TAXONOMIC AND PLUMAGE RELATIONSHIP BETWEEN RED-BACKED BUZZARDS *Buteo polyosoma* AND *Buteo poecilochrous*

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INTRODUCTION

The Gurney's Buzzard *Buteo poecilochrous* and the Variable Buzzard *B. polyosoma* are two closely related neotropic species (Lerner *et al.*, 2008). The first is found all along the Andean chain from Colombia to the north of Argentina y north of Chile, and always above 3000 m in altitude. This species occurs in habitats like open paramos, mountain ridges and altiplano, with the exception of an established population at 2000 m above sea level and restricted along the borders of the Loa river, which in a deep canyon crosses the Atacama desert in the Antofogasta region in Chile, at the limit of its south western distribution. According to Lehmann (1945) this species occupies in SW Colombia also an altitude of around 2000 m, but Cabot *et al.* (2006) have indicated that these specimens refer to the White-tailed Buzzard, *B. albicaudatus*.

Buteo polyosoma, in contrast, has a more extensive distributional range from the west of South America, from Colombia to the extreme south of the sub continent, including the Falkland Islands and the Juan Fernández archipelago.

Gore y Gepp (1978) indicate that *B. polyosoma* is rare in Uruguay and Reichholf (1974) mentions this species for NW Brasil.

B. polyosoma occurs in a great variety of habitats in a wide altitudinal range (Cabot, 1991; Jiménez, 1995) preferable xerophytic regions with different climatic and physical conditions, including high Andean altitudes 4000 m, Andean valleys and mountain slopes to the low level plains of El Chaco and the pampas region, as well as southern Chile and Argentina.

MATERIAL AND METHODS

The present study is based on the examination of feathers and body measurements taken from nearly 500 skins of both species, from collections in European and South American museums (mentioned in the acknowledgement section). Since 2000 the moult process was observed by JC, on *B. polyosoma* (four birds) and *B. poecilochrous* (six birds), legally imported from Peru, on the changes in plumage from specimens of *Buteo polyosoma* (four) and *B. poecilochrous* (six). Also four chicks of *B. polyosoma,* hatched in captivity in 2008, were observed over the years. Field data was taken in irregular patterns in Ecuador, Peru Bolivia and Chile from 1981 until 2008. The specimens were sexed by body measurement and molecular techniques (Ellegren, 1996).

The taxonomic affinities study was sequenced in one segment of 620 bases of the cytochrome b mitochondrial DNA following standard procedures. Identification was according the measurements and details mentioned in Cabot y de Vries (2003).

RESULTS AND DISCUSSION

A complex taxonomic history

The history of the taxonomic relations between the two species is long and controversial. Traditionally, these two forms have been considered separate species, albeit closely related. However, they have also been considered as co-species, in other words different at the sub-species level, but in neither case has there been any fundamental back-up to justify these designations of status. Brown and Amadon (1968) point to the altitude variant to distinguish one from the other. At present, they are recognised as two separate species based on the biological species concept (Cabot and de Vries, 2003; 2004).

The reasons for this long taxonomic debate are varied and basically stem from:

- The high variability in plumage in both species due to ontogenical changes of plumage depending on sex, morph and age over a period of six years, complicated further by males acquiring temporarily similarities with the female plumage. Some patterns are very similar between the two species (Vaurie, 1962; Cabot and de Vries, 2005).
- The lack of valid criterion to determine the specific difference, in the hand as well as in the field.
- The non-familiarity, of the taxonomists involved, with these species, and the scarcity of a series to determine the sequence of changes of the plumages of specimens in ornithological collections.
- The overlapping geographic ranges and altitudes, body measurements and the plumage patterns occurring in these species added to the debate.

The first species described was *B. polyosoma* from an adult male dark morph specimen originating in the Falklands (Quoy and Gaynard, 1824). Several authors have treated the taxonomy e.g. Hellmayr, 1932; Johnson, 1945; Housse, 1945; Lehmann, 1945; Vaurie, 1962; Brown and Amadon, 1968; Farquhar, 1998; Cabot and de Vries,200; the latter considering biological and ecological aspects). Three subspecies in *B. polyosoma* have been discussed, *B. p. polyosoma, B. p. peruviensis, B. p. exsul*, the latter confined to the Juan Fernández Island.

The complicated and tortuous road towards the systematic relationship started 55 years later with the description of *Buteo poecilochrous* Gurney 1879. A larger species, in which there is a considerable overlap in some male body measurements, compared with the *B. polyosoma* females. Two subspecies have been described for *B. poecilochrous.* The nomínate form and *B. p. fjelsai* from northern Peru, Bolivia, NW Argentina and Chile (Cabot and de Vries, 2009).

European and North American ornithologists, who were partially or completely unfamiliar with these species in their natural environment, only had a few skins available in museums, which represented, in a small and incomplete way, the complex plumage mosaic proper to these strongly polymorphic species. The taxonomists were faced with a complex diversity of shapes, designs and sizes which consisted of a heterogenic sample with elements which were difficult to understand and classify. Even if some plumages were duplicated in the series of museums, others could be absent and, at the same time, similar plumages were found in specimens of different sizes.

In addition, it was found that specimens of both species could have the same or similar geographic origin, or that within the series there might be specimens whose sex had not been determined or wrongly determined, (even by the collector), as well as a considerable number of males classified as females (Jiménez, 1995; Cabot and de Vries, 2003), since they carried the red dorsal patch characteristic of the definitive plumage of adult female (Vaurie, 1962). However, this characteristic is also present in immature males (Pávez, 1998; Cabot and de Vries, 2004).

Examples from other species, wrongly classified as *B. polyosoma* or *B. poecilochrous*, have been found in outstanding scientific collections from Europe. Inter alia: *B. swainsoni*, *B. ventralis, B. albicaudatus* and *B. albigula*, which were presumably used in taxonomic studies of red-backed buzzards.

Unfortunately, the criteria devised by the taxonomists only complicated matters further. One of these, the one which was the most widely disseminated, is known as the Stresemann rule (1925). This criterion became the only guideline available to ornithologists to separate *B. poecilochrous* from *B. polyosoma*. It is based upon the relative distances between the tips of the third and fifth most external primaries: longer in *B. polyosoma* than in *B. poecilochrous*. Our results have shown that this rule is not met in *B. poecilochrous* (Cabot and de Vries, 2003), since in this species both feathers are practically the same and, in nearly half the specimens, the third primary is much longer than the fifth. There are even specimens that have one formula for one wing and the reverse for the other, as in the case of the type specimen. In this way, the same individuals were classified and reclassified several times over, according to the criterion of the ornithologist (Vaurie, 1962), as has occurred with some paratypes of Chilean origin of the subspecies *B. poecilochrous fjeldsai*, recently described by Cabot and de Vries (2009), specimens referred in Hellmayr (1932), Hellmayr and Conover (1949).

Another criterion used in the study of plumage was the difference in categories for adults and for juveniles according to the pattern of the markings and the coloration of the tail (Farquhar, 1998). Birds with a white tail and a subterminal black band were considered adults, and those with a greyish-brown tail with irregular dark lines, juveniles. This separation does not match up to reality since the subadults (also with a white tail) are considered as adults, ascribing a greater degree of polymorphism to the latter than is in fact true. This made it difficult to study plumage and to understand the differences between the species.

For a long time, South American ornithologists with direct knowledge of both forms, have been asserting that the plumage of *B. polyosoma* and *B. poecilochrous* are the result of a plumage succession pattern relating to age, from the first basic plumage of the juvenile to the definitive adult plumage with different patterns in the sequences, according to morph, sex and age (Housse, 1945; Lehmann, 1945; Goodall *et al.,* 1951; Torres-Barreto, 1986). This occurs also in other related species *B albicaudatus* (Lehmann, 1945; Torres-Barreto, 1986; Johnsgard, 1990) and *Geranoaetus melanoleucus* (Hudson, 1945; Lehmann, 1945; Goodall *et al.,* 1951; Johnson, 1965; Jiménez y Jaksic, 1990). These results were not widely circulated internationally since they were published in Spanish. Because of this, later studies were made without taking into account these results, for example the recent study by Farquhar (1998) which attributes plumage variability to chance; while, at the same time, Pávez (1998) describes in detail an ordered sequence of changes in plumage, subject to a pattern, from juvenile to adulthood. The suggestion of con-specificity between *B. polyosoma* and *B. poecilochrous* based on a climal gradient of size depending on altitude (Farquhar, 1998) should not be taken into account. This gradual change does not exist (Cabot y de Vries, 2003).

Each species shows characteristic morphometric values and has its own ranges which give it different proportions (de Vries, 1973), which is also the case at high altitudes over 3.800 m at the Altiplano in Bolivia (Cabot and de Vries, 2003). So far no intermediate forms are known, in museums or in the field. Cabot and de Vries (2003) demonstrate that specimens from the Andean Altiplano above 3800 m are morphologically different from *B. poecilochrous* and, moreover, *B. polyosoma* at the Altiplano are of smaller size than their conspecifics at lower altitude in the Falkland Islands. Also, no gradient in size and in clinal process in body sizes have been detected in species of the genera of *Geranoaetus, Buteo*, *Falco, Circus*, which occur at high Andean altitudes as well as in the lowlands.

In order to disentangle the systematic relations between similar taxa, an accurate identification of each one of the specimens which represent these taxons is required. In the case of *B. polyosoma* and *B. poecilochrous*, incorrect identification of the individuals has been the core of the long and distended debate between these two species.

Buteo polyosoma and *B. poecilochrous* are identifiable by body measurement, by plumage pattern as well as by its silhuette and flight. The specific differences in morphology (measurements, plumage patterns and percentage of color morphs), ecologic aspects and behavior, represent biological barriers which favor specific isolation between both forms.

Cabot (1988, 1991) found both species coexistent in the puna region in northern Bolivia. B.*polyosoma* wintering in this area shows a solitary behavior and occurs in mainly flat areas, whereas B.*poecilochrous* is sedentary, living in pairs and is distributed in hilly country, with ridges and gorges. Similarily JC found this coexistence in the Atacama dessert near Calama, Chile, where *B.polyosoma* occured in a xerophytic hábitat and *B. poecilochrous* in the oasis of the river Loa

Distinct species of recent origin

Mutations in the sequences of DNA bases of the mitochondrial cytochrome b, because of its constant mutational rate, constitute a biological clock which quantifies the period of time taken to differentiate between the biological forms under study. The rate of substitution of nucleotides is assumed at between 2% and 10% per million years (Irwin *et al.*, 1991). It could be assumed that the older the genetic divergence of the forms, the greater the biological differences should have been between them. Nevertheless, it is not always so; selective pressures can act in a qualitative and quantitative differential way, upon the organisms in very short distances in mountain ecosystems (Fjeldså, 1992). The effect of a differential pressure from the natural selection between the populations and the variability in the flexibility of adaptation of the organisms, as a response to this pressure, will mould the populations differently.

Riesing *et al.* (2003) state that, according to analysis of a segment of mitrochondrial DNA of 606 bases of cytochrome b, *B. polyosoma* and *B. poecilochrous* have identical sequences. We have obtained similar results over one sector of mitochondrial DNA with 620 base pairs that *B. polyosoma* and *B. poecilochrous* have identical sequences , also of the same material and similar bases number. The specimens, two examples of *B. polyosoma peruviensis* and four *B. poecilochrous,* were obtained from Peru. The results indicate the nonexistence of intraspecific variation in the first species.

This results is not an indicator of co-specificity (as assumed by Farquhar, 1998 and Riesing *et al.*, 2003), but that the evolutionary process of speciation has been very recent and has not yet left its mark on the chain of nucleotides of the cytochrome c, due to its scant variability (Haring *et al.*, 1999).

Analysis carried out on fragments of the pseudoregion control (Ψ), which has a greater mutational rate, shows inter-specific differences in the sequences, which in passing also shows a close affinity of both species to *B. albicaudatus,* with which they constitute a definite cluster (Riesing *et al.*, 2003). The variations in the pseudoregion control finely reflect the evolutionary processes within the genus *Buteo* (Riesing *et al.*, 2003).

Lerner *et al.* (2008) found genetic support in the CR_1 control region for independent origins of *polyosoma* and *poecilochrous* from *albicaudatus*, thus supporting their status as distinct species.

The hypothesis on the speciation of *B. polyosoma* and *B. poecilochrous* relates to a recent parapatrics respective differentiation starting with *B. albicaudatus.* These situations are common in the speciation process of High

Andean ornithofauna (Garcia-Moreno and Fjeldså, 2000).

In the southern Colombian Andes, *B. albicaudatus* reaches medium altitudes (Lehmann, 1945) and its diet is centred on rabbits *Sylvilagus brasiliensis,* similarly, *B. poecilochrous* also bases its diet on this prey. Additionally, in this zone it is the only place where *B. albicaudatus* shows sexual dimorphism with a greater expansion of red over the shoulders of the females, and even over the back (Lehmann, 1945). This points to the latter form becoming different starting with *B. albicaudatus*, when it ascended and adapted to high altitude areas, free of ice after the last ice age, a few millennia ago, and inhabited the upper mountain levels following *S. brasiliensis,* which is very common in the paramo.

In fact both species of buzzards are very similar in size and plumage, especially in the pattern of the ventral parts of the dark morph, (Figure 5 in Cabot and de Vries, 2005). This similarity is mentioned by Gurney in the description of the type specimen *B. poecilochrous*. As a matter of fact, three study skins of *B. poecilochrous*, deposited in the museum of Stockholm, collected at Pichincha and Antisana (Ecuador) between 11.500-12.000 feet, were identified by Lönberg and Rendhall (1922) as *B. albicaudatus*. In this same museum a specimen of *B. albicaudatus* (NHRM 568608) was identified as *B. poecilochrous*, collected by Sneidern at Rio Timbio, Cauca, Colombia.

Buteo polyosoma could have originated in medium altitudes starting with those forms deriving from *B. albicaudatus,* already red-backed, which were climbing the slopes; spreading towards the south, reaching the extreme south where the ice was melting at those latitudes, and benefitted by the advance of mammals of Nearctic origin, reaching the south of the subcontinent. This species colonized the Falklands and diversified in some populations, as in the case of *B. polyosoma peruviensis* which inhabits the coastal desert of Peru and southern Ecuador.

Plumages

The two species of red-backed buzzards are sexually dimorphic in their two forms of coloration: light and dark (Cabot and de Vries, 2004). One outstanding fact (unusual in the *Buteo* genus) is that both species take six years to acquire their definitive plumage. This occurs in both coloration morphs and adheres to patterns depending on sex and age (Pávez, 1998; Cabot and de Vries, 2004, 2009). In this process in both species, subadult males acquire in both morphs (light and dark) red dorsal patches, similar to the females in their definite plumage. All the females show in the definitive plumage the upperparts grey with an extensive brick-red dorsal patch in the mantle, whereas for all the males in the definite plumage the mantle is dorsal grey (Cabot and de Vries, 2005).

The *B. poecilochrous* dark morph specimens are more common than pale morph specimens and this relation seems to occur all along its range of distribution. *B. polyosoma* dark morph specimens are very rare and infrequent in relation to the light morph, but increases to the extreme south of its range (Reynolds, 1938). Certain plumage patterns of the dark morph related to age and sex were considered aberrant forms by Housse (1945).

The converging of plumages between *B. polyosoma* and *B. poecilochrous* of the same sex, age and coloration morph is remarkable. Plumage repetition also occurs in both morphs of *B. albicaudatus,* with small variations. This long delay in acquiring definitive plumage is also manifest in *Geranoaetus melanoleucus* (Lehmann, 1945; Torres-Barreto, 1986; Jiménez and Jaksic, 1990; Goodall *et al.*, 1951; Hudson, 1945; Johnson 1965) closely related to the White-tailed buzzards (Riesing *et al.*, 2003). An unusual plumage of *Geranoaetus melanoleucus* is identical to the adult definitive pale morph of *B. albicaudatus* (Cabot and de Vries, 2008b).

In both species, there are three stages in the process for changing plumage:

Juvenile: first and second calendar year. They show very different plumages from the adults and subadults. At this age there exists already sexual dimorphism in plumage color. Males in their basic background plumage show more uniform plumage and with darker background with fewer paler marks than females, which show warmer brown plumages, with clear markings, but less pale as in males, in upper as well in lower parts. Juvenile females, especially in *B. poecilochrous*, have the small feathers of the bend of the wing and the border of the tail feathers, reddish, a characteristic not found in juvenile males.

Pale morph, underparts: brown markings on a whitish creamy to tannish cream background, brown or greyish brown tail with narrow, transversal, irregular blackish bands.

Dark morph, underparts: uniform brown to black brown background with pale markings; tail as above.

Immature: Their plumage becomes similar to the definitive plumage of the adult female but the background colour on upperparts is greyish brown, not pure grey as in the adult. The males show pale reddish patches on the mantle (and also a reddish or brown reddish feathers in median lowerparts in the dark morph). They imitate the females in the same phase, but always with less purity and richness of color and less surface and defined area.

The subadult females are extensively erythristic, as though trying to distance themselves from the males who are imitating them. They show an extensive red dorsal patch which spreads to the flanks and neck sides (pale morph) until the neck or under parts extensively red or brown red (dark morph). These are birds in their third and fourth livery.

Adults: The sexual dimorphism is accentuated.

Males: A tendency to differentiate from the females. They show a uniformly grey back with white underparts (pale morph) or mainly grey (dark morph): usually smooth and uniform coloring without markings in *B. polyosoma,* and strong white and grey barring usually in *B. poecilochrous* along the flanks, thighs, belly and undertail coverts. However some *B. poecilochrous* specimens have upper and median underparts uniform grey with some whitish marks on flanks, thighs, and grey and white upper and undertail coverts.

Females: Extensive red dorsal patch. White underparts in pale morph females, as for the males in the same phase. Dark morph *B. polyosoma* females show uniform grey upperparts with a red breast band usually without marks on under parts. *B. poecilochrous* females on the other hand, have no red band in their definitive plumage and the under parts are similar to the males in the same phase.

The significance of polymorphism

The significance of the delayed maturation process in these two species and between other related buzzards remains a mystery.

The coloration differences between sexes and ages in *B. poecilochrous* may be related to the coexistence of several individuals within a restricted area and with high food availability.

Individual variations in the duration of this process may occur which is frequent in processes of delayed maturation, but this is poorly known. We have observed in some study skins some feathers corresponding to two earlier phases, more easy detectable in immature birds and new adults. These individual variations need further studies, but may be related to stress in subadult males with female characteristics, in situations of dominancy and hierarchy.

De Vries (*pers. obs.*) has observed that juveniles enter those territories, where they were born the previous year, without aggression, and are fed by their parents who at the time are breeding growing chicks. Also, there are breeding females, which have not reached their definitive plumage. (Solís and Black, 1985; Coello, 1997). This has been proved in dark morph birds which are easily distinguishable by their reddish breast band. This is more difficult to detect in females of the light morph as both in subterminal and definite plumage the ventral part is white.

The reproductive behaviour observed in groups of up to five individuals could explain why subadult males take on the appearance of females in order to minimize aggression and to cooperate in the breeding process in view of the scarcity of territory. These helpers are assumed to be male, because of their plumage, although in one case at least there appears to have been one other female in addition to the reproductive female. These were not sexed by measurement or molecularly.

These observations on several helpers were carried out in Ecuador. There are no similar data available for other Andean areas, Bolivia, Northern Chile and Argentina, where there are no *Sylvilagus brasiliensis*.

In *B. poecilochrous* males which form part of pairs have a grey mantle as do alpha males living with male helpers, but also red-backed immature males may be present in the same territory (Solís and Black, 1985; Coello, 1997; and field data). Also red-backed males were observed together hunting along the river Loa (northern Chile), where hunting grounds are restricted along the borders of the river, an oasis in this desert region. The study skin (MCINB 199) in the National Museum Bolivar in Ambato (Ecuador) with grey and red feathers on the back is an example of a male loosing the red feathers of the mantle. Birds in Bolivia (EBD 6917 and BMNH 1902.318. 1601) are grey mantled with just one grey-red feather what could indicate a quicker molt where no gregarines is known.

Male helpers may therefore remain for a longtime red-backed, whereas other males will have the normal and quicker sequency in molting to the definite plumage.

Gregarious behaviour has not been seen in *B. polyosoma*. Also its diet is more varied, and the availability of food in its wide and diverse distribution area can be subject to seasonal changes. There are also cases of subadult breeding females (Reynolds, 1935).

B. polyosoma nests in pairs, so far no groups have been observed, except for some threesomes defending a territory (Alvarado and Figueroa, 2006). In captivity stressed males remain with red feathers on the back, dominant males are completely grey.

It remains to be discovered if the duration and sequence of changes is subject to individual changes which can be shortened, lengthened or the process arrested, as occurs in some species. The potential effect exercised by social factors, such as the size and components of the reproductive group, also needs to be investigated.

Plumage recognition of *B. poecilochrous* and *B. polyosoma*

We have described and illustrated the plumages of *B. polyosoma* (Cabot and de Vries, 2004) and *B. poecilochrous* (Cabot and de Vries, 2005, 2008) with comments on specific plumage patterns; in spite of the high individual and geographic variability of the plumages, especially and still for describing for *B. polyosoma*. In this work we give the plumage patterns features, of more detailed form, according coloration morph, age and sex (Table 1). The ontogenic process of plumage variation for dark male and dark female is showed for *B. polyosoma* (Figures 1, 2) and for *B. poecilochrous* (Figures 3, 4).

Recognition in the field

The species are recognisable by their silhouette (Cabot, 1991; Fjeldså and Krabbe, 1990). Identification is helped by knowing that *B. poecilochrous* is gregarious or usually flies in pairs along mountain rock faces or peaks and is found in high altitude ecosystems, whereas this is not the case with *B. polyosoma*.

There could be further complications with identification of wandering or solitary juveniles since their morphology differs from adults, with a proportionately larger tail in both species.

B. poecilochrous circles and forms a characteristic dihedral angle with its wings. The wing beats are slow and profound (Pávez, 2005), hovering frequently when hunting in

Table 1. Plumage recognition of *B. poecilochrous* and *B. polyosoma*.

DISTINCTIVE FEATURES IN PALE MORPH

Age	***B. polyosoma***	*B. poecilochrous*
1 year basic	Very variable. Upper-parts brown with white-cream to buff markings on wing-coverts and with dark barring on greater coverts, primaries and secondaries. Side of head, supercilium and under-parts pale cream to tawny. Obvious dark-brown malar stripe. White throat with variable black streaking; sides of neck with brown tear-shaped markings; central under-parts with rusty-brown arrowhead markings that become more spaced out towards thighs and belly; markings of the same colour on under wing-coverts. Tail grey-brown, normally with thin, irregular dark barring. Females are more mixed in colouration and with warmer tones than males.	Variable. Bigger and otherwise similar to equivalent in *polyosoma*. Brown upper-parts with uniform and darker mantle, pale to buff markings on scapulars and tertials. Sides of head (including subocular area and ear-coverts) and rest of under-parts whitish to intense buff-cinnamon with rusty to dark-brown markings. Noticeably long tail with grey brownish ground colour and more regular dark barring. Males are more uniform and darker, but with fewer, paler markings than in females, which usually have warmer plumage tones and feathers edged in buff-cinnamon.
2nd calendar year	Variable. Similar to preceding plumage type. Paler and upper underparts cream whithish more uniform; centre of chest and belly variabily barred or reticulated in rusty- orange to brown; females are more heavily marked. The markings get smaller and more spaced out on the thighs and under-belly. Wing under-coverts with markings of the same colour. Grey-brown tail with fine, blackish irregular transversal lines.	Variable. Similar to the equivalent in *polyosoma*, but with the sides of the head with more extensive pale colouration. Same patterning on under-parts, but browner, from cinnamon-brown to dark chestnut (occasionally rusty brown) and generally less rusty than equivalent in *polyosoma.* The ground colour of the under-parts ranges from creamy white to cinnamon. Females are generally more profusely marked on under-parts and are often washed with buff-cinnamon. Greyish tail with regular dark barring.

Immature	Variable. Head brown to darkgrey-brown with sides with white streaking. Whitish-cream underparts, rusty barring on centre of chest and thighs. Sides with rusty wash; rusty-brown markings on wing under-coverts. Brick-red patch, variable in size, on mantle that in females can merge into scapulars and tertials. Rectrices white and spotted with grey-brown at tips; rectrices also with fine transversal lines above a black subterminal band, which is sometimes incomplete.	Variable. Crown blackish brown with and pale sides to head. Back brown with pure reddish (or mixed with brown) patch. Scapulars with profusion of pale cream-to-buff markings; tertials with contrasting barring towards tips, also on upper side of the secondaries and primaries. Wing and median coverts similarly barred in females and sometimes in males. The barring on these feathers is obvious when the wing is closed and remains a constant feature in successive plumages in both colour morphs in this species. Under-parts cream-white to buff with chestnut-brown barring in the centre of the chest, but barring more spaced out and finer on belly and thighs. Under wing-coverts with chestnut-brown markings. Rectrices similar to equivalent, but more grey tinged and with the transversal barring usually thicker and blacker.
Pre-definitive	Variable. Head brown to brown greyish- and brown-black, with rest of upper-parts brown-grey, but more uniform and appearance and less barred than in equivalent plumage in *B. poecilochrous*. White under-parts with dark marks in centre of breast, flanks and on under wing-coverts. Female more densly barred underneath and with more extensive mantle patch, which reaches the nape and merges into the sides of neck, chest and flanks.	Variable. Top of head black to grey-black with white cheeks and the rest of the upper-parts grey-brown to dirty grey, with fewer pale markings; dorsal patch like the equivalent plumage in *polyosoma*, but often extending to scapulars, rump and tertials. In males the dorsal patch red with intermixed dark marks restricted to the upper mantle. Tertials distally dark barred. Uppertail coverts white dark barred
Definitive	Variable. Male. Crown and upper half of sides of head mid-grey to more pure pale grey. Upper-parts more uniform and under-parts purer white than in previous plumage. Barring and grey markings on sides. Female similar, but with darker back.	Variable. Male similar, but with steel-grey to slate-grey back; female with red mantle and sometimes with black crown, white sides of head (including ear-coverts and subocular feathers). Under-parts white with dark vermiculation in centre of chest and without obvious markings or grey streaking on sides. Greater under wing-coverts boldy dark barred.

DISTINCTIVE FEATURES DARK MORPH

The upper-parts are as in the previously described plumages and are only mentioned in passing here.

Age	*B. polyosoma*	66,231 mm
1 year basic	Variable. Uniform bituminous to dark brown with ochre markings on upper-parts, which are more abundant and warmer-coloured in females. Black-brown with pale spots on central under-parts and sides. Uniform underwing with a few pale spots. Males with fewer markings, darker more uniform than female.	Similar underneath to juvenile *B. albicaudatus,* with brown stripes on buff-tawny to rusty-ginger ground colour (blackish markings on white background in *albicaudatus*). Brown and sometimes blackish barring on buff background on sides of head and neck; broad brown-black malar stripe descend to sides of chest. Central underparts dark brown with pale markings that give reticulated appearance. Thighs and under tail-coverts with thick dark and pale barring. Under wing-coverts with profuse pale markings.
2nd calendar year	Variable. Brown to black-brown appearance, sometimes with varying degree of pale markings on the flanks and wing-coverts. Males at least seem fairly uniform, whilst females are more profusely marked.	Variable. Whole head blackish with striated appearance; neck and chest uniform brown with visible black feather shafts. Centre of chest blackish with feathers with pale emarginations, giving scale-like appearance; the rest of the under-parts and thighs barred in dark brown to cinnamon-ochre.
Immature	Variable. Head and bib uniform brown; central under-parts red-brown in male or red in female, usually without barring. Female with large dorsal patch.	Variable. Head and bib brown to grey-brown; males with red-brown chest and the rest of the under-parts brown with faint barring on lower under-parts; female with extensive red on under-parts with pale-bordered feathers and lower under-parts and thighs with pale or dark barring that reaches belly and blends into chest. Under wing-coverts whitish with dark barring.
Pre-definitive	Variable. Under-parts differ between sexes: males almost completely lead- to blue-grey with red feathers mixed in the mantle and centre of chest; female with grey head and extensive red areas on under-parts, with black sooty areas above all on sides, thighs and belly.	Variable. Males with bicolour reddish and grey on lower hindneck and upper mantle; head and bib greyish , centre of chest as far as belly reddish and the rest of the under-parts grey, with quite dense barring. The barring blends into the sides of the neck where it mixes in with the red pectoral band. Females similar, but with extensive dorsal patch and central under-parts reddish, and lower under-parts with white and grey barring. Under and upper tail coverts white.

Definitive	Variable. Usually no barring on chest and belly, rump and uppertail coverts grey. Sexes different underneath: male all uniform lead-grey above and below; female back like male, but with dorsal patch and red pectoral band, and with belly and thighs sooty black, and with under tail-coverts whiteish with sooty spots. Females from the Falklands Islands have barred lower under-parts, while some from the Central Valley of Chiles have fine pale barring in the middle of the chest and pale markings on the under wing-coverts.	Variable. Usually obvious barring on centre of chest and belly. Under-parts similar in both sexes. Chin and throat grey or white, black streaked, bib grey with white markings; centre of chest, thighs, belly and under wing-coverts with grey and white barring. Under and upper tail-coverts white. Some males are more uniform in appearance and lack markings on mid and upper under-parts, but have fine barring on flanks, thighs and belly.

a peculiar way (Walker, 2002, Cabot *et al.*, in this volume). It has the silhouette of an eagle, with a greater wingspan, and wings wider at the base (rounded at the back), and the tail proportionately shorter and rounder (fan shaped) than *B. polyosoma.* The latter is smaller in size, more graceful, with a rectilinear outline, narrow wings and a proportionately longer tail.

When perched, *B. poecilochrous* is more voluminous, with long, large secondaries leaving the distal extremities of the primaries very little exposed. The svelter *Buteo polyosoma* appears to have proportionately longer tarsals, especially those from the coastal desert of Peru and Ecuador.

In both species the wing tips overlap the tail in adults; this is from observation of captive birds and in the field. However, this criterion should not be used, since it does not serve to distinguish the species. Juveniles suffer from a notorious shortening of the tail on becoming subadults, especially in *B. poecilochrous.* Notable shortenings also occur in *B. albicaudatus* and in *G. melanoleucus* where they even change morphology.

Recognition by measurement

The following is a key to distinguish the species; measurements are expressed in millimeters:

Measurements above those indicated apply to *B. poecilochrous* and vice versa for *B. polyosoma.*

Over 1300 mm wingspan.
Distance from the tip of the eighth primary (P8) to the tip of P6 less than 8mm.
Wing width at centre (with the wings spread) less than 260 mm.
Distal width from P8 to the start of the dovetail more than 20 mm.
Distal width from P9 to the start of the dovetail more than 23 mm.
Distal width from P10 to the start of the dovetail more than 25 mm.
Wing length measurements less than 380 mm are characteristic of *B. polyosoma* males; length measurements over 445 mm apply to *B. poecilochrous* females.

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Figure 1. Age related changes for *B. polyosoma* dark morph male

Figure 2. Age related changes for *B. polyosoma* dark morph female

Figure 3. Age related changes for *B. poecilochrous* dark morph male

Figure 4. Age related changes for *B. poecilochrous* dark morph female