

A TAXONOMIC STUDY OF CRESTED CARACARAS (FALCONIDAE)

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ABSTRACT.—The taxonomic status of the crested caracara (*Caracara* spp., Falconidae) has been unsettled for many years. Current sources such as the AOU Check-list recognize a single species that includes three taxa formerly considered distinct, citing observations by Hellmayr and Conover (1949) on two specimens considered to be intermediate. We studied plumage characters and measurements of over 392 museum specimens and found no evidence of clinal change between the northern and southern continental populations. Sixteen specimens from localities near the Amazon River where these two populations sporadically meet exhibit a mosaic of plumage elements from both forms. Measurements of wing chord, bill length, and bill depth indicate that size is positively correlated with latitude north and south of the equator and that females are larger than males in the northern population. These populations do not meet in western South America. We conclude that three biological species can be identified in the crested caracaras: the insular Guadalupe Caracara (*Caracara lutosus*); and two continental species, Northern (*C. cheriway*) and Southern caracara (*C. plancus*), neither of which shows subspecific variation. Received 6 Oct. 1998, accepted 16 Feb. 1999.

The Florida population of the Crested Caracara (*Caracara plancus audubonii*) is considered threatened by the U.S. Fish and Wildlife Service (1987), a recognition that subjects that population to strict permit regulations and consideration for conservation efforts (Morrison 1996). Although the generic name given in the Fish and Wildlife Service listing is *Polyborus*, Banks and Dove (1992) have shown that the generic name should be *Caracara*. The threatened status, together with the uncertainty reflected by various taxonomic treatments at the species and subspecies levels, has led us to complement Morrison's (1996) detailed report by examining the taxonomy of crested caracaras throughout their range.

Ridgway (1876) treated the crested caracaras as three species in the genus *Polyborus* (now *Caracara*): *tharus* Molina, 1782 of southern South America; *cheriway* Jacquin, 1784 from northern South America to southern North America; and *lutosus* Ridgway, 1876 of Guadalupe Island, Mexico. Except for the replacement of the specific name *tharus* with the earlier *plancus* Miller, 1777 by Bra-

bourne and Chubb (1912), an action followed by Swann (1925) and all subsequent authors, this treatment remained unchanged for three-quarters of a century. Swann (1925) thought that birds from the northern part of the range of *C. plancus* in Brazil were "more or less intermediate in appearance" between more southerly *C. plancus* and *C. cheriway*, but gave no details. Hellmayr and Conover (1949), stating that *C. cheriway* "appears to us nothing else but a well-marked race of the Southern Caracara," were the first to unite the two continental populations into a single species, *C. plancus*. The chief distinguishing characters of blacker coloration and reduction of white barring both on rump and chest were considered by Hellmayr and Conover (1949) as "merely differences of degree." They also noted that the apparent gap in measurements between extreme southern *C. plancus* (Strait of Magellan) and *C. cheriway* was bridged by specimens from intermediate localities. Hellmayr and Conover (1949) admitted that they had seen *C. cheriway* only from north of the Amazon River but cited records of that form from Santarem and Rhomes, south of the river. At the same time, they reported that specimens from Marajó and Mexiana Islands, in the mouth of the Amazon, belonged to *C. plancus*. The only actual evidence of intermediacy mentioned by Hellmayr and Conover (1949:283–284) was based on two adult birds from Obidos, Brazil, classified as *C. cheriway*, "which, by more heavily barred lateral upper

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TABLE 1. Plumage characters of *Caracara cheriway* and *C. plancus*.

Character—area	<i>C. cheriway</i>	<i>C. plancus</i>
1 Breast	dark spots or wedge-shaped bars, heavier posteriorly	dark and light bars over entire breast area
2 Vent area	pale patch between thighs	dark feathers between thighs
3 Upper back/Scapulars	pale wedge-shaped patch with broad black bars, scapulars always black	finely barred, no wedge-shaped patch, scapulars usually heavily barred, only lightly in n. part of range
4 Lower back	black	barring continuous with upper back and tail
5 Upper tail coverts	white or faintly barred	barred

tail coverts, mark a decided step in the direction of *plancus*.”

Friedmann and coworkers (1950) and the American Ornithologists' Union (AOU 1957) retained *C. cheriway* as a species. Wetmore (1965) paraphrased Swann (1925) in mentioning intergradation south of the Amazon and accepted “the present-day tendency to unite” the two mainland forms. Brown and Amadon (1968) considered *C. plancus* and *C. cheriway* conspecific as did Blake (1977), who briefly noted “evidence of intergradation in Brazil.” Vuilleumier (1970) was the first to treat the insular *C. lutosus* as a well-marked subspecies of the combined *C. plancus*, apparently following the suggestion of Brown and Amadon (1968:736) that if *cheriway* and *plancus* were combined, then “it would be no great extension to include *lutosus*.” Stresemann and Amadon (1979) and Sibley and Monroe (1990) merged the continental forms but retained *C. lutosus* as an allospecies. The AOU (1983, 1998) merged all the taxa, noting the report of intergradation “near the mouth of the Amazon.” Thus, the merger of *C. plancus* and *C. cheriway* is based mainly on Hellmayr's and Conover's (1949:283) statement that color characters were “merely differences of degree”, and on the two specimens of *C. cheriway* from Obidos, Brazil, that they stated showed a “marked step” in the direction of *C. plancus*. The degree of intergradation or variation has never been thoroughly examined in the limited geographical area where the northern and southern populations meet, and the distinctiveness of *C. lutosus* has not been reviewed since Friedmann (1950).

METHODS

To reevaluate the taxonomic relationships of the crested caracaras at the species level, we compared five plumage characters and three body measurements of specimens from all continental geographic populations. All plumage color comparisons were made under museum Examolites® or in daylight. We took measurements on more than 392 specimens of wing chord, bill depth (at the cere), bill length (from the base of the bill to the tip), and tarsus of sexed adult birds from all parts of the species' range. Tarsal measurements were extremely variable within populations and were deemed not useful for comparison. Measurements of males and females were analyzed separately to determine sexual variation.

We used an early version of Table 1 to categorize plumage characters in specimens examined, and we asked colleagues at some other museums (see acknowledgments) to use that and xeroxed photographs of Fig. 1 to evaluate specimens for us, thereby avoiding the need of extensive loans of these large birds. Voice recordings and tissue samples of this species are insufficient for accurate analysis at this time.

Specimens from the northern populations were compared with those from Bolivia and southern Brazil south to Tierra del Fuego. Twenty-one specimens from localities in Brazil along the Amazon River and the northeastern coast of Brazil are from the contact zone of the two populations and were examined separately for plumage patterns. These were compared with northern and southern populations to determine the extent of variation within this region. Because this species is not sexually dichromatic in plumage color or pattern, adult specimens (definitive plumage) were not separated for plumage comparisons.

At the subspecies level we examined the purported characters of recently recognized taxa (Hellmayr and Conover 1949, Peters 1931), all of which were described long ago from the periphery of the range of the species.

South American collecting localities were confirmed using Stevens and Traylor (1983), Paynter (1988), and Paynter and Traylor (1991). Descriptive statistics, AN-

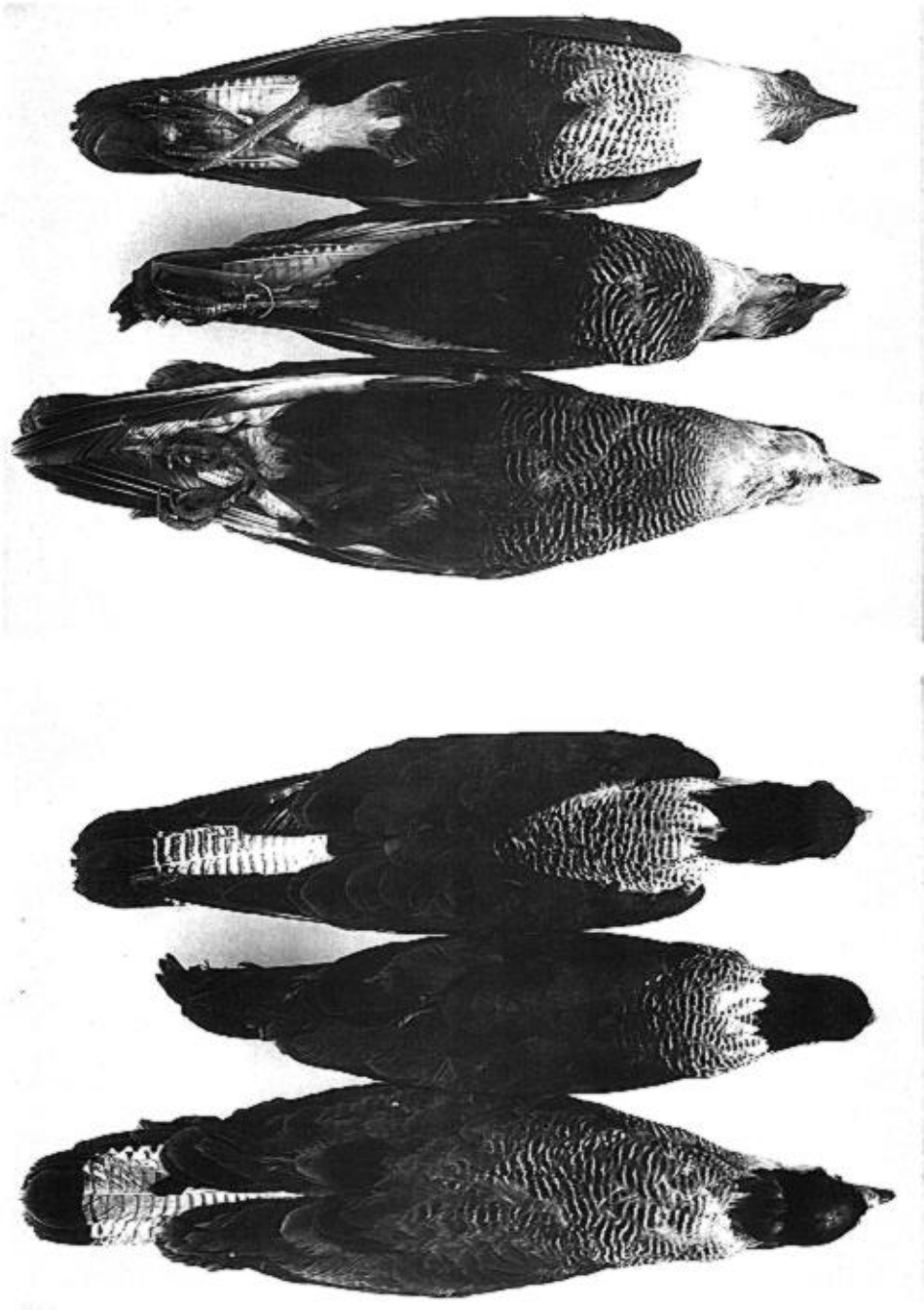


FIG. 1. Typical adult plumage, ventral (above) and dorsal (below) views of (top) *Caracara cheriway* (USNM 132707, Sonora, Mexico), (middle) specimen from zone of contact (USNM 276906, Maica, Brazil), and (bottom), *C. plancus* (USNM 284790, Argentina).

OVA's, and *t*-tests were done with SYSTAT (1992) version 5.0 for Windows.

RESULTS

Specific variation.—Typical adult crested caracaras from south (*C. plancus*) and north (*C. cheriway*) of the Amazon have clearly distinct color patterns (Fig. 1) with major differences in all five plumage characters. The plumage patterns of specimens from the northern and southern portions of the range do not overlap, and specimens from these populations can be identified and allocated unequivocally to either *C. cheriway* or *C. plancus* on that basis. All adult birds from northern Brazil (Roraima), Venezuela, Colombia, Ecuador, and Peru (Rio Chinchipe, Pacasmayo, and Catacaos) north to the United States (except Guadalupe Island) are of the *C. cheriway* type. Birds from southern Brazil (Bahia) and Bolivia to Tierra del Fuego are of the *C. plancus* type. In addition to the plumage differences evaluated (Table 1), the undertail coverts of *C. cheriway* are either all white, or faintly or incompletely barred, giving the base of the tail a whitish appearance, whereas the undertail coverts of *C. plancus* are finely barred with distinct wide white and narrow dark bars that extend completely across the feather. The base of the tail is more white than barred on *C. cheriway* specimens, but this character does not always hold true because some *C. cheriway* specimens have barring near the base of the tail.

Plumage patterns of specimens from the zone of contact.—The apparent zone of secondary contact for the two populations extends from the mouth of the Amazon River westward along the river and its southern tributaries to the Rio Tapajós (Fig. 2). It may extend west as far as the Rio Purus (Canutama), where two immature specimens (Field Museum of Natural History; FMNH 100805, 100806) having mosaic plumage tendencies were collected. A bird from farther west on the Rio Juruá (Museum of Comparative Zoology; MCZ 173161) is pure *C. plancus* and was not considered to represent the contact zone. The zone extends to the southeast from the mouth of the Amazon to approximately Morros de Mariana. The latest specimen collected from the contact zone that we found was dated 1937.

In two adult specimens (American Museum of Natural History; AMNH 241501, 241502) from well to the south at Remanso, on the Rio São Francisco, the plumage on the upper back/scapular area is similar to *C. cheriway*, but the lower back area is intermediate in color between *C. cheriway* and *C. plancus*. The breast of a bird (Naturhistorisches Museum, Vienna; NMWZ 39885) from Juazeiro, Bahia, was scored as *C. cheriway*. Specimens from other nearby Bahia localities (AMNH 163138, Salvador; The Natural History Museum; BMNH 73.3.19.4, Ilha de Itaparica; NMWZ 39884, Lago de Parnagua; NMWZ 39886, Barra) all are pure *C. plancus*. The appearance of these few *cheriway*-like characters well to the south may indicate a much wider zone of intergradation than we recognize, but the lack of available specimens from the intervening 500 km makes this conclusion problematical. This observation may merely be a reflection of the generally more variable plumage in the southern population. Gyldenstolpe (1951) also has commented on the lack of comparative material from parts of the range of this species.

Hellmayr and Conover (1949) mentioned birds from two other localities (Santarem and Rhomes) in the zone and we accepted their determination of those birds as *cheriway* (Table 2). We found no gradual intergradation in plumage characters but instead an abrupt shift in plumage type. There was no consistent pattern of intermediacy but rather a mosaic of plumage combinations. A summary of the plumage data shows that 54% of the 115 individual character states were like *C. plancus*, 40% were like *C. cheriway*, and 6% were intermediate. The lower back (character 4) received 4 of the 6 intermediate ratings. Specimens rated intermediate in this character have dark backs with white-tipped, not barred, feathers in the mid- to lower back region. No specimen was intermediate in more than one character. Seven of the birds from the contact zone were rated as pure for one or the other species.

The two specimens from Obidos that were the basis for the original merger of the species do not agree in plumage patterns. FMNH 101538 is typical *C. cheriway*, whereas FMNH 101539 has the breast and heavily barred tail pattern typical of *C. plancus* and

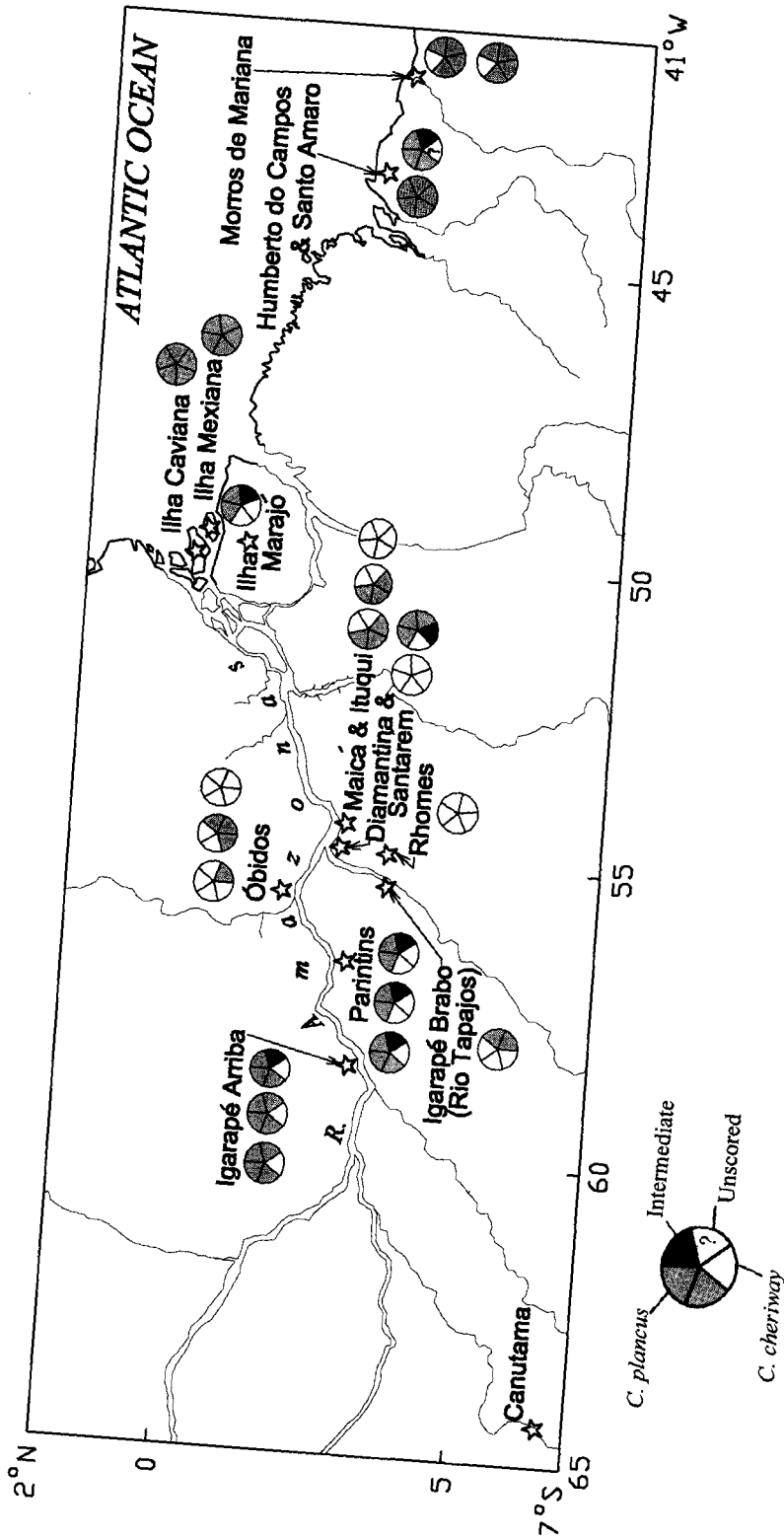


FIG. 2. Map of localities in zone of contact with icons corresponding to character states listed in Table 2.

TABLE 2. Summary of plumage characters (numbers from Table 1) of specimens from the zone of contact between northern and southern continental populations of crested caracaras. Localities without specimen numbers are included on the basis of records mentioned by Hellmayr and Conover (1949). C = *C. cheriway*, P = *C. plancus*, I = intermediate, ? = unscored.

Locality	Museum #	Character				
		1	2	3	4	5
Óbidos	FMNH 101538	C	C	C	C	C
	FMNH 101539	P	P	C	C	P
	BMNH 1908.8.21.17	P	C	C	C	C
Igarapé Arriba	FMNH 101424	P	P	C	P	P
	FMNH 101425	P	P	C	P	P
	FMNH 101427	P	P	C	I	P
Diamantina Parintins	USNM 121077	I	P	C	P	P
	AMNH 276706	P	P	C	I	P
	AMNH 277572	P	C	C	I	P
	AMNH 277573	P	C	C	I	P
Maicá Ituqui	USNM 276906	P	P	C	C	P
	FMNH 101157	C	P	C	P	P
	FMNH 101158	C	C	C	C	C
	AMNH 285747	P	P	C	C	C
Agarapé Brabo (Rio Tapajos)	AMNH 285747	P	P	C	C	C
Humberto do Campos (Maranhão)	FMNH 100401	P	P	P	P	P
Santo Amaro Maranhão	MCZ 92682	I	?	P	P	P
Morros de Mariana	AMNH 241499	P	C	P	P	P
	AMNH 241500	P	C	P	P	P
	BMNH 73.3.19.4	P	P	P	P	P
Ilha Mexiana	BMNH 73.3.19.4	P	P	P	P	P
Ilha de Marajó	MCZ 22996	P	I	C	C	P
Ilha Caviana	UM 7504	P	P	P	P	P
Santarem		C	C	C	C	C
Rhómes		C	C	C	C	C

the back pattern of *C. cheriway* with the wedge-shaped barring on the upper back and completely black mid- and lower back. An additional specimen from Obidos (BMNH 1908.8.21.17) is typical of *C. cheriway* except for the barring on the breast. Our efforts to locate the two other specimens from Obidos mentioned by Hellmayr and Conover (1949: 284) were unsuccessful.

Size variation.—We divided mensural data from the continental populations into four geographic sets as indicated in Table 3. A one-way analysis of variance shows significant differences among the four continental groups in wing length ($F = 27.8$, $P < 0.01$, $n = 336$), bill length ($F = 3.4$, $P < 0.02$, $n = 376$), and bill depth ($F = 4.2$, $P < 0.007$, $n = 391$), but body size, as estimated by wing chord measurements, was positively correlated with latitude (Fig. 3). Although individual variation in body size is extensive throughout the range, specimens from the extreme southern parts of South America are the largest. Northern and

southern populations were analyzed separately for sexual size dimorphism. *t*-tests of northern and southern populations revealed a significant sexual size difference in the northern population, with females being larger (wing length, $t = -5.50$, $n = 243$; bill length, $t = -5.96$, $n = 271$; bill depth, $t = -6.93$, $n = 277$; $P < 0.001$ in all measurements) but no difference in the southern populations (wing length, $t = -1.37$, $n = 77$; bill length, $t = -0.65$, $n = 84$; bill depth, $t = -0.84$, $n = 92$; $P > 0.05$ in all measurements). That the ostensible gap in measurements between *C. cheriway* and extreme southern birds was bridged by specimens from intermediate localities, was used by Hellmayr and Conover (1949) as an argument to justify conspecific treatment. Our data (Table 3, Fig. 3) show that these caracaras vary clinally within each hemisphere, and become smaller toward the equator. This is true for wing chord, bill length, and bill depth.

TABLE 3. Descriptive statistics for four geographic groups of continental crested caracaras and the Guadalupe Island caracara.

	Wing (mm)	Bill length (mm)	Bill depth (mm)
US, Cuba, Mexico	♂ $n^a = 85$	90	92
	R ^b = 343–409	28.6–36.7	16.2–19.9
	$\bar{x}^c = 382.51$	32.65	17.70
	SD ^d = 13.67	1.47	0.75
	♀ $n = 79$	84	86
	R = 363–415	29.8–38.7	16.5–22.0
	$\bar{x} = 391.27$	33.60	18.3
Central Am. & Northern South Am.	SD = 11.35	1.44	0.88
	♂ $n = 42$	51	51
	R = 353–409	29.5–35.0	14.8–19.2
	$\bar{x} = 374.17$	32.13	17.24
	SD = 12.14	1.27	0.84
	♀ $n = 37$	46	48
	R = 358–407	31.1–36.4	15.7–20.0
Contact Zone	$\bar{x} = 383.57$	33.28	18.05
	SD = 11.64	1.31	0.81
	♂ $n = 10$	13	14
	R = 351–401	30.2–34.7	16.3–18.9
	$\bar{x} = 379.5$	32.32	17.31
	SD = 16.15	1.41	0.88
	♀ $n = 6$	8	8
Southern South Am. Incl. S. Brazil	R = 359–406	29.2–33.8	17.3–18.8
	$\bar{x} = 386.00$	31.7	18.04
	SD = 16.54	1.55	0.48
	♂ $n = 35$	40	43
	R = 358–438	26.5–37.7	14.9–21.4
	$\bar{x} = 397.34$	32.49	17.92
	SD = 22.46	2.37	1.47
Guadalupe Island	♀ $n = 42$	44	49
	R = 361–455	28.2–37.3	15.7–21.4
	$\bar{x} = 404.45$	32.82	18.18
	SD = 22.84	2.28	1.44
	♂ $n = 1$		
	406	32.2	17.8
	♀ $n = 2$		
401.5	31.0	18.2	

^a n = number of specimens measured.

^b R = range.

^c \bar{x} = mean.

^d SD = standard deviation.

DISCUSSION

Species limits.—We conclude that there are 3 species of crested caracaras: *Caracara planicus*, *C. cheriway*, and *C. lutosus*. Our examination of nearly 400 specimens from the continental range of the crested caracaras (*Caracara*) revealed a mix in plumage characters of the northern and southern populations only in the limited zone of contact near the Amazon River in Brazil. We consider this limited character sharing a result of secondary contact, first suggested by Vuilleumier (1970). The

specimens indicate an abrupt shift in appearance from the northern to the southern plumage pattern, and most of the intermediate specimens exhibit a non-consistent mosaic of characters (back pattern, breast). Juvenile birds from the contact zone exhibit the same tendencies, but were not studied as extensively as adults.

The essential reproductive isolation of these populations is expressed by the low number of intermediate characters in specimens from the contact zone, and the relatively narrow

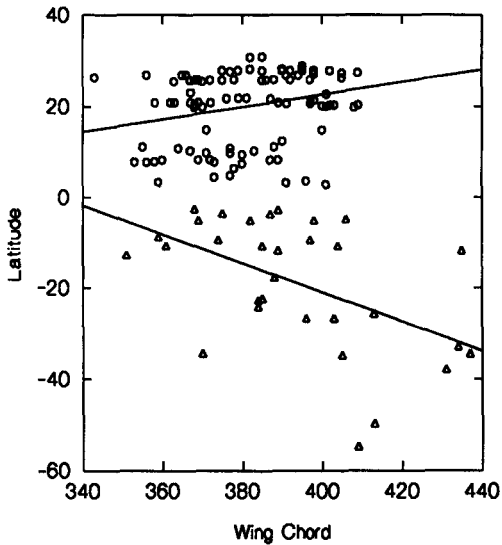


FIG. 3. Linear regression model of size (indicated by wing chord) and latitude of 196 specimen records. Triangles represent specimens from south latitude and circles represent specimens from north latitude.

area of overlap. Crested caracaras are not widespread in Amazonia east of the Andes, occurring only as wanderers in isolated patches of savanna in Amazonian Colombia, Ecuador, and Bolivia. Individuals of the two forms probably meet only infrequently when they wander into areas of sufficiently open habitat along the Amazon River. There is no record of contact of the populations in western South America. Localities of South American specimens reveal a distributional gap from northern Peru (excluding three *cheriway* specimens taken from coastal Peru and the Peru-Ecuador border) south to the middle of Chile. Parker and coworkers (1982) indicate that crested caracaras are uncommon or rare in southern Peru, and Johnson (1965) reports they are very scarce and confined to the sea coast in the two northernmost provinces of Chile (see map 77 in Brown and Amadon 1968).

Review of the Guadalupe Island species.—Morphologically, adults of the extinct Guadalupe Island population differ from those of North and South American mainland populations more than the latter two differ from one another. The crest of *C. lutosus* is brown rather than black, and the crest feathers are longer than those of mainland specimens. The throat

is buff to pale brown, not white. Ventral and dorsal surfaces of the rest of the body are entirely banded with brown and white or buff, and there is no solid abdominal patch as in the mainland populations. Remiges and some scapulars are solid brown rather than black; most upper-wing coverts are bordered narrowly with darker brown. Sexed adult representatives of extinct *C. lutosus* are rare in collections, and only three specimens were measured (see Table 3). They do not differ in size from mainland birds.

A few specimens from southern South America (e.g., U.S. National Museum, USNM 13926, Patagonia) show some resemblance to *C. lutosus*. These South American mainland birds are primarily brown rather than black, and most of the body, except for the thighs and a small abdominal patch, is banded. However, the banding is finer on the mainland birds than in *lutosus*. It was undoubtedly birds like this that Ridgway (1876:460) alluded to when he stated "This species resembles the *P. tharus* [= *C. plancus*] much more than *P. cheriway* . . ." An explanation for the morphological similarity of birds at opposite ends of the range, with birds of quite different appearance occupying the intervening continent, would be speculative at this stage.

We agree with Ridgway (1876) that the Guadalupe Island birds are specifically distinct. Recognition of that distinct and isolated population follows logically from our separation of *C. cheriway* from *C. plancus*, but we suggest that the extinct *C. lutosus* should be recognized at the species level regardless of the treatment of the mainland populations.

Intraspecific variation.—Both southern (*C. plancus*) and northern (*C. cheriway*) crested caracaras have been variously divided at the subspecific level by different authors. Populations of the Southern Caracara (*C. plancus*) from northern Paraguay to the Amazon have frequently been separated under the trinomial *C. p. brasiliensis* (Gmelin, 1788) on the basis of being darker and smaller (Swann 1925, Wetmore 1926, Peters 1931). The name *brasiliensis* cannot be applied to any caracara (Banks and Dove 1992), and Gyldenstolpe (1951) has indicated that the subspecific name *caracara* Spix, 1824 must be used if two forms of birds south of the Amazon are recognized. However, we are unable to document

any consistent difference in plumage pattern, color, or size among these birds, and so we follow most recent authors (Hellmayr and Conover 1949, Gyldenstolpe 1951, Blake 1977, Stresemann and Amadon 1979) in recognizing the populations south of the Amazon as being monotypic *Caracara plancus*.

Populations of the northern mainland species, *C. cheriway*, have been recognized by up to four subspecific names (*cheriway* Jacquin, 1784; *audubonii* Cassin, 1865; *pallidus* Nelson, 1898; *ammophilus* van Rossem, 1939). Divisions in this species have been based on the amount and intensity of black as opposed to brown on the wings and back, and on size. The amount of black is subject to individual variation, and depends on stage of molt and extensive fading related to the open habitat occupied by the species. Contrary to Griscom (1932), we do not believe that fading from black to brown occurs post mortem. Size varies less than some earlier writers have suggested and increases clinally from the Amazon to the north (Fig. 3), so that the birds in the southern United States tend to be among the largest. There are no major changes in these characters to warrant the recognition of van Rossem's (1939) *ammophilus* of Sonora, Mexico with a supposedly smaller bill and feet and more prominently barred tail, or, despite the present disjunction of range, the trinomial *audubonii* that Cassin (1865) based on Florida's larger birds. We agree with Stresemann and Amadon (1979) in considering those names synonyms of *C. cheriway*.

Nelson (1898) separated birds from the Tres Marias Islands off western Mexico under the subspecific name *pallidus*, on the basis of paler or lighter brown coloration and slightly smaller size. Grant (1965) agreed that the island birds are generally paler brown than those on the mainland but attributed the difference to greater fading of the island birds. We agree that the color is not diagnostic, and note that new feathers or those generally hidden from solar radiation are no paler on the island birds than on those from elsewhere in the range. Furthermore, AMNH 471349, taken by Nelson at the Tres Marias, is dark both dorsally and ventrally. Grant (1965) considered a shorter terminal tail band and a shorter wing and tarsus in males to be sufficient for recognition of *pallidus*, even though compa-

rable differences could not be demonstrated in females. However, tarsus length is too individually variable to be a useful taxonomic character. Wing and culmen lengths given by Nelson (1898) and Grant (1965) fit well in the range of variation of the much larger mainland sample we measured (Table 3). We believe that the minor difference in the length of the terminal tail band may be related to wear of the rectrices and that other differences of tail band characters mentioned by Grant (1965) are not sufficient to warrant separation of the Tres Marias population. Some specimens from the Tres Marias exhibit extensive barring on the abdomen, but this is within the range of variation of the mainland specimens. Thus, we synonymize *pallidus* with *C. cheriway*.

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