumage color of *Cercomacra tyrannina* is more pronounced in females than in males, a widespread trend among antbirds (Hellmayr 1929). For this reason, the spectrophotometric evaluation of color was restricted to females. Brown and rufescent plumage is susceptible to post-mortem color change over time. However, nearly all females used in this study were collected by M. A. Carriker, Jr., and K. von Sneidern in the 1940's, and so this limits potential biases caused by differences of post-mortem change. [The diagnosis of males is uncertain at present and will be addressed in a future paper.]

Colorimetric characters were described in terms of opponent-color coordinates (L, a, b) (Hunter and Harold 1987). The "LAB" system is based on the hypothesis that signals from the cone receptors in the human eye are coded by the brain as light-dark (L), red-green (a), and yellow-blue (b). The rationale is that a color cannot be red and green or yellow and blue at the same time. Therefore, "redness" and "greenness" can be expressed as a single value a, which is positive if the color is red, negative if green. Likewise, "yellowness" or "blueness" is expressed by b for yellows and $-b$ for blues. The third coordinate L, ranging from 0 to 100, describes the "lightness" of color; low values are dark, high values are light. For example, consider the opponent-color coordinates of breast color for two hypothetical specimens: (1) $L = 40$, $a = 20$, $b = 40$; and (2) $L = 50$, $a = 15$, $b = 35$. The breast of the first specimen is darker and more saturated with red and yellow than that of the second specimen.

Geographic coordinates of collecting localities were taken from Paynter and Traylor (1981). Elevational data were recorded from specimen labels whenever possible, otherwise from Paynter and Traylor.

I used principal components analysis (PCA) to reduce the dimensionality of data and to facilitate the analysis of color and morphology in two dimensions. Color analyses were performed on correlation matrices derived from untransformed variables, whereas morphology was analyzed with log-transformed variables and covariance matrices (Wilkinson 1989). Mensural differences between the taxa were evaluated with t-tests. When appropriate, α-levels (0.05) were adjusted for the number of simultaneous tests. Least-squares regression lines were projected on bivariate scatterplots for heuristic purposes, not for hypothesis testing. Clinal variation of plumage color and morphology in Colombia was illustrated by plots derived from trend-surface analyses of raw and principal components data (SURFER, Golden Software, 1987).

Cercomacra parkeri sp. nov.
Parker's Antbird

Holotype.—National Museum of Natural History (USNM), No. 436469; adult "laying" female from La Bodega, on the north side of the Río Negrito on the road from Sonsón to Nariño, ca. 5,800 ft. [1,768 m], on the eastern slope of the Cordillera Central, depto. Antioquia, Colombia; collected 16 June 1951 by M. A. Carriker, Jr.; original number 20461.

Diagnosis.—*Cercomacra parkeri* females are most similar to those of *C. tyrannina crepera* of Central America, but differ as follows: (1) auriculars of *C. parkeri* brownish-gray instead of rufescent; and (2) eyering and lores gray or brownish-gray rather than brown or rufescent. The white intrascapular patch, variable in size in *C. t. crepera*, is absent or vestigial in female *parkeri*. Male *C. parkeri* tend to have olivaceous rather than gray flanks but cannot be distinguished by plumage color from all specimens of *C. t. tyrannina*. Mean tail length of *C. parkeri* is significantly longer than that of Colombian populations of *C. t. tyrannina* (Table 1).

Description of holotype.—All qualitative color comparisons were made under Examolites (Macbeth Corp.). Crown gray with faint olive-brown tint becoming progressively more olive-brown on the mantle, scapulars, lower back, rump, and upper tail coverts (Table 2). Contrasting intrascapular patch absent. Outer webs of wing coverts, alula, remiges, and rectrices dull olive brown. Concealed inner webs of remiges dark grayish-brown. Lores and anterior half of eyering pale gray. Preorbital bristles black. Sides of neck and distal two-thirds of auricular feathers gray, concolor with the crown; rachi of auriculars basally white or pale buffy-white. Underparts from chin to undertail coverts rich rufescent, darkest and most saturated on the upper breast. Opponent-color coordinates (L, a, b) based on the average of three independent measurements: crown (27.1, 1.3, 7.4); back (27.2, 2.3, 10.7); and breast (46.3, 16.2, 39.4) (compare with Table 2). Soft part colors of dried specimen: upper mandible brownish-black; lower mandible horn-colored, brownish-black near the tomia; feet and tarsi, brownish-black.

Measurements of holotype (mm).—Wing (60.6), tail (61.7), tarsus (21.3), bill length (9.7), bill width (4.6).

Distribution.—Females are known from the western slope of the Cordillera Occidental and northern and eastern slopes of the Cordillera Central of the Colombian Andes (3,700 to 6,000 ft [1,128 to 1,829 m]) (Fig. 1). Males provisionally assigned to *C. parkeri* on the basis of elevation (collected above 1,000 m) occur on the western slope of the Cordillera Oriental, depto. Santander, in addition to known localities for females.

Etymology and dedication.—This taxon is named for my friend and brother-in-arms, Theodore A. Parker III (1953–1993), who put his life on the line for the cause of nature conservation. Those of us privileged to have known him witnessed the ascension of a savant—the most talented field ornithologist of our generation, and perhaps the best in history.

TABLE 1

RANGES, MEANS (± SD), AND SAMPLE SIZES OF SELECTED MEASUREMENTS (MM) OF COLOMBIAN POPULATIONS OF *Cercomacra tyrannina* AND *C. parkeri*. MALE SPECIMENS WERE ASSIGNED TO SPECIES BASED ON ELEVATION. SIGNIFICANT *P*-VALUES (TWO-TAILED T-TEST), BY SEX, BETWEEN *C. parkeri* AND *C. tyrannina*, WERE ADJUSTED FOR THE NUMBER OF SIMULTANEOUS TESTS, 0.05/10 = 0.005: * = *P* < 0.001

Characters	*parkeri*		*tyrannina*	
	♂	♀	♂	♀
Wing chord	61.7–66.8	58.1–63.0	60.8–66.5	56.2–64.4
	64.2 ± 1.6	60.8 ± 1.4	63.7 ± 1.6	60.3 ± 1.9
	n = 16	*n* = 11	*n* = 46	*n* = 47
Tail length	57.0–69.8	58.9–64.7	51.6–63.6	50.0–62.6
	* 63.3 ± 3.9	* 60.6 ± 2.0	57.1 ± 2.9	55.1 ± 3.3
	n = 14	*n* = 10	*n* = 45	*n* = 38
Tarsus length	21.1–24.1	21.1–23.8	21.0–23.9	20.6–23.4
	22.9 ± 0.9	22.4 ± 0.8	22.6 ± 0.8	22.0 ± 0.6
	n = 17	*n* = 11	*n* = 45	*n* = 45
Bill length	9.8–11.7	9.7–11.2	10.3–12.5	9.7–11.4
	10.6 ± 0.5	10.4 ± 0.6	11.0 ± 0.5	10.5 ± 0.5
	n = 16	*n* = 10	*n* = 39	*n* = 41
Bill width	4.0–5.0	4.1–4.8	4.3–5.4	4.3–5.4
	4.7 ± 0.3	* 4.4 ± 0.2	4.7 ± 0.3	4.8 ± 0.2
	n = 17	*n* = 11	*n* = 46	*n* = 46

Specimens examined (Colombia).—*Cercomacra parkeri* (females). Depto. Antioquia: La Bodega (USNM holotype); La Frijolera (AMNH 133482, USNM 256136 [formerly AMNH 133483]); Valdivia (USNM 402341, 402347, 402348). Depto. Bolívar: Volador (USNM 398011). Depto. Caldas: Hacienda Sofía (USNM 436463, 436464); La Selva (ANSP 158180). Depto. Valle del Cauca: "Salencio" on Novita trail (AMNH 111924).

Males provisionally assigned to *C. parkeri* on the basis of elevation (collected above 1,000 m). Depto. Antioquia: Botero (USNM 426347, 426348); La Bodega (USNM 436470); La Frijolera (AMNH 133484); Valdivia (USNM 402342, 402343, 402344, 402345, 402346, 402349). Depto. Caldas: La Selva (ANSP 158181); La Sofía (USNM 436466, 436467, 436468). Depto. Risaralda: Pueblorrico (ANSP 158179). Depto. Santander: Virolín, 6,000 ft. (USNM 373602). Depto. Valle del Cauca: Palmira (AMNH 108924, 108925).

Cercomacra tyrannina (females, sample size in parentheses). Depto. Antioquia: El Pescado

TABLE 2

SPECTROPHOTOMETRIC MEASUREMENTS (RANGE, MEAN, AND STANDARD DEVIATION) OF OPPONENT-COLOR COORDINATES (*L, A, B*) OF FEMALE *Cercomacra parkeri* AND TRANS-ANDEAN COLOMBIAN POPULATIONS OF *C. tyrannina*. SIGNIFICANT *P*-VALUES (TWO-TAILED T-TEST) WERE ADJUSTED FOR NUMBER OF SIMULTANEOUS TESTS 0.05/9 = 0.0056: * = *P* < 0.001; ** = *P* < 0.0001

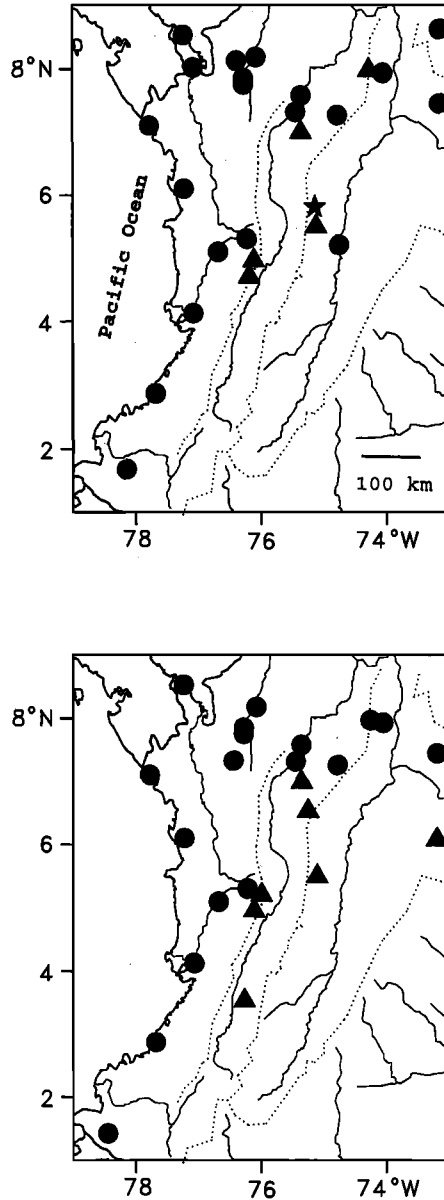|		Color characters		
		Lightness *L*	Red *a*	Yellow *b*
parkeri	Crown	25.3–28.9	1.3–1.9	5.9–8.2
(n = 11)		27.4 ± 1.3	** 1.6 ± 0.2	** 6.8 ± 0.9
	Back	26.3–29.9	1.7–2.6	6.3–10.7
		* 28.1 ± 1.1	2.1 ± 0.3	* 8.0 ± 1.3
	Breast	40.0–49.0	15.9–18.8	36.7–43.0
		45.2 ± 3.0	17.3 ± 1.1	39.8 ± 1.8
tyrannina	Crown	24.3–32.6	1.8–4.3	8.4–16.8
(n = 47)		29.1 ± 2.0	2.8 ± 0.6	11.8 ± 1.6
	Back	26.2–35.0	1.7–3.5	5.8–15.3
		30.5 ± 2.1	2.5 ± 0.5	10.7 ± 2.2
	Breast	37.9–55.8	12.0–20.1	34.2–42.8
		47.5 ± 4.4	16.5 ± 2.0	39.2 ± 2.1

FIG. 1.   Distribution of examined specimens of *Cercomacra tyrannina* (circles) and *C. parkeri* (triangles) in Colombia: (top) females; (bottom) males provisionally assigned to species by elevation—*C. tyrannina* (sea level to 1,000 m) and *C. parkeri* (above 1,000 m). The type locality of *C. parkeri*, La Bodega, depto. Antioquia, is indicated by a star. Some symbols represent two localities. Dotted lines approximate the divides of the three Andean cordilleras. Degrees of north latitude and west longitude appear along the side and bottom.

(2); Hacienda Belén (4); Tarazá (1); Puerto Valdivia (2). Depto. Antioquia/Cordoba: Quimarí (1). Depto. Cordoba: Quebrada Salvajín (2); Socorré (3); Tierralta (4). Depto. Bolívar: Santa Rosa (6). Depto. Cauca: Río Saija (1). Depto. Chocó: Acandi (3); Alto del Buey (3); Andagoya (2); Río Jurado (3); Unguía (1). Depto. Nariño: Barbacoas (1). Depto. Norte de Santander: Bellavista (1). Depto. Risaralda: Santa Cecilia (1). Depto. Santander: Hacienda Santana (4). Depto. Tolima: Honda (1). Depto. Valle del Cauca: Punto Muchimbo (2).

Males assigned to *C. tyrannina* by elevation (sea level to 1,000 m). Depto. Antioquia: El

Pescado (1); Hacienda Belén (4); Tarazá (1); Valdivia (3); Villa Arteaga (1). Depto. Bolívar: Puerto Nuevo (2); Santa Rosa (6); Volador (2,500 ft) (1). Depto. Cauca: Rio Saija (1). Depto. Chocó: Acandí (3); Alto del Buey (1); Andagoya (1); Río Jurado (3). Depto. Cordoba: Quebrada Salvajín (3); Socorré (3); Tierralta (2). Depto. Nariño: Guayacana (3). Depto. Risaralda: Santa Cecilia (2). Depto. Santander: Hacienda Santana (5). Depto. Valle del Cauca: Punto Muchimbo (4).

Large series of *C. tyrannina* from Middle America (Mexico, Honduras, Costa Rica, Panama), Ecuador, Venezuela, and Brazil were also examined, as well as smaller series of *C. laeta, C. serva, C. manu, C. cinerascens, C. nigricans,* and *C. nigrescens.*

Behavior, vocalizations, and ecology.—Unknown.

RESULTS

I addressed the relationship of *C. parkeri* and *C. tyrannina* along the lines broached by the following questions.

(1) Are patterns of plumage color and morphological variation within *tyrannina* and *parkeri* different?

(2) Does *parkeri* represent the end point of a phenotypic continuum that corresponds to elevational gradients?

(3) Do environmental or physical barriers separate the elevational ranges of the two taxa?

(4) Should *parkeri* be recognized as a subspecies of *C. tyrannina* or as a separate species?

PLUMAGE COLOR

Color correlates among plumage regions.—Colorimetric values from the three plumage regions (crown, back, breast) of female *C. tyrannina* specimens were significantly correlated (Table 3). For example, lightness of the crown, back, and breast were positively correlated. Redness of plumage regions was also positively correlated. By comparison, only the crown and back exhibited significantly correlated values for yellow. Lightness values were uncorrelated or negatively correlated with the saturation of red and yellow. In other words, darker specimens of *C. tyrannina* were more richly colored.

None of the color correlates for *C. parkeri* (Table 3) were significant when *P*-values were adjusted for the number of simultaneous tests ($n = 36$). Nevertheless, the relationship among colorimetric characters in *C. parkeri* seems to differ substantially from those exhibited in *C. tyrannina*. For example, when the signs of the correlation coefficients for *C. parkeri* and *C. tyrannina* (Table 3) were compared, only 16 of 36 possible pairwise correlations had the same sign for both species—about the number that would be expected by chance. Most significantly, the lightness of the back and redness of the crown were positively correlated in *C. parkeri*, whereas lightness and redness of the dorsal plumage (crown and back) of *C. tyrannina* were negatively correlated.

Plumage color differences between C. tyrannina *and* C. parkeri.—The crown of *C. parkeri* was significantly less saturated with red and yellow than in *C. tyrannina*, whereas the back of *C. parkeri* was both lighter and less yellow than that of *C. tyrannina* (Table 2). Most significantly, values for yellowness of the crown of the two species did not overlap, unlike breast color. A bivariate plot of factor scores for plumage color confirms the difference between the two taxa (Fig. 2, Table 4).

Geographic variation of C. tyrannina.—Annual rainfall ranges from approximately 1,500 mm in the middle Cauca and Magdalena valleys to more than 8,000 mm in the headwaters of the Atrato and San Juan rivers on the Pacific slope of the Cordillera Occidental (see Haffer 1967, 1975; Fig. 1.3 in Instituto Geográphico "Agustin Codazzi" 1982). In general, annual rainfall increases westward along transects drawn from the lower Río Magladena to the Gulf of Urabá on the Caribbean coast and the depto. Chocó on the Pacific coast.

Female plumage color ($n = 47$ individuals) appeared to vary along rainfall gradients. Trans-Andean populations are currently divided into two subspecies, *C. t. tyrannina* and *C. t. rufiventris.* Wetmore (1972: 190) noted that *C. t. rufiventris* was "merely a transition from the northern *crepera* [which ranges from southern Mexico to central Panama] to typical *C. tyrannina tyrannina,* found through most of Colombia, southern Venezuela and northwestern Brazil . . . occasional specimens in the area assigned to *rufiventris* are as pale as the average *tyrannina.*" Spectrophotometric measurements confirm his observations; *C. t. tyrannina* and *C. t. rufiventris* specimens are combined in the following analyses.

Lightness of the back ($r^2 = 0.18$, $P < 0.01$) and breast ($r^2 = 0.09$, $P < 0.05$), but not the

TABLE 3

PEARSON CORRELATION COEFFICIENTS OF OPPONENT-COLOR COORDINATE/PLUMAGE CHARACTERS OF FEMALES, WITH *Cercomacra parkeri* ABOVE THE DIAGONAL, *C. tyrannina* BELOW THE DIAGONAL. SIGNIFICANT P-VALUES FOR EACH SPECIES WERE ADJUSTED FOR NUMBER OF SIMULTANEOUS TESTS, 0.05/ 36 = 0.0013: $* < 0.001$; $** P < 0.0001$

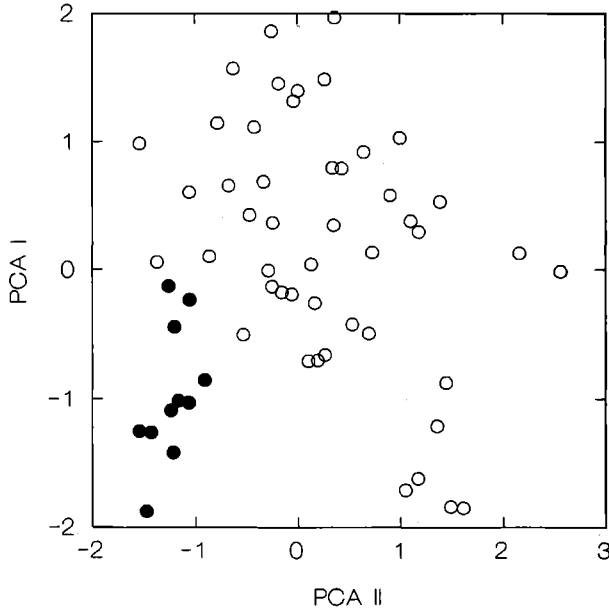|		(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
(1) Crown	L	—	0.41	0.01	0.30	0.11	-0.22	0.11	0.23	-0.30
(2) Back	L	0.47*	—	0.53	0.75	0.25	-0.23	0.04	-0.28	0.44
(3) Breast	L	0.47*	0.53*	—	0.36	0.41	-0.55	0.06	0.10	0.73
(4) Crown	a	-0.14	-0.53*	-0.37	—	-0.11	-0.08	0.50	-0.37	0.29
(5) Back	a	-0.27	-0.42	-0.20	0.69**	—	-0.18	-0.45	0.04	0.33
(6) Breast	a	-0.43	-0.45	-0.64**	0.49	0.34	—	-0.13	-0.73	0.13
(7) Crown	b	0.15	-0.26	-0.10	0.77**	0.47*	0.38	—	0.18	-0.09
(8) Back	b	-0.08	-0.52*	-0.02	0.57**	0.76**	0.28	0.58**	—	-0.46
(9) Breast	b	0.02	0.13	0.41	-0.05	-0.03	0.33	0.20	0.20	—

FIG. 2. Bivariate plot of factor scores (PCA I and II) from a principal components analysis of plumage color in female *Cercomacra tyrannina* and *C. parkeri* (see Tables 2, 3, and 4).

crown ($r^2 = 0.06$, $P > 0.10$), was negatively correlated with longitude, which in turn appears to be roughly correlated with rainfall. Saturation of dorsal (crown and back) and ventral (breast) plumage with red was positively correlated with longitude: crown ($r^2 = 0.33$, $P < 0.0001$); back ($r^2 = 0.39$, $P < 0.0001$); and breast ($r^2 = 0.14$, $P < 0.01$). Saturation of yellow in dorsal, but not the ventral plumage, also was positively correlated with longitude: crown ($r^2 = 0.22$, $P < 0.001$); back ($r^2 = 0.22$, $P < 0.001$); and breast ($r^2 = 0.01$, $P > 0.50$).

Specimens from the Pacific coast in the Chocó region and the Gulf of Urabá are darker and significantly more saturated in pigments expressed as red and yellow (Fig. 3). Clinal gradients are steepest near the base of the northern tip of the Central Andean Cordillera (compare Fig. 1 and Fig. 3). These data are conveniently summarized by PCA I (Fig. 4), which was positively correlated with longitude ($r^2 = 0.26$, $P < 0.001$). PCA 2 was uncorrelated with longitude ($r^2 = 0.00$, $P > 0.87$).

Only lightness and yellow of the breast ($r^2 = 0.46$, $P < 0.0001$) were positively correlated

TABLE 4

FACTOR LOADINGS FROM A PRINCIPAL COMPONENTS ANALYSIS OF OPPONENT-COLOR COORDINATES (*L, A, B*) of Female *Cercomacra parkeri* AND TRANS-ANDEAN COLOMBIAN POPULATIONS OF *C. tyrannina* (SEE FIG. 2)

		PCA Axes	
		I	II
Crown	lightness *L*	0.10	0.79
	red *a*	0.92	0.06
	yellow *b*	0.84	0.35
Back	lightness *L*	−0.14	0.80
	red *a*	0.84	−0.10
	yellow *b*	0.87	0.07
Breast	lightness *L*	−0.09	0.83
	red *a*	0.29	−0.73
	yellow *b*	−0.00	0.09
Percent variance explained		34.9	29.4

CROWN YELLOWNESS

BREAST YELLOWNESS

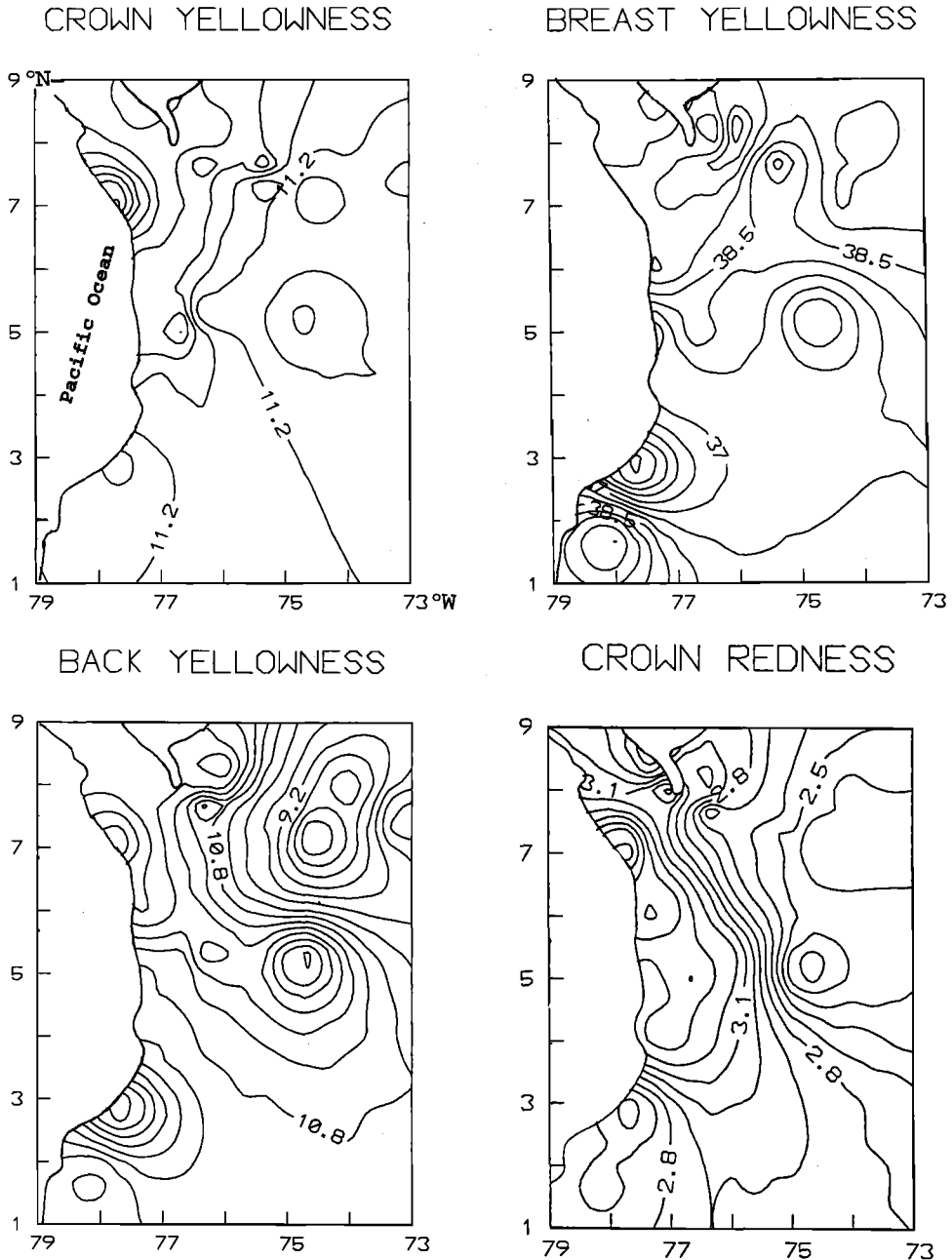## BACK YELLOWNESS

CROWN REDNESS

FIG. 3. Geographic variation of crown redness, and yellowness of crown, back, and breast of female *C. tyrannina* in Colombia (see Table 2). Note the difference in isoline orientation between dorsal and ventral yellowness. Degrees of north latitude and west longitude appear along the side and bottom.

with latitude. Color clines of the dorsal and ventral plumage thus appeared to be somewhat orthogonal to one another. PCA 1 ($r^2 = 0.03$, $P > 0.25$) and PCA 2 ($r^2 = 0.02$, $P > 0.42$) were uncorrelated with latitude (Fig. 3). In sum, geographic variation in female plumage of *C. tyrannina* is consistent with the expectations of Gloger's ecogeographic rule, which posits that populations in more humid environments tend to be more heavily pigmented.

Elevational variation of C. tyrannina *and* C. parkeri.—Although the elevational range of *C. tyrannina* is narrow in Colombia (sea level to 915 m in the Serranía del Baudo), significant
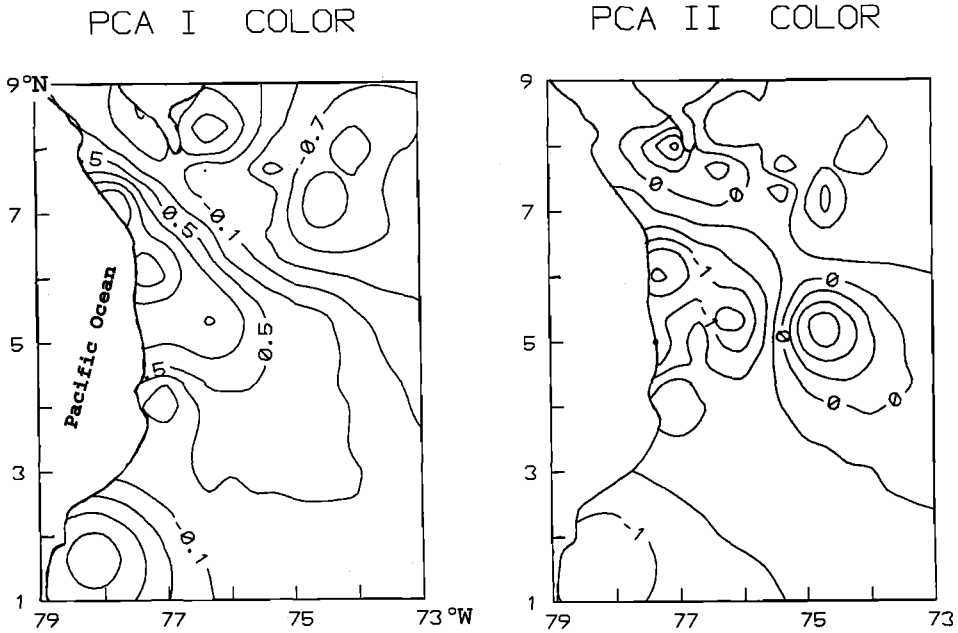
PCA I COLOR

PCA II COLOR

FIG. 4. Trend surface analysis of factor scores from a principal components analysis of plumage color of female *C. tyrannina*. Degrees of north latitude and west longitude appear along the side and bottom.

elevational clines in plumage color were observed. Two of the nine possible color/plumage characters of female *C. tyrannina* were negatively correlated with elevation: yellowness of the crown ($r^2 = 0.11$, $P < 0.03$) and back ($r^2 = 0.10$, $P < 0.03$), although these probabilities fall above the adjusted *P*-value when all characters are considered simultaneously (Table 5). In general (8 of 9 correlation coefficients were negative), plumage color was less rufescent at higher elevations.

Perhaps owing to small sample size ($n = 11$) of female *C. parkeri,* none of the colorimetric variables were significantly correlated with elevation (Table 5). However, the relationship between elevation and plumage coloration in *C. parkeri* differed qualitatively from that in *C. tyrannina* (Fig. 5). Only two of nine correlation coefficients had the same sign for both species (Table 5)—a result not expected by chance (binomial test, $P < 0.01$). Collectively, these data demonstrate the distinctiveness of *C. parkeri.*

TABLE 5

PEARSON CORRELATION COEFFICIENTS OF THE RELATIONSHIP BETWEEN COLORIMETRIC VARIABLES AND ELEVATION FOR FEMALE *C. parkeri* AND *C. tyrannina.* NONE OF THE P-VALUES WAS SIGNIFICANT WHEN ADJUSTED FOR THE NUMBER OF SIMULTANEOUS TESTS FOR EACH SPECIES $\alpha = 0.05/9 = 0.0056$

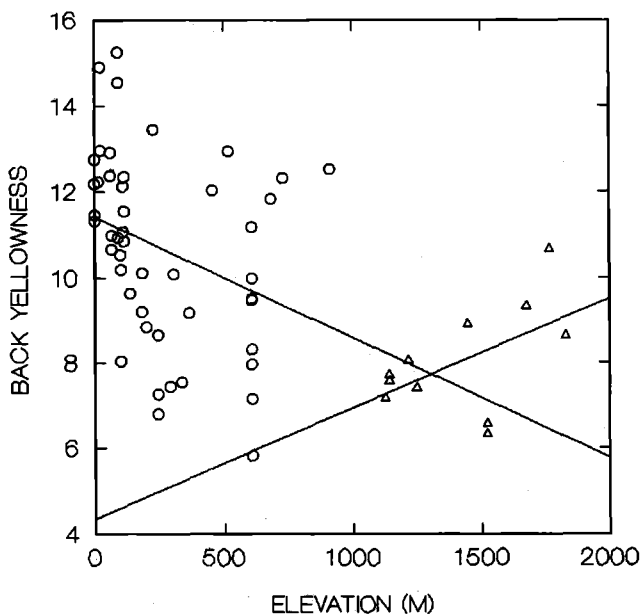|		*parkeri*	*tyrannina*
Crown	lightness (*L*)	0.14	−0.14
	red (*a*)	−0.08	−0.19
	yellow (*b*)	−0.20	−0.33
Back	lightness (*L*)	0.21	−0.05
	red (*a*)	0.61	−0.21
	yellow (*b*)	0.53	−0.32
Breast	lightness (*L*)	0.43	−0.11
	red (*a*)	−0.46	0.07
	yellow (*b*)	0.13	−0.07

FIG. 5.   Relationship of the "yellowness" of back plumage of female *C. tyrannina* (circles) and *C. parkeri* (triangles) with elevation. Least-squares regression lines for the two species are illustrated for comparison.

MORPHOLOGY

Morphological correlates within subspecies.—The correlative relationships among morphological variables of female *C. tyrannina* and *C. parkeri* (Table 6) differ significantly. Seven of ten correlation coefficients for pairs of variables of the two species had the same sign. Wing chord/tarsus and wing chord/bill length correlations were significantly positive for *C. tyrannina* but strongly negative for *C. parkeri*. These differences reflected a fundamental dissimilarity in morphological shape.

Morphological differences between C. tyrannina *and* C. parkeri.—From pooled samples of specimens (Table 1), the tail of male and female *C. parkeri* was significantly longer than that of *C. tyrannina,* and the bill width of female *C. parkeri* was significantly narrower.

Geographic variation of C. tyrannina.—Although this study focused on a fraction of the species' geographic range, females exhibited significant patterns of morphological variation in Colombia (Table 7). Wing chord and tail length were significantly correlated with longitude. Factor scores (PCA 1) derived from a principal components analysis of wing chord, tail length, and tarsus length were significantly correlated with longitude ($n = 36$, $r^2 = 0.34$, $P < 0.0002$) and uncorrelated with latitude. The size of females increased from the Pacific slope eastward to the upper Magdalena Valley (Fig. 6).

PCA I factor scores derived from morphology (wing, tail, tarsus) were significantly correlated with PCA I scores derived from the analysis of nine plumage color variables ($n = 36$, $r^2 = 0.17$,

TABLE 6

PEARSON CORRELATION COEFFICIENTS OF MORPHOLOGICAL MEASUREMENTS OF FEMALES. *C. parkeri* (N = 9–11) ABOVE THE DIAGONAL, *C. tyrannina* (N = 33–46) BELOW THE DIAGONAL: $* = P < 0.005$, $** = P < 0.0005$

	Wing	Tail	Tarsus	Bill length	Bill width
Wing	—	0.21	−0.57	−0.34	0.02
Tail	0.35	—	−0.41	−0.27	0.18
Tarsus	0.51**	−0.09	—	0.35	0.02
Bill length	0.44*	0.03	0.42	—	0.37
Bill width	0.06	0.22	0.05	0.16	—

TABLE 7

PEARSON CORRELATION COEFFICIENTS FOR THE RELATIONSHIP BETWEEN MORPHOLOGICAL
MEASUREMENTS AND LATITUDE AND LONGITUDE FOR FEMALE *C. tyrannina.* SAMPLE SIZE IN
PARENTHESES. SIGNIFICANCE: * = $P < 0.01$, ** = $P < 0.005$.

	Latitude	Longitude
Wing	0.03 (47)	* −0.39 (47)
Tail	0.19 (38)	** −0.61 (38)
Tarsus	−0.18 (45)	−0.17 (45)
Bill length	−0.26 (41)	0.11 (41)
Bill width	−0.28 (46)	0.22 (46)

$P < 0.024$). This suggests that both morphology and plumage color are labile and respond adaptively to environmental gradients.

Elevational variation of C. tyrannina *and* C. parkeri.—Two of five morphological characters of female *C. tyrannina* were positively correlated with elevation (Table 8). Populations inhabiting the Andean foothills and the Serranía del Baudó, depto. Chocó, had longer wings and tails and presumably greater body masses than lowland populations. In contrast, body size of *C. parkeri* (wing, tail, tarsus) was uncorrelated with elevation. However, bill length was negatively correlated with elevation (Fig. 7). These data reinforce the conclusions drawn from the analyses of plumage color—that *C. parkeri* was morphologically distinct and did not represent the end point of an elevational cline of *C. tyrannina.*

DISCUSSION

Subspecies of Cercomacra tyrannina *in Colombia.*—Patterns of geographic variation in color and morphology among Colombian females of *C. tyrannina* are complex and defy simple taxonomic categorization. In general, populations from the drier interior were paler in color and larger than those from coastal localities. However, trend-surface projections demonstrated that clinical patterns varied among the chosen color characters, often discordantly. Should the smaller, darker Pacific slope populations, "*T. c. rufiventris,*" continue to be recognized taxonomically? Although color clines appear to be steepest near the northern end of the Cordillera Central, where does one draw the dividing line between *rufiventris* and nominate *tyrannina*? Any such division would be arbitrary at best. I agree with Haffer and Fitzpatrick (1985) that subspecies
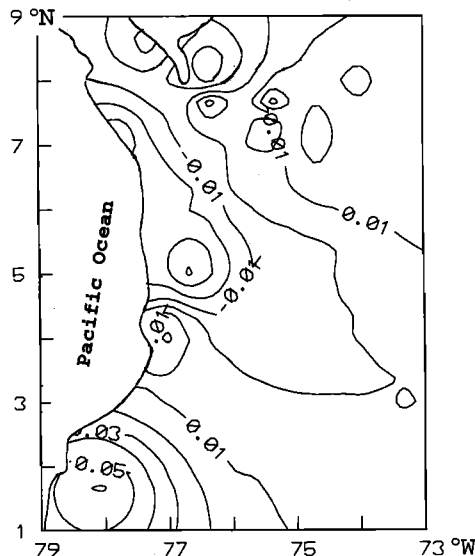

FIG. 6. PCA I factor scores from an analysis of body size of female *C. tyrannina.* Degrees of north latitude and west longitude appear along the side and bottom.

TABLE 8

PEARSON CORRELATION COEFFICIENTS FOR THE RELATIONSHIP BETWEEN MORPHOLOGICAL
MEASUREMENTS AND ELEVATION FOR FEMALE *C. parkeri* AND *C. tyrannina.* SAMPLE SIZE IN
PARENTHESES. SIGNIFICANCE: $*$ = $P < 0.05$; $**$ = $P < 0.005$

	parkeri	*tyrannina*
Wing	0.03 (11)	** 0.43 (46)
Tail	0.21 (10)	** 0.34 (38)
Tarsus	0.32 (11)	0.02 (44)
Bill length	* −0.74 (10)	0.13 (40)
Bill width	0.21 (11)	0.13 (45)

names should be applied only to populations that exhibit relatively uniform character "plateaus" separated by zones of rapid phenotypic change. Applying trinomials to a series of populations whose phenotypes imperceptibly grade into one another denies statistical reality. In the absence of well-defined subdivision between coastal and interior populations, I recommend that *C. t. rufiventris* (Lawrence) be placed in the synonymy of *C. t. tyrannina* (Sclater).

The roughly parallel clines in size and color of female *C. tyrannina* that corresponded to rainfall gradients suggest ecophenotypic adaptation, although environmental induction also may be partially responsible (James 1983). Color variation in this species is the best-documented case of Gloger's rule in the Neotropics. Size variation is subtle, but the statistically significant trend toward larger birds from drier interior locations and at higher elevations is consistent with the expectations of Bergmann's ecogeographic rule (see James 1970; Murphy 1985).

Is C. parkeri a species or a subspecies of C. tyrannina?—In contrast to the clinal variation among lowland populations, the distinction between highland (*C. parkeri*) and lowland (*C. tyrannina*) "dusky" antbirds is discrete. The intraspecific relationship of morphological and color characters differed between the two taxa, as did the relationship between plumage and morphological variables and elevation. No evidence of plumage intermediacy between the two taxa was found.

A narrow elevational hiatus may occur between the two species. *C. tyrannina* has been recorded up to 730 m in the Andean foothills, well below the range of *C. parkeri* (ca. 1,130–1,830 m). Females of both species have been collected along elevational transects at two localities (Table 9). Based on M. A. Carriker's specimens, catalogs (1947–1948), and field maps (deposited in USNM), elevational gaps of 885 m and 518 m, respectively, were recorded between *C. parkeri* and *C. tyrannina* along the El Pescado-Valdivia and Santa Rosa-Volador transects. Carriker did not distinguish between the two taxa in his field catalog and collected specimens of both opportunistically. In other words, he made no special effort to obtain "dusky antbirds" at higher elevations, perhaps because they were relatively common throughout the humid lowlands of northern Colombia. Thus, the actual width of the elevational hiatus at the two localities in the late 1940's could have been much narrower or nonexistent. In any event, there is no evidence of physical or environmental barriers between the two taxa. Ecological, behavioral, and biochemical data are needed to conclusively determine the specific relationship of *parkeri.* However, specimen data and elevational distributions indicate that *parkeri* is a biological species rather than a subspecies of *C. tyrannina.* I cautiously suggest that the burden of proof lies with those who would disagree.

Within the genus *Cercomacra,* at least three taxa appear to be restricted to the lower slopes of the Andes: (1) *C. parkeri* from Colombia; (2) *C. nigrescens aequatorialis* (Zimmer 1931) from eastern Ecuador; and (3) *C. nigrescens notata* (Zimmer 1931), including *C. n. jelashtei* (Carriker 1933), from eastern Peru. The elevational limits of a fourth taxon, *C. tyrannina vicina* (Todd 1927), are imperfectly known, but it may be restricted to the foothills of the eastern slope of the Cordillera Oriental in Colombia and the Andes of Venezuela.

Zimmer (1931) noted that *Cercomacra nigrescens aequatorialis* and *C. n. notata* were more similar in coloration to one another than either taxon was to *C. n. fuscicauda,* of the adjacent lowlands. Whether or not the lowland and highland populations of *C. nigrescens* are in genetic contact is unknown. However, the finding of discrete differences between *C. parkeri* and *C. tyrannina* suggests the possibility that a similar situation may occur between highland and lowland taxa of *C. nigrescens.*
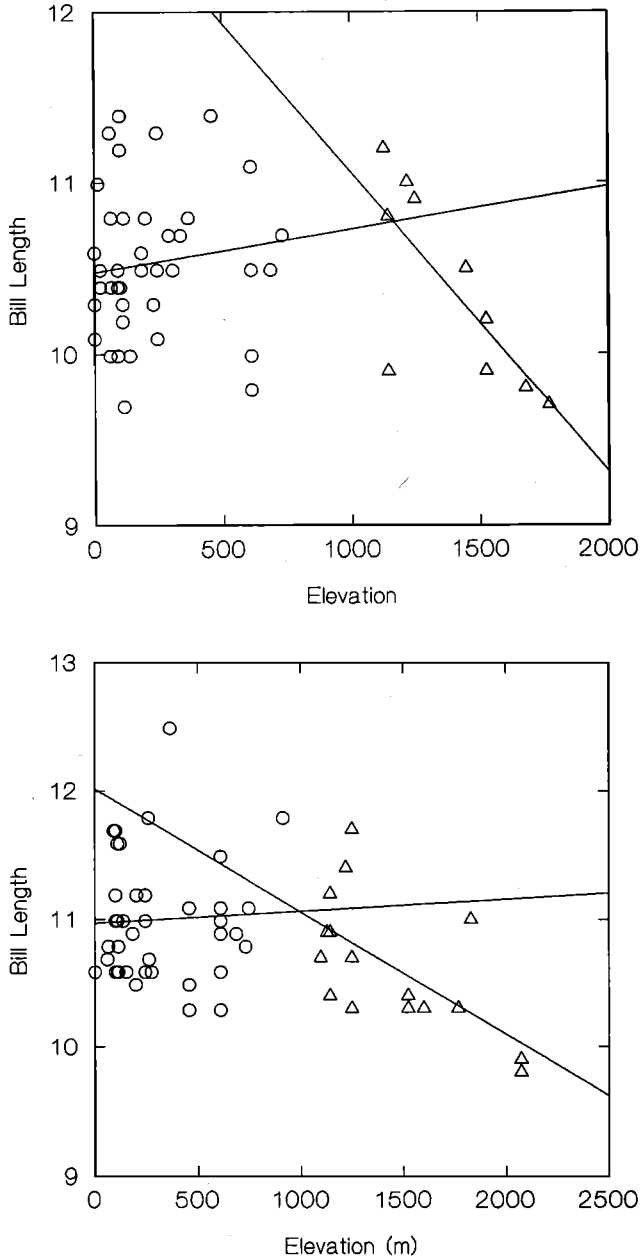
FIG. 7. Relationship of bill length and elevation for *C. tyrannina* (circles) and *C. parkeri* (triangles): females (top); males (bottom). Note that the slopes of the least-squares regression lines were of different sign for the two taxa. Intercepts and slopes for females were 10.48 + 0.00025 × elev. for *tyrannina* and 12.82 − 0.00175 × elev. for *parkeri*; for males, 10.97 + 0.00009 × elev. for *tyrannina* and 12.02 − 0.00096 × elev. for *parkeri*.

EPILOGUE

Speciation.—Although our knowledge of cryptic sibling species in the Andes is rudimentary (e.g., Graves 1987; Arctander and Fjeldså 1994; Whitney 1994), allopatric distributions may be the rule among recently evolved, geminate taxa (Mayr 1963). Because of the relatively short distances between the lowlands and the crest of the Andes, genetic isolation and differentiation

TABLE 9

LOCALITIES (ELEVATIONS) WHERE FEMALE *C. parkeri* AND *C. tyrannina* HAVE BEEN COLLECTED
ALONG THE SAME ELEVATIONAL TRANSECT

Transects	
El Pescado-Valdivia, depto. Antioquia	Santa Rosa-Volador, depto. Bolívar
tyrannina	*tyrannina*
El Pescado	Santa Rosa
198 m (USNM 402360)	610 m (USNM 392645)
335 m (USNM 402361)	(USNM 392815)
	(USNM 392875)
Puerto Valdivia	(USNM 392876)
110 m (AMNH 133489)	(USNM 392878)
	(USNM 398012)
parkeri	*parkeri*
Valdivia (above Sevilla)	Volador
1220 m (USNM 402341)	1128 m (USNM 398011)
1250 m (USNM 402347)	
1448 m (USNM 502348)	
La Frijolera	
1524 m (AMNH 133482)	
(USNM 256136)	

of *C. parkeri* (vis-a-vis *C. tyrannina*) is unlikely to have occurred along elevational gradients in the Colombian Andes (Graves 1988). A likely scenario is that *parkeri* evolved in allopatry in the lowlands, perhaps in the Cauca Valley, and was later displaced by *tyrannina* to mid-elevation foothills of the Andes after secondary contact.

Conservation.—*Cercomacra parkeri*, like many other Andean forest birds (Graves 1985, 1988), has a limited geographic distribution and elevational range. These factors translate to small population sizes and vulnerability to extinction. Mid-elevational forest in Colombia is rapidly disappearing (Hilty 1985), and most remaining forest patches are second growth or have been degraded by selective cutting. Because *Cercomacra* antbirds occur frequently in second growth, tangled thickets, forest edge, and stream-side vegetation, *C. parkeri* may be better off than primary forest obligates.

Summation and the future.—Avian speciation in the Andes and adjacent lowlands, especially the ecological and evolutionary processes that permit the co-existence of sister taxa, remain *terra incognita* despite more than a century of study. In a field in which narrative models are the norm, few hypotheses regarding differentiation and speciation have been tested quantitatively. The study of geographic variation in Neotropical birds also has a long tradition, but, again, only a few papers have quantitatively explored variation in morphology or plumage color or the ecological or evolutionary implications of character gradients. Why? Not only are pertinent data difficult to obtain but also the few ornithologists specializing on the systematics, taxonomy, and evolutionary biology of Neotropical birds have been reluctant to embrace quantitative methods. As a consequence, the poverty of our collective knowledge of quantitative patterns of geographic variation and their relationship to environmental gradients and speciation is overwhelming.

Ted Parker did not spend his time performing statistical analyses of character gradients or formulating null models of mixed-species flocks, but more importantly he collected data and observations that made my research on these topics possible. That was part of his genius. In a letter written many years before his death, Ted expressed his philosophy and work ethic: " . . . as long as I can see and hear and write I'll be ready for any kind of field work." He was an incredible resource of unique and unpublished data on Neotropical birds. Ted amazed his colleagues and inspired generations of students. Now, we go it alone.

In homage to his spirit, we must abandon the comfort of our academic offices for the wild parts of the planet while there is still time and rededicate our efforts to discover new facts— new information about the ecology, behavior, genetics, morphology, systematics, and distributions of birds. In final tribute to Ted's life, we must then do meaningful things with what we have learned.

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