BUTEO POLYOSOMA AND B. POECILOCHROUS, THE "RED-BACKED BUZZARDS" OF SOUTH AMERICA, ARE CONSPECIFIC[1]

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Abstract. The Puna Buzzard (= Variable Buzzard or Gurney's Buzzard, *Buteo poeciloch-rous*) and the Red-backed Buzzard (*B. polyosoma*) are two morphologically similar and closely related South American raptors that have been and are currently separated as species mainly on the basis of wing length and "Stresemann's wing formula." I reexamined wing formula, wing length, geographic variables, and plumage in adults and immatures, and adult vocalizations. For both adults and immatures, wing formula and wing length are not reliable taxonomic characters because of their continuous clinal relationship. In both age classes, wing tip contour changes allometrically with changes in wing length, which is itself a function of body size and mass. Thus, neither of the currently accepted morphometric characters examined here serve to separate taxon *polyosoma* from *poecilochrous*. There are at least 27 distinct adult plumage morphs (formerly five) in this species group, perhaps more than any other in Falconiformes, with no relationship to morphometric variables and only minor geographic variation. Immature plumages are similarly ineffective in diagnosing taxa. Vocalizations are similar among adults from widely varying latitudes and altitudes. I therefore propose dropping *poecilochrous* (Gurney 1879) in favor of *polyosoma* (Quoy and Gaimard 1824) for all forms in this group, as the latter has priority. The English common name applied to this group should be Variable Buzzard, with the exception of the isolated population in the Juan Fernandez Archipelago which should for now remain the Juan Fernandez Buzzard (*B. p. exsul*), although it may well be elevated to species rank with further data.

Key words: allometry, Buteo poecilochrous, Buteo polyosoma, *polymorphism, raptors, systematics, taxonomy.*

Resúmen. El gavilán cordillerano (= gavilán variable, *Buteo poecilochrous*) y el aguil-ucho de espalda colorada (*B. polyosoma*), son dos rapaces del occidente de América del Sur que morfologicamente son muy semejantes. Al presente están separados como especies según la medida del largo del ala y la "formula de ala" de Stresemann. Porque puede haber influencia alométrica, ecomorfológica, y de dimorfismo en tamaño sexual en los caracteres en consideración he reexaminado medida de ala, formula de ala, y variables morfométricos y geográficos para adultos y juveniles, plumaje de adultos y juveniles, y vocalizaciones de adultos. Este estudio demuestra para ambos adultos y juveniles que no se puede tener confianza en la medida del largo de ala y formula de ala para hacer deciciones taxonómicas porque las dos variables exhiben una relación clinal continua. Para las dos clases de edad, el contorno de la punta del ala cambia alometricamente de acuerdo con cambios en lo largo del ala, lo cual es una función de tamaño y peso del cuerpo. De esta manera, ningunos de los dos caracteres taxonómicos principales examinado aquí sirven para separar taxon *polyo-soma* de taxon *poecilochrous.* Hay por lo menos 27 (anteriormente cinco) morfos de plumaje en los adultos de este grupo, quizás más que cualquier otro miembro de Falconiformes documentado, sin relación de cualquiera con variables morfométricos y con solo mínima variación geográfica. Plumaje juvenil también es inútil para distinguir entre *polyosoma* y *poecilochrous.* Vocalizaciones de adultos de diferentes latitudes y altitudes son semejantes. Por lo tanto, yo propongo rechazar el nombre *poecilochrous* (Gurney 1879) en favor del nombre *polyosoma* (Quoy and Gaimard 1824), que tiene prioridad, para todos los morfos de este grupo. El nombre común designado para este grupo debe ser gavilán variable, con la excepción de la población aislada del aguilucho de Más Afuera (*B. p. exsul*) en el archi-pélago de Juan Fernandez que debe permanacer como es, aunque datos colectados en el futuro podrán servir para elevarlo al rango de especie.

Palabras claves: alometría, Buteo poecilochrous, Buteo polyosoma, *polimorfismo, ra-paces, sistemáticas, taxonomía.*

INTRODUCTION

Two nearly identical and thus presumably very closely related South American raptors, the Puna Buzzard (= Variable Buzzard or Gurney's Buzzard, *Buteo poecilochrous*, Gurney 1879) and the Red-backed Buzzard (*B. polyosoma*, Quoy and Gaimard 1824), have endured a long history of systematic and taxonomic confusion (e.g., Hellmayr and Conover 1949, Amadon and Bull 1988). Despite these uncertainties, the two taxa, which are collectively referred to as the "red-backed hawks" of South America (Vaurie 1962), continue to be regarded as separate species (e.g., Sibley 1993, del Hoyo et al. 1994).

Two subspecies are currently recognized in *polyosoma; poecilochrous* is monotypic (Stresemann and Amadon 1979). *B. p. polyosoma* (Stresemann 1925) has an extensive latitudinal distribution in western South America. It not only occurs patchily in the Andes (páramo and puna habitats) from southwestern Colombia through Chile and Argentina, in the arid coastal lowlands of western Ecuador, Perú, Chile, in Patagonia (shrub-steppe habitat), and the Argentinean Pampas (Vuilleumier and Simberloff 1980, Vuilleumier 1986, Travaini et al., 1994), but it also inhabits several islands (e.g., Tierra del Fuego Archipelago, Falklands) (Cobb 1933, Marchant 1960, Fjeldså and Krabbe 1990). *B. p. exsul* (Salvin 1875), the Juan Fernandez Buzzard, an insular endemic, breeds primarily on Alexander Selkirk Island of the Juan Fernandez Archipelago (Murphy 1936, Navarro 1970) but was recently introduced to nearby Robinson Crusoe Island where it appears to be "thriving" (Brooke 1987). Other formerly recognized subspecies (e.g., *peruviensis* Swann 1922, *simonsi* Swann 1922, *unicolor* d'Orbigny 1836) have been suppressed without major objection (Stresemann and Amadon 1979). *B. poecilochrous* is considered a high Andean endemic, occurring from northern Ecuador through northwestern Argentina; a range broadly overlapping, or parapatric with, that of *polyosoma* (Vaurie 1962, Solis and Black 1985, Jimenez and Jaksic 1990). Many field observers have relied upon elevation to distinguish the taxon, although this cannot always be reliable as *polyosoma* can occur at higher elevations (Hilty and Brown 1986, Fjeldså and Krabbe 1990, Cabot 1991).

Both *polyosoma* and *poecilochrous* are highly polymorphic in definitive basic (adult) plumage.

All adult plumage types (morphs) are united by the possession of a distinctive white, faintly to heavily barred tail with a wide black subterminal band nearly identical to that of the White-tailed Hawk (*B. albicaudatus*). Vaurie (1962) grouped the various plumages into a series of five morphs, four of which he suggested were identical in both species, whereas the fifth was restricted to *polyosoma* (Hellmayr 1932, Hellmayr and Conover 1949). Variable amounts of reddish, chestnut or rufous pigmentation commonly are found in the dorsal feathers both laterally across shoulders to marginal and lesser coverts, and longitudinally from nape to upper tail coverts of adults of either sex but more frequently on females; hence the term "red-backed hawks." Gray backs are not uncommon but are found on more males than females (Vaurie 1962).

Major systematic treatments of *polyosoma* and *poecilochrous* lack consensus and reflect a need for more detailed information. The two forms have traditionally been classified as allospecies in a superspecies complex (Amadon 1966, Amadon and Short 1976, 1992) which also includes *albicaudatus* (Stresemann and Amadon 1979, Amadon and Bull 1988). Voous (1968) suggested that the Galápagos Buzzard (*B. galapagoensis*) also might be allospecifically related. Sibley and Monroe (1990) regarded *albicaudatus* and *galapagoensis* as allospecies, but excluded *polyosoma* and *poecilochrous* from the superspecies entirely, citing the occurrence of "too much distributional overlap," and suggesting that these latter two taxa should instead be regarded as full and separate species. In a recent revision, however, Sibley (1993) deferred to the opinion of Amadon (in Peters 1979:367) which considered *polyosoma, poecilochrous*, and *albicaudatus* as allospecies (= superspecies). Suspected hybridization in zones of overlap (Vaurie 1962) has led some authors to suggest that *poecilochrous* should be considered an altitudinal variant (e.g., subspecies) of *polyosoma* (Brown and Amadon 1968, Amadon and Bull 1988). Allospecies status for *polyosoma, poecilochrous*, and *albicaudatus* , but not *galapagoensis*, is accepted in the American Ornithologist's Union checklist (AOU 1983) with the caveat that the taxonomic relationship among them is uncertain.

Gurney (1879) originally separated *poecilochrous* from *polyosoma* on the basis of the former's greater wing length and body size but

gave no details on the ranges of these values for diagnostic purposes. Stresemann (1925) later developed a wing formula consisting of the difference in relative lengths of the sixth and eighth primaries counting from the inside, rather than from outside as in Gurney (1879) and Vaurie (1962). Often referred to as "Stresemann's wing formula," the eighth primary should be longer than the sixth in *polyosoma,* whereas *poecilochrous* should show the reverse. However, Stresemann (1925) apparently neither examined the type of *poecilochrous* (holotype, 8751330; British Museum of Natural History, BMNH) nor made note of Gurney's (1879) description of it, because presumably he would have realized that the eighth primary was clearly *longer* not shorter than the sixth in that specimen (Gurney 1879: 177, Hellmayr and Conover 1949:91, Farquhar, unpubl. data). Discrepancies notwithstanding, ornithologists working with *polyosoma* and *poecilochrous* have, in general, adopted Stresemann's wing formula as the standard and most reliable diagnostic character. As it is difficult at best to distinguish relative primary lengths on volant raptors in the field, many field observers regard Stresemann's wing formula as a geometric basis for the observable "roundedness" (or "pointedness") of the wing tip contour (Fjeldså and Krabbe 1990, Cabot 1991). Rounded wing tips suggest wing formulas consisting of small values (p8 ≤ p6), thus identifying *poecilochrous,* whereas large values (p8 > p6), represented in pointed wing tips, identify *polyosoma.* Other characters used with less frequency and success in diagnosis between these two buzzards have included purported differences in juvenal plumage (paler, more variegated in *polyosoma* than in *poecilochrous*), and in altitudinal distribution (*polyosoma* < 3,500 m, *poecilochrous* > 3,500 m) (Hellmayr and Conover 1949, Vaurie 1962, Fjeldså and Krabbe 1990).

Regardless of whether the type of *poecilochrous* has the "wrong" wing formula, one might not be able to rely on this character, or on wing length, due to confounding relationships. For example, wing morphology (e.g., wing tip contour) and body size (e.g., wing length) are allometrically related in birds (Rayner 1988). These two characters are thus potentially misleading for a diagnosis, especially if they are clinally or randomly distributed in morphometric space. Therefore, reversed sexual size dimorphism, as is exhibited in these species, could be expected

to confound a diagnosis based solely upon wing formula or wing length. In addition, because these buzzards occur across expansive altitudinal (0 to 5,000 m) and latitudinal (6°N to 55°S) zones, there may be geomorphological correlations to consider (Johnson and Selander 1971, Nolan and Ketterson 1983).

In this paper I address the systematic and taxonomic problems in this group by examining characters relevant to diagnosis between *polyosoma* and *poecilochrous* including morphometrics, adult plumage, and vocalizations. Analysis of these data reveal that no reliable characters exist for species diagnosis between these taxa and, therefore, they should be merged into one; namely, *Buteo polyosoma,* because it has priority over *B. poecilochrous.*

METHODS

For the morphometric portion of this study I examined 199 adult and 95 immature specimens (skins) deposited in 18 major museums. All specimens analyzed for this study were carefully checked for molt and wear prior to measurement. I measured the following characters: lengths (from carpal joint to tip of feather, wing flat) of five outermost primaries, nine (p9), eight (p8), seven (p7; = wing length, WL), six (p6), and five (p5), which form the wing tip; and, wing formula, WF, length of p8 minus that of the sixth primary p6 (Baldwin et al. 1931). Measurements of bilateral characters were generally taken on the right side, or the left, if damaged feathers were present. All measurements of primary lengths were made with the same wing rule, in whole millimeters. I obtained data on altitude (ALT), latitude (LAT), and longitude (LONG) either directly from the specimen tags or from ornithological gazetteers (Paynter 1975, 1977, 1981, 1985, 1988, Stephens and Traylor 1983).

To remove geographic effects from morphometric variables, I regressed raw data for a given morphometric variable against the variables whose linear effects I wished to control (e.g., latitude, longitude, altitude, and interactions), and saved the residuals. These residuals were then used in subsequent statistical analyses. All morphs of both species were pooled for statistical analyses of mensural characters. Data outliers were identified and removed prior to analyses using the Mahalanobis D^2 test in JMP statistical software (SAS 1989). Correlation and re-

gression analyses were conducted using JMP and SYSTAT (1992). Level of significance was $P \leq 0.05$.

In examining plumage morphs, I visually inspected all specimens using natural daylight, and followed Vaurie's (1962) descriptions of both adult and immature (juvenal) plumages as a guide in order to minimize confusion and maximize consistency. For both age classes I compared plumage morph with wing formula, wing length, altitude, and latitude to note any association useful for taxonomic diagnosis. There may be some confusion initially between adult plumage designations proposed by Vaurie (1962) and those developed here because I decided to remain with capital letters to designate plumage morphs. Because an author's name will likely be associated with the morphs no matter what the designations, the names or symbols applied to the morphs will become less important.

For specimens in adult plumage, Vaurie (1962) noted general color (chestnut, gray, and white) and pattern (solid or barred) on the dorsal (mantle) and ventral (throat, breast, abdomen) regions. Other regions of the body, e.g., crown, nape, wings, are too uniform in color (typically some shade of gray, except for a very rare completely erythristic morph) across the majority of specimens to be of any importance in diagnosis. Instead of chestnut or rufous, I chose the term "reddish" as it connotes a wider array of hues and brightnesses inherent in the expression of that pigment in these taxa. The area of the back covered by reddish pigmented feathers is quite variable and continuous between successive specimens, ranging from extensive (completely reddish feathers found both laterally across shoulders to marginal and lesser coverts, and longitudinally from nape to upper tail coverts) to quite sparse with less than six feathers exhibiting traces of reddish pigment, the remainder being gray. The gray coloration in the feathers also is variable, ranging from near black to light gray precluding reliable categorization of the various shades. I placed specimens devoid of pattern, such as barring, into pure (clear) color groups. Thus, specimens with only a few feathers containing a different pigment, e.g., small amount of reddish on otherwise gray feathers, were placed in a separate category, e.g., reddish-gray. Barring, generally restricted to the posterior portion of the ventral feathering, included the abdomen, thighs, and flanks (see Pettingill

1985). However, only the abdomen was considered in this study because if the abdomen is barred then the thighs and flanks also are barred; the converse is usually, but not always, true.

Vaurie's (1962) general description of immatures in juvenal plumage was that *polyosoma* is "paler, more variegated and more streaked" on the underparts than *poecilochrous*. Thus, I grouped specimens according to pattern of ventral pigmentation (e.g., streaking, mottling, and/or pure). As Vaurie suggests, the contour and flight feathers of virtually all specimens exhibit highly variable shades of brownish, rufous or chestnut, often with a lighter ground color of buff to ochraceous buff so as to make actual color less useful in diagnosis. All juvenal plumages are distinguished from adults by having tails with closely spaced, thin brownish-gray bars on an otherwise grayish background. In contrast, adults all have tails with more widely spaced brownish to grayish bars on a background of pure white, and with a wide (ca. 2–4 cm) black subterminal band.

Vocalizations emitted in a territorial context by adults (e.g., as when human observers approach nest areas, often considered "alarm calls;" see Farquhar 1992) were recorded in the field using a Sony TC-D5 Pro II cassette recorder and a Sennheiser MKH 70 shotgun microphone fitted with a Zeppelin wind screen. Adult females representing ranges of wing formula (e.g., wing tip contour, rounded, or pointed) and wing length (relatively longer or shorter) were selected for recording in each of four sites: (1) bird with long, rounded-wing—recorded at nesting area, 3,700 m above sea level (masl), approximately 28 km ESE Quito, Ecuador, on the road to Papallacta, along a volcanic ridge known locally as "Cerro Paluguillo," approximately 21 km WNW of Volcán Antisana; (2) bird with short, pointed wing—recorded at nesting area, 60 masl, along main road 1.8 km E Ancón, Ecuador; (3) bird with short, pointed wing—recorded at nesting area, 70 masl, along main highway 23 km ESE Santa Elena, Ecuador, near Cerro Chucacunduy; and (4) bird with long, pointed wing, recorded at nesting area, near Santiago, Chile, 2,800 masl. I generated spectrograms of the calls using Canary (v. 1.0, Cornell Laboratory of Ornithology, Ithaca, New York).

RESULTS

The following analysis is divided into three parts. The first focuses on morphometrics. Spe-
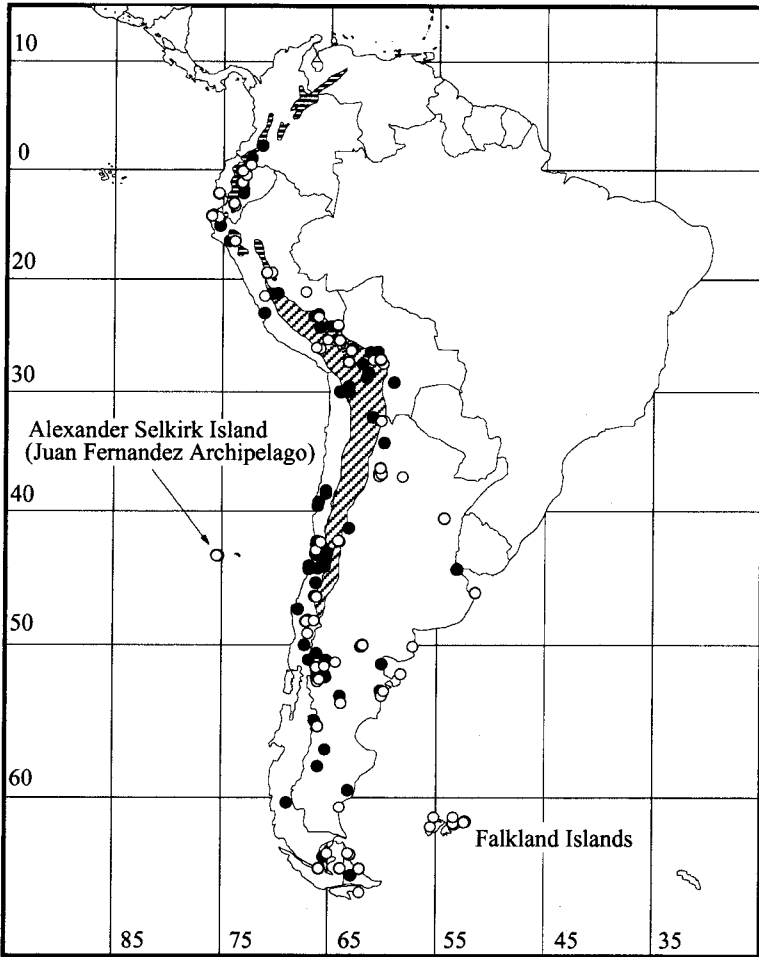
FIGURE 1. Distribution of collecting localities for the specimens of adult (dark circles) and immatures (open circles) of *Buteo polyosoma* and *B. poecilochrous* used in this study. Shaded areas represent páramo (horizontal hatching) and puna (diagonal hatching) habitats above 2,000 m above sea level (after Vuilleumier and Simberloff 1980).

cifically, the discriminatory power of the two most commonly used diagnostic characters: wing formula (WF) and wing length (p7). The second part of the analysis deals with identification and grouping of plumage morphs. For the preceding two analyses I examined two age classes, adults ($n = 83$ males, 116 females, and 38 specimens of unknown sex) and immatures (in juvenal plumage; $n = 50$ males, 45 females, 42 specimens of unknown sex), a sample which uniformly represents the geographic range of both *polyosoma* and *poecilochrous* (Fig. 1). In the third part of the analysis I qualitatively compare adult vocalizations among individuals

(adult females) of varying wing formulas and wing lengths recorded in the field in four widely separated geographic regions.

MORPHOMETRICS

Figure 2 displays, for both adults and immatures, the regression between residuals (removing linear effects of latitude, longitude, altitude, and interactions) for wing formula (WF) and wing length (p7). Note that no discrete groups appear around which to hypothesize a taxonomic boundary for either age class. Rather, the distribution of data points is clinal. In both sexes of adults the relationship (slope) is allometric and
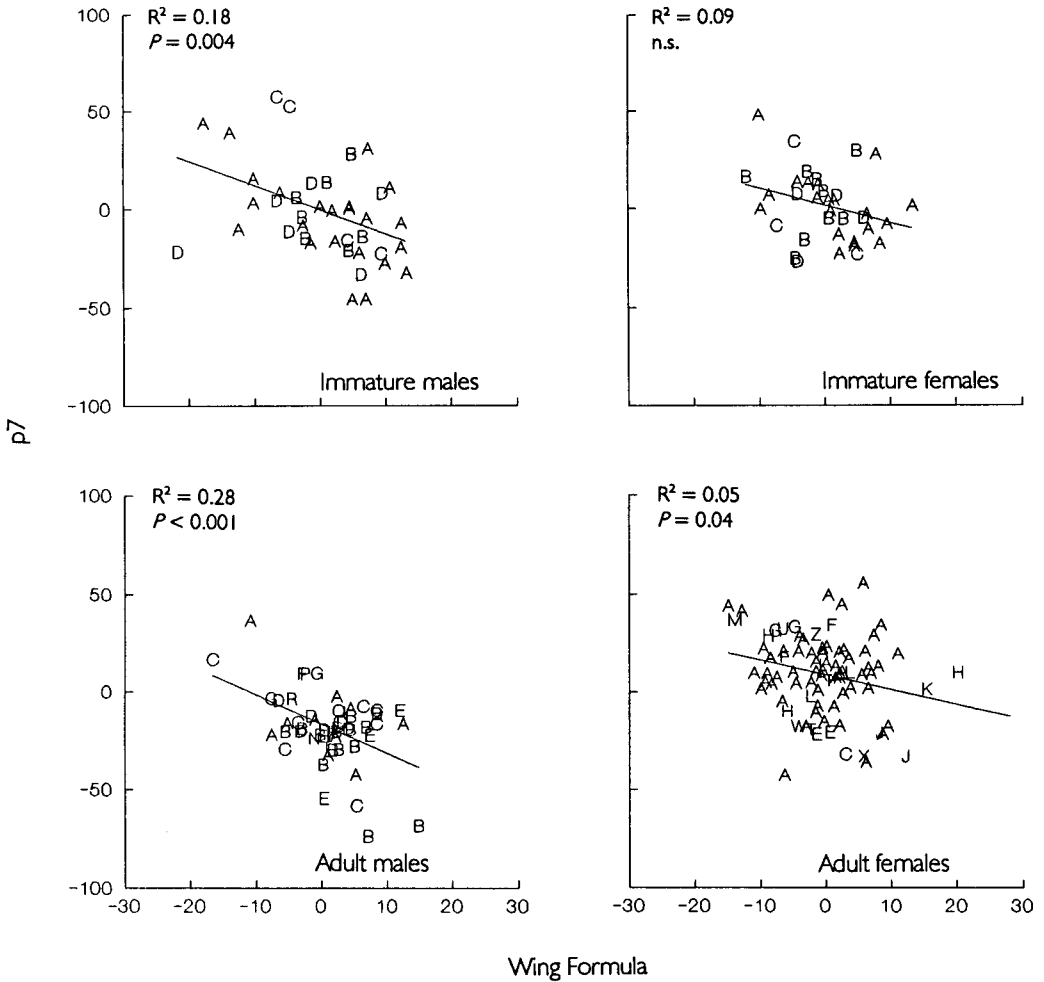
FIGURE 2.   Regression curves for residuals (see Methods) of wing formula and wing length (p7) for immature males and females (upper plots) and adult males and females (lower plots). Both taxa, *B. polyosoma* and *B. poecilochrous,* are pooled. Letters indicate plumage morph (see text; Tables 1 and 2).

statistically significant ($P < 0.05$), but for immatures the relationship is significant only in males.

The slopes of the regression lines for all except immature females suggest that as wing length (p7) increases, wing formula decreases (tends toward negative values), and vice versa. Thus, it follows that wing tip shape, or contour, likewise changes with wing length (a function of body size). To further examine the relationship between size, i.e., wing length, and wing shape, I relied upon a widely used field identification technique for adults of these species (Fjeldså and Krabbe 1990, Cabot 1991), in which wing tip contour is described in terms of

its "pointedness" or its "roundedness." Figure 3 displays, for all specimens of adults and immatures, the set of outer primary lengths (p5 through p9). Note that for both age classes wing tip contour noticeably changes from a "pointed" shape at the shorter extremes (bottom of figure) to a more "rounded" shape at the longer extremes (top of figure). This change is associated with allometric changes in primary lengths, and it can be safely stated that it is not under the influence of geographic effects, i.e., altitude, latitude, and longitude, because these were removed prior to the analysis.

Finally, I regressed wing length against altitude using raw data because this has been a
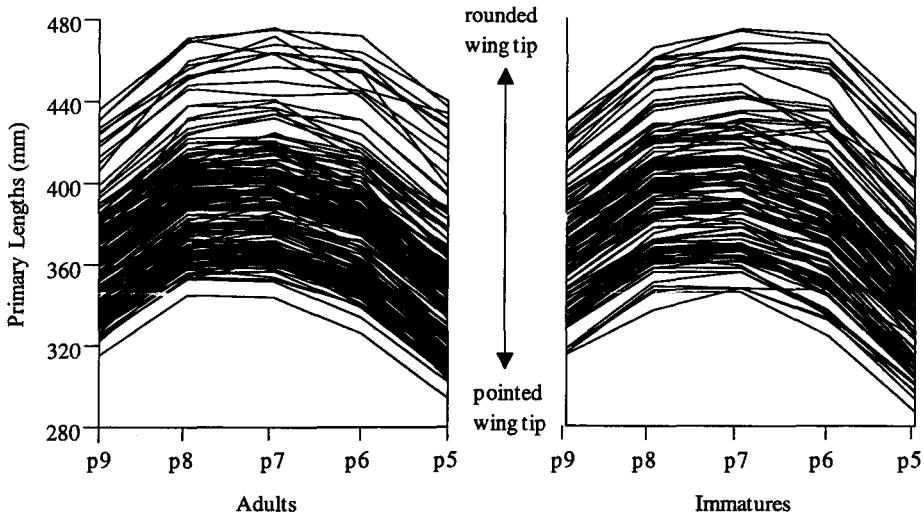
FIGURE 3. Lengths for primaries 9 through 5 for both adults (left) and immatures (right) are connected with lines to describe the wing tip contour (see text); each line represents a single specimen. Note that for shorter wing lengths (p7) inner primaries (p6 and p5) are shorter than outer primaries (p9 and p8), resulting in a more "pointed" wing tip. As wing length increases, the inner primaries increase in length at a greater rate than do the outer primaries, resulting in a more "rounded" wing tip. Both taxa, B. polyosoma and B. poecilochrous, are pooled.

source of some contention in assigning species status to these birds, for example, *poecilochrous,* the larger of the two purported taxa, is thought to be restricted to the highlands. Thus, Figure 4 shows that indeed there is a statistically significant positive relationship. In this case, a second-order polynomial function best fits the data for both age classes and both sexes, and the points are clearly clinal in distribution.

PLUMAGE MORPHS

Adults. My analysis of adult plumage morphs reveals that, instead of five as envisioned by Vaurie (1962), there are at least 27 (Table 1). Following are representative specimens for each plumage morph: (A) BMNH 19023131600, holotype; (B) American Museum of Natural History (AMNH) 165544; (C) National Museum of Natural History (NMNH) 48809; (D) Field Museum of Natural History (FMNH) 101171; (E) BMNH 1902-3131603, holotype; (F) Royal Museum of Scotland (RMS) 190114786; (G) BMNH 87511321, syntype; (H) FMNH 99435; (I) AMNH 123949; (J) AMNH 165542; (K) AMNH 235758; (L) AMNH 470790; (M) BMNH 441071; (N) Yale Peabody Museum (YPM) 22405; (O) BMNH 192961413; (P) BMNH 9612314; (Q) BMNH 8751330, holotype; (R) FMNH 217629; (S)

FMNH 123726; (T) BMNH 19023131598; (U) BMNH 1903128142; (V) FMNH 47161; (W) FMNH 62274; (X) RMS 19587111893; (Y) YPM 22664; (Z) BMNH 1903128145; (Aa) BMNH 19031281153.

Each of Vaurie's (1962) five morphs (lettered A through E, Table 1) appears in my groupings, but many were apparently either overlooked or simply combined into one of the five. Numbers of specimens assigned to each morph are very much skewed toward a few types, with the majority being represented by only one. By far, the most common morph is A (Vaurie's B), in which the throat and breast is pure white, the abdomen barred, and the back reddish. This type represents 45.1% of all specimens examined, although the majority of these are females (78 of 107, 72.8%). The next most common morph (B, not described by Vaurie) is pure white below (throat, breast, abdomen) and gray on the back, accounting for 11% of all specimens examined and these are mostly, if not all, males (two of the 24 specimens are unknown sex but small enough to be males).

White is actually the most frequently encountered color on the underparts of all specimens. Eighty percent of specimens (73 males, 90 females, 26 unknowns) examined in this study
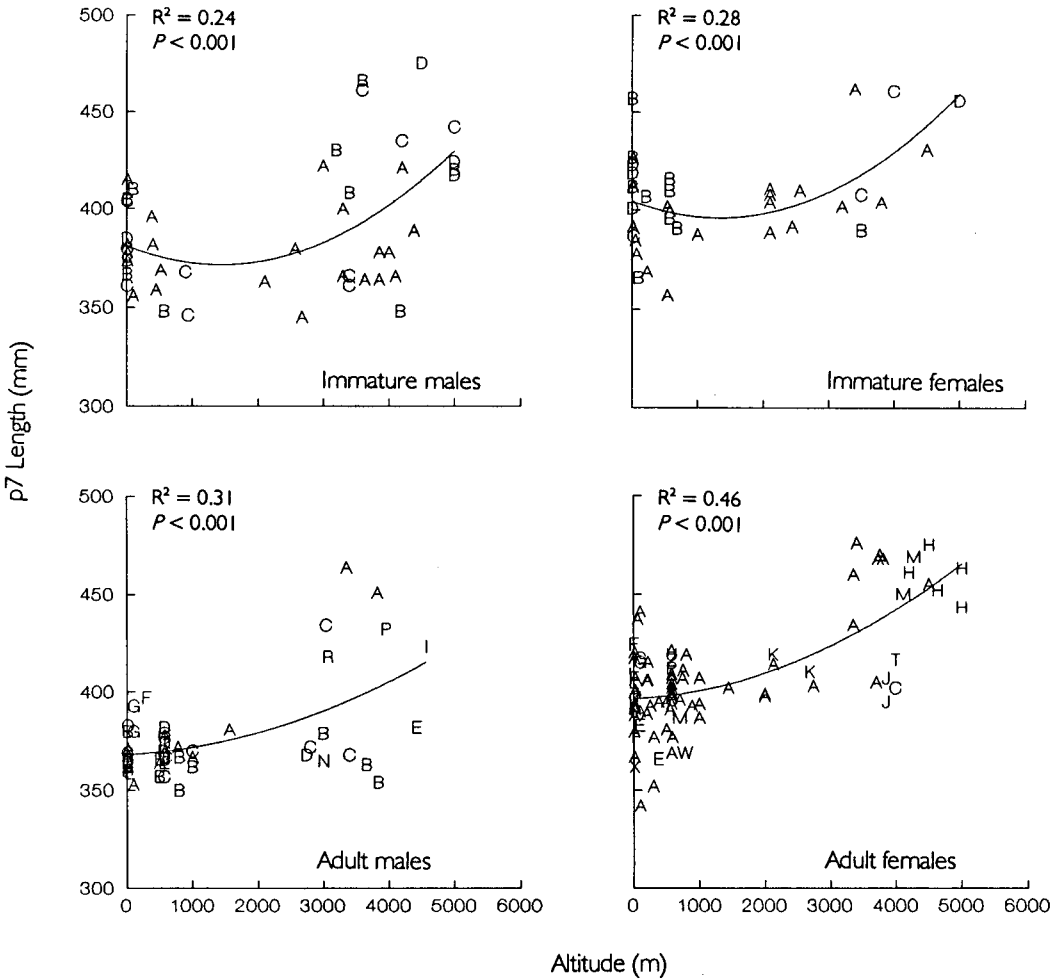
FIGURE 4.   Regression curves for wing length (p7) and altitude for immature males and females (upper plots) and adult males and females (lower plots). Both taxa, *B. polyosoma* and *B. poecilochrous*, are pooled. Letters indicate plumage morph (see text; Tables 1 and 2).

have white throats and breasts. Approximately three-quarters (40 males, 85 females, 18 unknowns) of this sample also have barred abdomens; thus specimens with pure white underparts are relatively uncommon. Pure gray morphs (Vaurie's C) are quite rare in collections (five of 237 specimens). Likewise, pure reddish morphs (Type 12) are represented by only 4 specimens.

One plumage morph (G) is found only in *exsul*, the insular endemic. This morph not only exhibits a bluish cast to its gray feathers (all other specimens have neutral gray), but also has distinctly white-edged feathers on the back in approximately the same area as are found red-

dish feathers on the red-backed specimens. Moreover, no reddish feathers are known to occur on the backs of either sex of this subspecies (Chapman 1926) belying the term "red-backed hawks." Reddish backs (R and SR, see Table 1) are neither universal in this group, representing 75% of all specimens of known sex, nor restricted just to females (73%). Females with gray backs are quite few (3.5% of specimens of known sex), however, and most of these (5 of 7) are *exsul*.

Vaurie's morph A (K here), represented by "dark sooty brown, or dark slate" throat, reddish breast and abdomen, and reddish back, considered unique to *polyosoma*, accounts for only

4 (1.7%) of the specimens I encountered. These specimens have the "correct" wing formula for *polyosoma* (p8 > p6), but so do most of the other morphs; therefore, I see no reason why this morph should be restricted to *polyosoma,* or used to distinguish it from *poecilochrous.*

It is important to note that for all specimens examined, Stresemann's wing formula, designating *poecilochrous* (p8 < p6), is found in only 11 (4.6%) specimens, unevenly distributed among five morphs: A (Vaurie's B; 1 male, 4 females, 1 unknown), C (Vaurie's D; 1 male), H (1 female, 1 unknown), M (Vaurie's E; 1 unknown), and N (1 unknown). Thus, none of the morphs exclusively exhibit negative wing formulae. Rather, the specimens with negative wing formulae are mixed in with the others exhibiting positive wing formulae (i.e., for *polyosoma*). Clearly, there is no general, discernible pattern with respect to plumage morph and Stresemann's wing formula (also see Fig. 2). One morph (H: gray throat and breast, barred abdomen, red back), which occurs probably only in females, was collected exclusively at high elevations, i.e., > 4,000 masl (Fig. 4).

Immatures. Although there was a notable degree of overlap between specimens regarding pattern of pigmentation on the breast and abdomen, I was able to distinguish four general immature plumage morphs (see Table 2): (A) breast clear (pigmented, but devoid of markings) or streaked, abdomen streaked (e.g., Academy of Natural Sciences at Philadelphia, ANSP 145510,); (B) breast heavily streaked or mottled, breast mottled (e.g., AMNH 470786); (C) breast mottled, abdomen mostly or entirely clear (e.g., YPM 81356); (D) breast and abdomen mostly or entirely clear (e.g., YPM 11780).

As in adult morphs, there was no discernible pattern between wing formula, wing length, and plumage morph which would have offered some utility in species diagnosis. The majority of specimens (63 of 137, 46%) fell into the A plumage morph, which Vaurie (1962) suggests is most often found in *polyosoma.* However, specimens labeled *polyosoma* predominate in each of the other three plumage morphs. Additionally, there is no apparent association between plumage morph and either wing formula, wing length, or altitude (also see Fig. 2 and 4).

VOCALIZATIONS

Spectrograms from adult females recorded in the field in Ecuador (one in the highlands, two in the lowlands) and Chile (one at medium altitude) are displayed in Figure 5. Note the overall similarity in frequency modulation among all plots. Each consists of an initial note which typically rises slightly at the beginning then tapers off, followed by a series of monosyllabic notes of shorter duration repeated throughout the remainder of the call, up to 7 sec, in some cases.

DISCUSSION

If wing formula (Stresemann 1925) and wing length (Gurney 1879) were good diagnostic characters for separating *Buteo polyosoma* from *B. poecilochrous,* then plotting the two variables should show discrete groupings that could be used to hypothesize taxonomic boundaries. No such groups were detected in either adults or immatures.

The question thus is no longer whether these two taxa can be separated on the basis of wing formula or wing length, but why do some individuals clearly have large wing formula values (p8 > p6), whereas others have small wing formula values (p8 ≤ p6)? To that end, wing formula and wing length (p7), measured for both sexes in this study, suggest that wing formula changes clinally and allometrically with wing length. Thus, large birds tend to have smaller wing formula values and small birds tend to have larger wing formula values. This allometric relationship, also sex-biased, is further demonstrated in relationships between wing length and wing tip contour.

Larger birds have more massive bodies than smaller birds. Thus, more "rounded" rather than more "pointed" wings would accommodate the greater wing loading requirements of larger birds, and the opposite would be true for smaller birds (Greenewalt 1962, 1975, Rayner 1988). Clearly, the smaller birds measured in this study had wings that were not only more pointed, but also more narrow, than those of larger birds. Therefore, it is possible to predict that within a mated pair the smaller male should have more pointed (and more narrow) wings than the larger female. I have observed and photographed this phenomenon in the field. Therefore, the character which may have been useful to discriminate between species is actually discriminating between sexes; such errors are not new to the fields of taxonomy and systematics (Mayr 1982).

Regressions between wing length and altitude

TABLE 1. Adult plumage morphs for specimens labeled *Buteo p. polyosoma* (poly), *B. p. peruviensis* (peru), *B. p. exsul* (exsul), and *B. poecilochrous* (poec) are grouped according to feather color (white, W; reddish, R; sparsely reddish, SR [see text]; gray, G) and pattern (barred, *; solid color superior to barring, color/*; white-edged, #) on the throat (Th), breast (Br), abdomen (Ab) and back (Ba). Mean and standard deviation (SD) are of primary length (p7) and wing formula (wf) for males, females, and those of unknown sex. *n* (%) indicates sample size and relative frequency, respectively. Sample reference specimen for each morph is listed in text.

This study	Vaurie 1962	Th	Br	Ab	Ba	Taxon	Male p7 mean ± SD (n, %)	Male wf	Female p7 mean ± SD (n, %)	Female wf	Unknown p7 mean ± SD (n, %)	Unknown wf	Totals n (%)
A	B	W	W	*	R	poly	376.1 ± 23.6 (15, 6.3)	14.2 ± 6.0	399.1 ± 18.7 (71, 30.0)	12.3 ± 6.3	408.5 ± 26.0 (11, 4.6)	9.7 ± 7.8	107 (45.1)
	B	W	W	*	R	poec	464.0 (1, 0.4)	−3.0	453.8 ± 29.2 (7, 2.9)	6.2 ± 8.3	464.5 ± 10.7 (2, 0.8)	4.5 ± 7.8	
B		W	W	W	G	poly	362.9 ± 8.4 (24, 10.1)	14.7 ± 3.8			366 (2, 0.8)	5.5 ± 3.5	26 (11.0)
C	D	W	W	*	G	poly	368.3 ± 7.2 (10, 4.2)	14.4 ± 7.2	402.0 (1, 0.4)	11.0	365.7 ± 4.7 (4, 2.0)	12.7 ± 7.0	18 (7.6)
	D	W	W	*	G	poec	401.5 ± 46.0 (2, 0.8)	3.0 ± 14.1			425.0 (1, 0.4)	2.0	
D		W	W	*	SR	poly	370.3 ± 6.0 (10, 4.2)	13.5 ± 4.0	368.0 (1, 0.4)	16.0	374.7 ± 10.2 (3, 1.3)	6.5 ± 6.4	14 (5.9)
E		W	W	W	SR	poly	378.7 ± 10.6 (4, 1.7)	17.0 ± 5.3	364.5 ± 2.1 (2, 0.8)	13.0 ± 1.4	363.0 (1, 0.4)	17.0	9 (3.8)
		W	W	W	SR	peru	361.0 ± 2.8 (2, 0.8)	21.0					
F		W	W	W	R	poly	379.0 ± 25.4 (3, 1.3)	12.5 ± 3.5	407.0 ± 17.0 (2, 0.8)	6.0 ± 5.6	404.0 (1, 0.4)	9.0	8 (3.4)
		W	W	W	R	peru			377.0	9.0	352.0 (1, 0.4)	17.0	
G		W	W	*	G#	exsul	386.5 ± 9.2 (2, 0.8)	6.5 ± 4.9	416.0 ± 1.1 (5, 2.1)	5.2 ± 1.5			7 (2.9)
H		G	G	*	R	poec	383.5 ± 26.7 (4, 1.7)	11.2 ± 3.9	457.7 ± 11.1 (6, 2.5)	9.7 ± 15.9	464.0 (1, 0.4)	−9.0	7 (2.9)
I	C	G	G	G	G	poly					375.0 (1, 0.4)	20.0	5 (2.1)
J		G	G	R	R	poly			399.3 ± 6.6 (3, 1.3)	21.0 ± 2.8	405.5 ± 2.1 (2, 0.8)	4.0 ± 1.4	5 (2.1)
K	A	G	R	R	R	poly			414.5 ± 6.4 (3, 1.3)	27.0	381.0 ± 28.3 (2, 0.8)	11.0 ± 8.5	4 (1.7)
L		R	R	R	R	poly			402.3 ± 8.3 (3, 1.3)	9.7 ± 3.0	402.0 (1, 0.4)	6.0	4 (1.7)

TABLE 1. Continued.

This study	Vaurie 1962	Th	Br	Ab	Ba	Taxon		Male p7	Male wf	Female p7	Female wf	Unknown p7	Unknown wf	Totals n (%)
M	E	G	G	R/*	R	poly	mean ± SD	387.0		387.0		384.0	7.0	4 (1.7)
							n (%)			1 (0.4)		1 (0.4)		
	E	G	G	R/*	R	poec	mean ± SD			459.5 ± 13.4	0.5 ± 3.5			
							n (%)			2 (0.8)				
N		G	G	*	G	poly	mean ± SD	365.0	16.0			424.0	2.0	3 (1.3)
							n (%)	1 (0.4)				1 (0.4)		
		G	G	*	G	poec	mean ± SD					414.0	−1.0	
							n (%)					1 (0.4)		
O		G	G	G	SR	poly	mean ± SD	383.0	7.0 ± 9.9					2 (0.8)
							n (%)	2 (0.8)						
P		G	G	RG	R	poly	mean ± SD	432.0	8.0	412.0				2 (0.8)
							n (%)	1 (0.4)		1 (0.4)				
Q		G	GR	*	R	poly	mean ± SD					412.0	3.0	2 (0.8)
							n (%)					1 (0.4)		
		G	GR	*	R	poec	mean ± SD					464.0	4.0	
							n (%)					1 (0.4)		
R		W	G	*	R	poec	mean ± SD	418.0	5.0					1 (0.4)
							n (%)	1 (0.4)						
S		W	RG	R/*	R	poec	mean ± SD				38.0			1 (0.4)
							n (%)			1 (0.4)				
T		G	G	G/*	G	poly	mean ± SD			416.0	5.0			1 (0.4)
							n (%)			1 (0.4)				
U		G	GR	R	R	poly	mean ± SD			419.0	7.0			1 (0.4)
							n (%)			1 (0.4)				
V		G	RG	R/*	R	poec	mean ± SD			436.0	20.0			1 (0.4)
							n (%)			1 (0.4)				
W		G	RG	RG/*	SR	poly	mean ± SD			369.0	10.0			1 (0.4)
							n (%)			1 (0.4)				
X		G	GR	RG	SR	poly	mean ± SD			362.0	15.0			1 (0.4)
							n (%)			1 (0.4)				
Y		RG	R	R	R	poly	mean ± SD			389.0	7.0			1 (0.4)
							n (%)			1 (0.4)				
Z		GR	GR	R	R	poly	mean ± SD			416.0	12.0			1 (0.4)
							n (%)			1 (0.4)				
Aa		R	R	R	SR	poly	mean ± SD	13.0						1 (0.4)
							n (%)	1 (0.4)						
Total								83 (35.0)		116 (48.9)		38 (16.0)		237

TABLE 2. Juvenal plumage morphs for specimens labeled *Buteo p. polyosoma* (*poly*), *B. p. exsul* (*exsul*), and *B. poecilochrous* (*poec*) are grouped according to pigmentation pattern (clear, streaked, mottled) on the breast (Br) and abdomen (Ab). Mean and standard deviation (SD) are of primary length (p7) and wing formula (wf) for males, females, and those of unknown sex. n (%) indicates sample size and relative frequency, respectively. Sample reference specimen for each morph is listed in text.

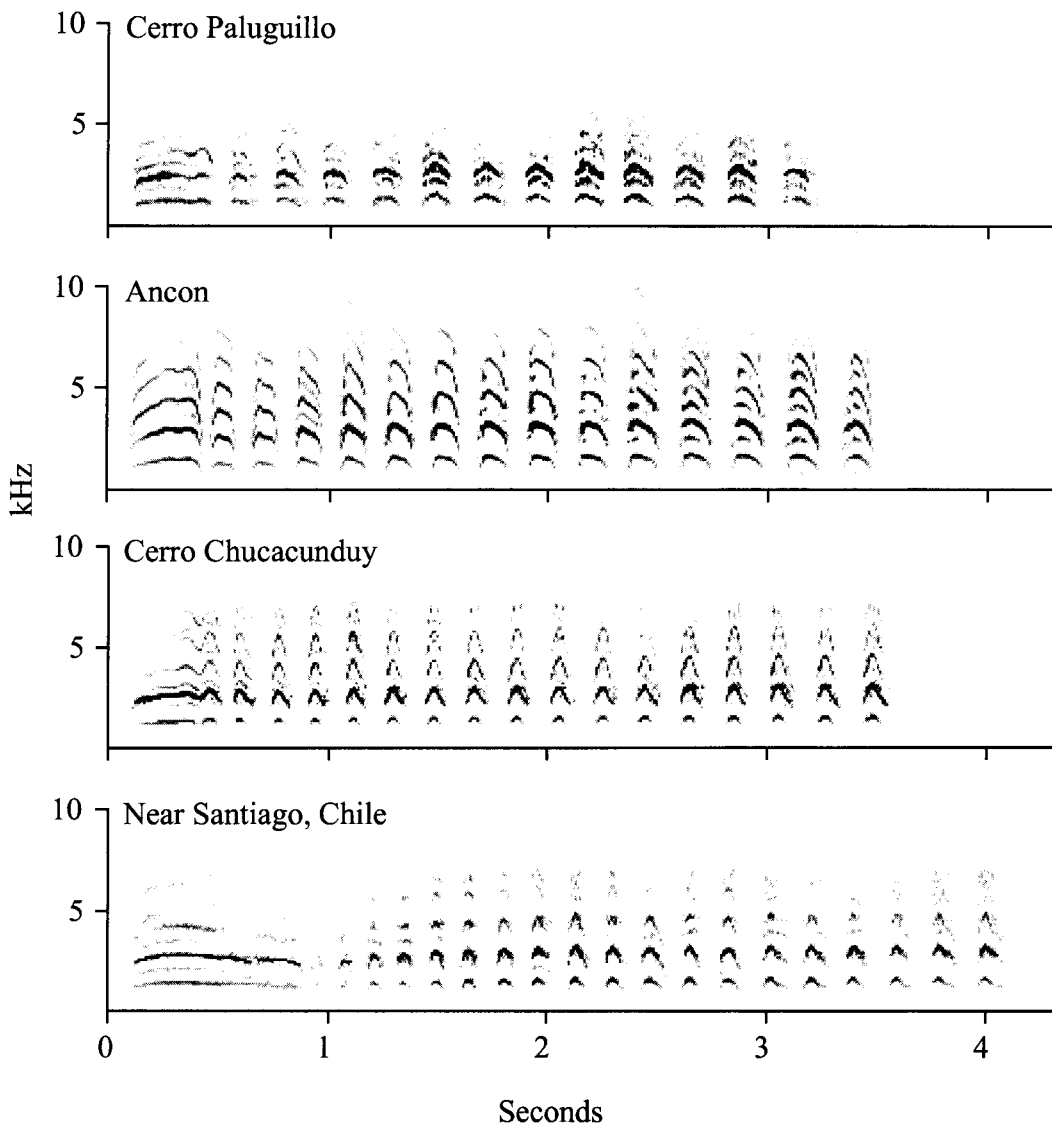| This study / Br / Ab	Taxon		Male p7	Male wf	Female p7	Female wf	Unknown p7	Unknown wf	Totals n (%)
A clear, streaked / clear, streaked / streaked	*poly*	mean ± SD	374.0 ± 16.7	16.1 ± 5.9	399.0 ± 21.8	13.8 ± 6.9	393.0 ± 23.4	13.5 ± 7.7	63 (46.0)
		n (%)	23 (16.8)		23 (16.8)		17 (12.4)		
clear, streaked / streaked	*poec*	mean ± SD	422.0 ± 0.7	1.5 ± 4.9	431.0	−9.0 ± −1.0	455.0 ± 19.1	−6.0 ± 8.5	5 (3.6)
		n (%)	2 (1.5)		1 (0.7)		2 (1.5)		
clear, streaked / streaked	*exsul*	mean ± SD					390.0 ± 2.1	7.5 ± 0.7	2 (1.5)
		n (%)					2 (1.5)		
B hvy streak, mottled / hvy streak, mottled / mottled	*poly*	mean ± SD	387.0 ± 29.2	9.3 ± 10.7	411.0 ± 20.7	12.7 ± 5.5	401.0 ± 23.8	11.7 ± 6.0	33 (24.1)
		n (%)	10 (7.3)		11 (8.0)		12 (8.9)		
hvy streak, mottled / mottled	*poec*	mean ± SD	443.0 ± 32.5	2.0 ± 2.8			450.0 ± 21.9	−0.5 ± 2.1	4 (2.9)
		n (%)	2 (1.5)				2 (1.5)		
hvy streak, mottled / mottled	*exsul*	mean ± SD			366.0				1 (0.7)
		n (%)			1 (0.7)				
C mottled / mottled / clear	*poly*	mean ± SD	369.0 ± 18.3	16.9 ± 5.0	398.0 ± 14.8	7.3 ± 8.1	387.0	20.0	10 (7.3)
		n (%)	7 (5.1)		2 (1.5)		1 (0.7)		
mottled / clear	*poec*	mean ± SD	446.0 ± 13.5	0.3 ± 7.6	461.0	−2.0			4 (2.9)
		n (%)	3 (2.2)		1 (0.7)				
D clear / clear / clear	*poly*	mean ± SD	385.0	13.0	416.0 ± 22.9	15.2 ± 6.6	422.0 ± 41.6	8.5 ± 7.2	12 (8.7)
		n (%)	1 (0.7)		5 (3.6)		6 (4.4)		
clear / clear	*poec*	mean ± SD	446.0 ± 41.0	−7.5 ± 4.9	456.0	−5.0			3 (2.2)
		n (%)	2 (1.5)		1 (0.7)				
Totals			50 (36.5)		45 (32.8)		42 (30.6)		137

FIGURE 5. Spectrograms generated from field recordings of adult females in Ecuador (Cerro Paluguillo, Ancón, and Cerro Chucacunduy) and Chile (near Santiago). The darkest tracing, all between 2 and 3 kHz in each sonogram, represents the dominant frequency.

exhibit statistically significant positive relationships for both adults and immatures. Because the distribution of data points in the plots is clinal in both sexes and both age classes, delineation of any taxonomic boundaries is ruled out. Other authors have suggested that birds identified as *poecilochrous* may be merely altitudinal variants of *polyosoma* (Brown and Amadon 1968, Amadon and Bull 1988), in which case they may be considered as subspecies instead of full species.

It is common to see small bodied individuals with pointed wing tips in the lowlands, and larger bodied individuals with rounded wing tips in the highlands, but this is not an absolute difference; rather, it is one of scale. Due to the clinal nature of the morphometric relationships examined here, neither species nor subspecies designation for *poecilochrous* is warranted.

This species probably has the most highly variable plumage of any of the Falconiformes

yet documented. The variability in color and plumage pattern on the underparts combined with either reddish or gray backs makes for an extraordinarily high amount of plumage morph variation. However, the actual number of morphs for all populations discussed here is probably unknown and unknowable, and it is essentially irrelevant to the taxonomic question at hand. Regardless, some discussion of the magnitude of variation must be presented.

If one restricts the possible combinations to those found in this study, where:

N_1 = five possible throat types: white, gray, reddish, grayish-red, reddish-gray;

N_2 = five possible breast types: white, gray, reddish, grayish-red, reddish-gray;

N_3 = ten possible abdomen types: white, gray, reddish, grayish-red, reddish-gray, barred, red above barred, gray above barred, reddish-gray above barred, grayish-red above barred; and,

N_4 = four possible back types: gray, reddish, sparsely reddish, white-edged;

then simple counting procedures would yield the following possible number of plumage morphs:

$$(N_1)(N_2)(N_3)(N_4) = (5)(5)(10)(4) = 1,000.$$

The populations on the Juan Fernandez Archipelago (*exsul*) and the one in the region of coastal SW Ecuador and NW Perú seem to lack the polymorphism that is characteristic of the rest of the group. Whether these populations formerly had, or will eventually exhibit, greater polymorphism is unknown and is probably a function of geographic isolation and local adaptation.

It is interesting that although the adults in the coastal population of SW Ecuador and NW Perú appear to be represented mainly by morphs E and F, there is some evidence that darker morphs occur in the area. However, there is only one record of such an occurrence. Color images (35 mm transparencies) taken by T. S. Schulenberg 10 July 1979 near Piura, Provincia de Piura, Perú, show an adult with a blackish gray throat and breast, dark rufous abdomen and extensively rufous back. The position of the bird and lighting in the photographs did not allow accurate determination regarding the presence of barring on the abdomen, so it could have been either morph J or M, or perhaps an entirely new one.

The general lack of polymorphism in the coastal SW Ecuador/NW Perú population makes it somewhat unique among continental forms. However, the morph itself is not unique because identical specimens have been taken from coastal regions of Argentina (Provincia de Buenos Aires) and Chile (Provincia de Santiago). Subspecies status (*B. erythronotus peruviensis* Swann 1922 = *B. polyosoma peruviensis,* Chapman 1926) was based originally upon smaller wing length, but my analysis shows this to be only the shorter end of a continuous range of wing lengths in this group. In addition, cooperative breeding is exhibited in Ecuador in both the highland population (Solis and Black 1985; M. Coello, unpubl. data) and the coastal population (Farquhar, unpubl. data). I therefore concur with Hellmayr and Conover (1949) and Stresemann and Amadon (1979) that subspecies *peruviensis* status be dropped.

Morph G, belonging to *exsul,* has a bluish cast to the gray on the back, in addition to the white-edged interscapular feathers on both sexes. No other specimens encountered possessed either of these characters. One color image (35 mm transparency) of an immature in juvenal plumage taken by M. de L. Brooke, ca. 1986, shows it to be in a typical A morph. The divergent nature of the adult plumage suggests that subspecies status for this population should remain unchanged until further data are acquired and evaluated.

Aside from the aforementioned examples of geographic variation in adult plumage, the variability in the remainder of the populations in this species is most likely due to a genetic polymorphism. Evidence for this can be seen in that the morphs do not fall out along any recognizable geographic gradient, and adults of different morphs are routinely seen interbreeding throughout their range (M. Coello, unpubl. data). Preston (1980) suggested that in Red-tailed Hawk (*B. jamaicensis*) morphs, which also have variable ventral plumage patterns, were most often associated with perch sites which increased their crypticity, thus making them less conspicuous to prey. Although such ecological factors could be at work in maintaining a polymorphism, evidence of differential reproductive success related to perch sites and color morphs is lacking. Alternatively, Paulson (1973) invoked a form of frequency-dependent selection termed apostatic selection (Clarke 1962) in which it is advantageous for the morph of an avian predator to be different from the majority of other morphs in the area such that it will be less familiar to

their potential prey. The slight advantage in prey capture thus accrued would presumably lead to a balanced polymorphism. However, Preston (1980) argued effectively against such selection pointing out that (1) no evidence exists to show that prey develop an "avoidance image" of common avian predator morphs, (2) it would be maladaptive for prey to focus on ventral plumage pattern while ignoring other cues indicative of a predator (e.g., silhouette), and (3) the fact that prey within the territory of an avian predator may encounter only one morph and should learn to avoid it no matter what its plumage pattern (Arnason 1978).

Adult vocalizations are not useful in discriminating between taxa in this study. Spectrograms have very similar dominant frequencies (darkest tracing in each spectrogram) and, although they show some differences in call rate and frequency modulation, fall well within the variation seen in the closest relative to this group, the White-tailed Hawk (Farquhar 1992). Although small, the sample of calls examined for the present study was taken from a wide range of geographic localities and represents the possible ranges of wing lengths and wing formulas which might otherwise serve to discriminate among taxa.

I conclude that wing length, Stresemann's wing formula, plumage morphs, and adult female vocalizations are ineffective in separating *polyosoma* from *poecilochrous*. Furthermore, as these characters are currently the only ones recognized to separate the two taxa, I suggest that *polyosoma* and *poecilochrous* be considered conspecific, at least until further data are available to show that this taxonomic merger is erroneous. The name, *poecilochrous* (Gurney 1879), should be synonymized with the older name, *polyosoma* (Quoy and Gaimard 1874), which should thus be applied to all forms in this group. Finally, as the English name "Red-backed Buzzard" inaccurately describes this highly polymorphic group in which many adults are not "red-backed," I suggest that the name "Variable Buzzard" be used for all forms except *B. polyosoma exsul*, which should remain the Juan Fernandez Buzzard. The Juan Fernandez Archipelago is of volcanic origin from the Tertiary or Pleistocene (Stuessy et al. 1984, Bourne et al. 1992), and if any population is likely to be different it will be this one because it probably has been isolated from mainland forms for a considerable amount of time. Vocalization and genetic studies are needed to confirm its systematic relationship to the mainland group.

ACKNOWLEDGMENTS

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