

THE UNIFICATION OF THE VARIABLE BUZZARD (*GERANOAEETUS POLYOSOMA*) AND GURNEY'S BUZZARD (*GERANOAEETUS POECILOCHROUS*) IS UNJUSTIFIED: COMMENTS ON FARQUHAR'S PROPOSAL OF CONSPECIFICITY

La unificación del aguilucho variable (*Geranoaetus polyosoma*) y aguilucho de la puna (*Geranoaetus poecilochrous*) es injustificada: comentarios sobre la propuesta de conspecificidad de Farquhar

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RESUMEN.- Farquhar (1998) propuso que el aguilucho variable (*Geranoaetus polyosoma*) y el aguilucho de la puna (*G. poecilochrous*) sean unificados dentro de la primera especie, ya que él no encontró diferencias morfológicas y vocales que garanticen su estatus de especies separadas. Re-examinamos los análisis hechos por Farquhar (1998) y detectamos que el autor no separó a los especímenes de cada especie a simple vista ni utilizó correctamente el criterio de Stresemann (1925) para identificarlos. El autor trató un conjunto de mediciones corporales y descripciones de plumaje, respectivamente heterogéneas, como si fueran muestras homogéneas. Los análisis de Farquhar (1998), en los que incluyó aves mal sexadas, inducen a error, y no permiten caracterizar a cada especie con base en sus respectivas proporciones corporales y los patrones de plumaje. Además, el autor no consideró que el polimorfismo dentro de cada especie está determinado por dimorfismo sexual, la existencia de morfos de color (pálido y oscuro) y la maduración tardía del plumaje. La interpretación que hizo el autor de las voces de alarma fue subjetiva. Todo lo anterior debilita la propuesta de unificar al aguilucho variable y aguilucho de la puna en una sola especie, por lo cual proponemos que sigan siendo consideradas especies separadas.

PALABRAS CLAVE: cambios alométricos, fórmula alar, llamadas de alarma, morfo oscuro, morfo pálido, plumaje sexualmente dimórfico.

ABSTRACT.- Farquhar (1998) proposed the unification of the Variable Buzzard (*Geranoaetus polyosoma*) and Gurney's Buzzard (*G. poecilochrous*) into the first species because he did not find morphological and vocal differences that would guarantee their status as separate species. We reviewed the work of Farquhar (1998) and we detected that the author did not separate specimens from each species by simple sight nor did he use the Stresemann (1925) criterion correctly to identify them. The author treated body measurements and plumage descriptions, respectively heterogeneous, as if they were homogeneous samples. Analyzes by Farquhar, which included mis-sexed birds, are misleading as they do not allow for characterizing species based on their respective body proportions and plumage patterns. Furthermore, the author did not consider that the polymorphism of both species is due to sexual dimorphism, the existence of pale- and dark-morphs, and the late maturation of the plumage. The author's interpretation of alarm calls was subjective. These observations weaken the proposal to unify the Variable and Gurney's Buzzard into a single species. Therefore we propose that they continue to be considered separate species.

KEY WORDS: alarm calls, allometric changes, dark morph, pale morph, sexually dimorphic plumage, wing formula.

Following Gurney (1879), ornithologists generally considered the Variable Buzzard (*Geranoaetus polyosoma*) and Gurney's Buzzard (*G. poecilochrous*) as separate species until Farquhar (1998) questioned the validity of the former. After re-examining wing morphometrics, plumage coloration related to age, adult vocalizations, and geographical distribution of both species, Farquhar (1998) concluded that (i) wing formula and wing length are not reliable taxonomic characteristics due to their continuous clinal relationship; (ii) wing-tip contours change allometrically with changes in wing length, which is itself a function of body size and mass; and (iii) these changes are linked to altitude such that the largest birds occur at higher altitudes and the smallest at lower altitudes. He also found that (i) plumages vary randomly; (ii) there are at least 27 adult plumage morphs; (iii) immature plumages are similarly ineffective for diagnosing species; and (iv) vocalizations are similar in adults of both species from widely varying latitudes and altitudes. Because Farquhar did not find reliable characteristics with which to differentiate both species, he grouped the Variable Buzzard and Gurney's Buzzard into the Variable Buzzard.

Despite Farquhar's arguments, there is abundant documentation from respected ornithologists that indicates the Variable and Gurney's Buzzard are morphometrically separable, and that their range of body measurements are different at the interspecific level (Stresemann 1925, Hellmayr & Conover 1949, de Vries 1973, Cabot 1991, Cabot & de Vries 2003, Cabot & de Vries 2010a). Other authors highlight that plumage patterns do not vary randomly, but that in these species there is a prolonged succession of changes leading to the final definitive plumage (Chapman 1926, Housse 1945, Pavez 1998, Cabot & de Vries 2010a). Along with this, each species presents two color morphs (pale and dark; Fig. 1) with different rates of occurrence (Vaurie 1962, Jiménez 1995) and plumage variations related to sexual dimorphism, especially among dark birds (Cabot & de Vries 2010a). Additionally, the body sizes of both species vary inversely latitudinally (Jiménez 1995, Cabot & de Vries 2009), and exhibit differences in vocalizations (Fjeldså & Krabbe 1990, Walker 2002).

Despite the extensive evidence that morphologically separates the Variable from Gurney's Buzzard and justifies the variability of their polymorphic plumages, Farquhar and others still consider them to be a single species. We re-examined the information and procedures used by Farquhar (1998) with the objective to argue against the proposal of conspecificity.

Review of Farquhar's proposal

We meticulously reviewed Farquhar's (1998) work and contrasted his results with the available information on

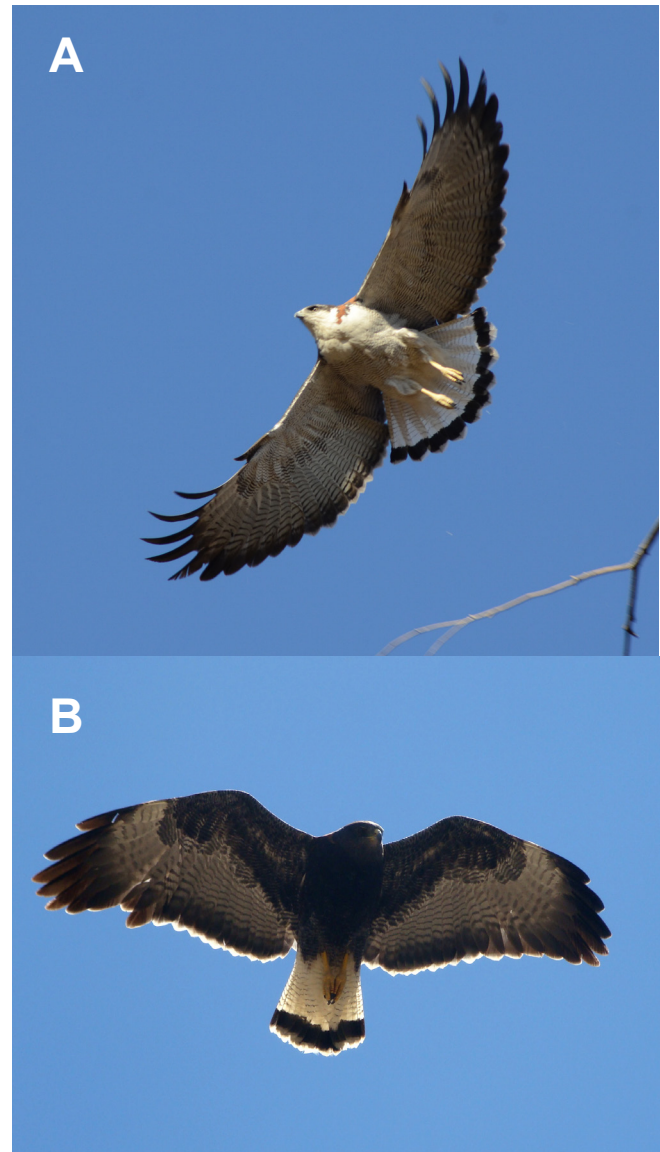


Figura 1. Adult female Gurney's Buzzards (*Geranoaetus poecilochrous*). A. Pale morph (photo: Sergio Alvarado). B. Dark morph (photo: Flavio Martínez).

the distribution, behavior, and systematics of the Variable and Gurney's Buzzard. We statistically reanalyzed some morphometric measurements on which the author based his conspecificity proposal. As we argue below, Farquhar's work contains faulty analysis and unwarranted conclusions. For the common names in English of both species we follow Cabot & de Vries (2010b).

Misuse of Stresemann's wing formula

Two of the reasons why Farquhar's interpretations are wrong are because they fail to recognize visible external morphological differences and misuses Stresemann's (1925) wing formula in separating Variable from Gurney's Buzzards. Taxonomists such as Chapman (1926), Hell-

mayr (1932), Vaurie (1962), and Farquhar (1998) changed Stresemann's original description "approximately as long" to "more than" or "less than" when referring to the lengths of the third and fifth primaries counting from the outside.

Counting from the inside, Stresemann (1925) found that in the Gurney's Buzzard, the sixth primary (p6) was "approximately" as long as or longer than the eighth primary (p8), and that the overall wing length was over 400 mm. In the case of the Variable Buzzard, Stresemann (1925) found that the p6 was shorter than the p8 and that the wing/tail ratio in adult specimens was > 0.46 and in juvenile specimens > 0.51 . Stresemann (1925) also provided wing lengths for males and females of both species. Given the small distance between the tips of the p6 and the p8 in the Gurney's Buzzard (de Vries 1973), it is inevitable that in some individuals the p8 will be slightly longer than the p6 and vice versa (Vaurie 1962). Thus, the incorrect application of Stresemann's criterion possibly led in the past to identify some specimens of the Gurney's as Variable Buzzards

Vaurie (1962) provided ranges of wing lengths for both sexes that did not overlap between species and noted that the plumage patterns of dark-morph specimens differed between species (Variable Buzzard: 89 males and 131 females, Gurney's Buzzard: 19 males and 17 females), as reported by Gurney (1879), Stresemann (1925) and, subsequently, by Cabot & de Vries (2010a).

Although Farquhar (1998) recognized that, the Gurney's Buzzard "probably has the most highly variable plumage of any of the Falconiformes yet documented" and that "the actual number of morphs for all populations discussed here is probably unknown and unknowable," he did not consider an analysis of the molt sequences.

Age- and sex-related plumages, phases, and interspecific differences

Farquhar (1998) ignored the published descriptions of interspecific differences in plumage patterns between the dark-morph adults of the Variable and Gurney's Buzzard (Gurney 1879, Stresemann 1925, Hellmayr & Conover 1949, Brown & Amadon 1968). Such differences are apparent in the plates in Brown & Amadon (1968), Fjeldså & Krabbe (1990) and Ferguson-Lees & Christie (2001). Interspecific differences are also detectable in immature individuals (de Vries 1973, Cabot & de Vries 2010a), especially in the dark morph of the Gurney's Buzzard (Vaurie 1962), that resembles the immature individuals of the Black-chested Buzzard Eagle (*G. melanoleucus*) (Fjeldså & Krabbe 1990).

Farquhar (1998) also failed to realize that both species have plumage patterns that change with age and show two typical color morphs (pale and dark; Chapman 1926,

Housse 1945); that the occurrence of the color morphs differ between species (Hellmayr & Conover 1949, Brown & Amadon 1968, de Vries 1973); and that the proportion of dark and pale Variable Buzzards varies geographically (Reynolds 1935).

Given the limitations in Farquhar's analyses and his failure to notice the differences in the successive post-juvenile and basic plumage patterns in the skins that he examined, we believe that it was impossible for him to even contemplate and decipher the nature of the polymorphism in both buzzard species. He did not detect any abnormal plumages due to errors when sexing and identifying buzzards, which becomes obvious when he mentions (as in Vaurie 1962) that grey-back specimens are more frequent in males than in females. Both the Variable and Gurney's Buzzard are sexually dimorphic in plumages and males in definitive adult plumage have a grey back, while adult females in definitive plumage have a red dorsal patch (but not a grey back) and immature males have a small reddish dorsal patch. The reddish dorsal patch is also present in subordinate males of the polyandric Gurney's Buzzards (Cabot & de Vries 2010a). Farquhar omitted the description of the Gurney's Buzzard in Gurney (1879) and assumed that this species is only separable from the Variable Buzzard by body size and wing length. The original description of the Gurney's Buzzard based on plumage patterns that differ from the Variable Buzzard, and on the greater length of the wing chord, tarsi, tail, and middle toes of seven female Variable Buzzards and six White-tailed Buzzards (*G. albicaudatus*).

Both Farquhar (1998) and Vaurie (1962) mistakenly believed that Variable Buzzards with white tails are adults with plumage patterns that do not change over time, in what these authors described as a highly polymorphic species. This contradicts Hellmayr & Conover (1949) who concluded, "It is now an established fact that this buzzard occurs in various mutational strictly alternative plumages".

The polymorphic plumage of the Variable and Gurney's Buzzard is the outcome of a long process of age-related changes, first described by Chapman (1926) and later by Pavez (1998), in the pale morph of the Variable Buzzard. Subsequently, Cabot & de Vries (2004, 2010a) described these changes in both color morphs of both buzzard species, and highlighted interspecific differences. For example, the adult definitive basic plumage in both pale males and females of the Variable Buzzard is white ventrally; however, males have grey backs and females a brick-red patch on their mantle. In the dark morph of the Variable Buzzard, the sexual dimorphism is different. On the upperparts, males and females resemble the pale phase but on the underparts males are uniformly grey; females have a reddish dorsal patch, a broad uniform breast band of

the same color, a grey head and bib, and on the rest of their underparts and thighs a uniform unbarred blackish grey or sooty brown. Rarely some dark male specimens of Variable Buzzards from northern Chile show lower underparts grey with faint white bars similar to the dark Gurney's Buzzards (Hellmayr & Conover 1949, Brown & Amadon 1968).

The adult pale-morph plumage pattern in the Variable Buzzard is similar in the Gurney's Buzzard. However, coloration patterns differ in the pre-basic definitive plumages of dark-morph individuals. Dark juvenile Gurney's Buzzards are brownish with black malar streaks, pale cheeks, and very pale underparts (de Vries 1973), and usually have mid- and lower underparts and thighs that are coarsely barred. Dark juvenile Variable Buzzards are uniform dark-to-sooty brown with pale spots on the flanks (Cabot & de Vries 2004). After their first molt, individuals appear blackish brown with more uniform underparts (Chapman 1926, Cabot & de Vries 2004, 2010a).

Morphometrics and reversed sexual size dimorphism

Farquhar (1998) used wing length (distances from the carpal joint to the tip of the five outermost primaries) and wing formula (Baldwin *et al.* 1931) as variables in his analysis of the two groups that he separated by tail color (white or brown). His analysis was less thorough than that by de Vries (1973) and did not take into account variations associated with sex-related size differences (both species show considerable reversed sexual dimorphism in size).

Farquhar (1998) was also unable to discriminate both buzzard species because he combined wing measurements, sexes, and color morphs (Tables 1 and 2 in Farquhar 1998). Thus, his results do not coincide with the values reported by other authors (Hellmayr & Conover 1949, de Vries 1973, Cabot 1991, Cabot & de Vries 2003). The very wide-ranging standard deviation values reported by Farquhar (1998) indicate that he sexed incorrectly the specimens in his sample.

Farquhar (1998) unsuccessfully used biometrics to separate morphs. By plotting wing length against wing formula of buzzards grouped by sex and tail color, he identified brown-tailed specimens as juveniles or immatures, and white-tailed specimens as adults. However, he did not take into account that Variable Buzzards have brown tails during their first two years (Stresemann 1925, Chapman 1926) and that in subsequent ages the immature individuals have white tails until they attain their definitive adult plumage.

Farquhar's regression analysis between wing length and wing formula showed that they are not linearly related. His correlation analysis yielded negative results in three of the four groups, which means that 75% of them achieved no statistical significance. Farquhar then trans-

formed this group of correlations into a clinal gradient for which he did not provide initial values nor quantified how one variable changes with respect to another at any point along the gradient. Furthermore, he altered the correlations using an allometric process stating, "Rather, the distribution of data points is clinal. In both sexes of adults, the relationship (slope) is allometric and statistically significant ($P < 0.05$), but for immatures the relationship is significant only in males." However, the correlations he obtained between wing length and wing formula were wrong because he included measurements taken from mis-sexed specimens. When Farquhar (1998) plotted wing length against wing formula, the data points of the mis-sexed specimens occupied different positions on the x-axis (wing length). Given the buzzard's reversed sexual size dimorphism, that erroneous data increased the dispersion of points, and prevented well-differentiated subgroups from forming. Thus, correlations appear at random because the buzzards with greater wing lengths had a small wing formula and vice versa.

Farquhar (1998) stated that wing-tip contours change from pointed to round as the wing length increases. His claim is based on a non-quantified interpretation of the contours of wing tips superimposed one on another with respect to their respective wing lengths, which the author presented separately in two figures—one for adult buzzards (white-tailed specimens) and the other for immature buzzards (brown-tailed specimens)—again with no distinction according to sex (Fig. 3 in Farquhar 1998). In those two figures, one for each age class, the specimens with shorter wing lengths shows more "pointed" wing tips than those with longer wings, which have blunter wing tips. Between these two extremes, there are overlapping wing tip contours among specimens with intermediate wing lengths (female Variable and male Gurney's Buzzard) which are difficult to interpret. Farquhar's representation is misleading since it lumps together the buzzards' wing tip contours of both sexes with respect to wing lengths without considering the differences caused by reversed sexual size dimorphism.

Supposed clinal and allometric changes

Farquhar (1998) reported that size and wing length were related as a cline or at random in a morphometric space (Rayner 1988). He provided an artificial example in a hypothetical relationship based on data linking wing length and wing tip shape. At the interspecific level, this relationship between a buzzard's size and wing length is not simple (Rayner 1988). Proof of that is that southern Variable Buzzards are heavier (Humphrey *et al.* 1970, Jiménez 1995, Jaksic *et al.* 2002) but have shorter wings than Gurney's Buzzards (Cabot & de Vries 2003). That demonstrates a gap or discontinuity between body mass and wing length at

the interspecific level. This clinal discontinuity also occurs between sexes at the intraspecific level. Male and female buzzards have differing relationships between body mass and wing lengths. Male Variable and Gurney's Buzzards have smaller wing loads than their respective females (Cabot & de Vries 2003), as occurs in other diurnal and nocturnal raptors (Johnson 1965, Brown & Amadon 1968, Mueller *et al.* 1981).

Farquhar (1998) argued in favor of an increase in wing length with altitude based on second-order polynomial correlations derived from data of two different-sized species with overlapping altitudinal ranges, even though each has altitudinal preferences. The Variable Buzzard, with smaller wingspan, occurs commonly at lower altitudes (< 3000 m s.n.m) but sometimes at higher altitudes (Fjeldså & Krabbe 1990, Cabot 1991), while the longer-winged Gurney's Buzzard occurs almost exclusively at higher altitudes (> 3000 m s.n.m; Cabot *et al.* 2010). Moreover, the polynomial correlations confound the relationships between variables as they suggest a behavior that is not real (Conte & Deboor 2018).

Farquhar (1998) did not provide initial nor final values for the clinal gradient he proposed, including the rate of change according to altitude. It is apparent by analyzing Figure 4 in his paper that the data did not group homogeneously. The data points in each of the four regression graphics form two more or less well-defined sub-groups: 0-1000 m a.s.l. and > 3000 m a.s.l. However, Farquhar provided very little data for buzzards at intermediate altitudes; only one white-tailed female at 1000-2000 m a.s.l., and six and five brown-tailed and white-tailed females at 2000-3000 m a.s.l.

Another major problem in Farquhar's analysis is that he combined the information from both buzzard species and then analyzed the variables and adjusted the model as if it were a single homogeneous sample. This is evident when examining the values of the variables in Table 1. For example, the means and standard deviations for the p7 are different between female Variable and Gurney's Buzzards (399.1 ± 18.7 mm vs 453.8 ± 29.2 mm, respectively). The confidence intervals $CI_{95\%} = (394.7-403.5$ mm) vs $CI_{95\%} = (426.8-480.8$ mm) for the Variable and Gurney's Buzzard, respectively, does not overlap and differences are significant in the contrasted measures. This also occurs when calculating the corresponding coefficients of variation (CV = 4.7% for the Variable Buzzard, CV = 6.4% for the Gurney's Buzzard) as well as between its means (*t*-test for means: $t = -6.99$; $P = 0.000$). Our brief statistical exploration reveals that the combination of heterogeneous data into a single sample masks the variability and the effects of covariates on the fit. Conclusions would have been very different if Farquhar had treated the variables separately,

and adjusted the slopes and coefficients, for example, using a mixed model or, where appropriate, a multilevel model (McCullagh & Nelder 1989, McCulloch & Searle 2001).

The measurement of mis-sexed specimens throws up data points at different positions along the wing length axis from the correctly sexed specimens, thereby giving rise to a spurious correlation between the variables.

Farquhar (1998) committed a further error when he linked morphological changes in buzzards to a single geographical variable, and assumed that a specimen is a faithful reflection of the morphological types present in space and time at that locality. He did not consider documented seasonal movements for the two species. Likewise, he ignored the fact that the Variable Buzzard increases in size at greater latitudes (Vaurie 1962, de Vries 1973, Jiménez 1995, Cabot & de Vries 2003) and that the opposite occurs in the Gurney's Buzzard. In fact, the southern Gurney's Buzzards (*G. p. fjeldsai*) are smaller than those more northerly buzzards from the nominal subspecies (Cabot & de Vries 2009).

Farquhar (1998) linked wing dimensions exclusively to the altitude of the capture locality without considering that Variable and Gurney's Buzzards differ in geographic ranges and altitudinal distribution, respectively. He combined in a single global distribution two geographical ranges that overlap partially in the Andes (Fjeldså & Krabbe 1990), thereby assuming an as-yet not demonstrated inter- and intra-taxonomic spatial and temporal homogeneity. He based his assumptions on a limited number of museum skins taken from an extensive geographical area. Most specimens were from lowland localities from southernmost South America or the Falkland Islands. Although only a little under half (Figs. 1 and 4 in Farquhar) of the specimens were from the Andes, he still insisted on a supposed generalized process of morphological changes (clinal and allometric changes) along a region that extends from Colombia to the far southern tip of the South American continent. For a correct analysis of morphological variations in terms of geographical factors, (a) it is essential to quantify the number of buzzard species present in specific localities during the complete annual cycle to be able to determine the buzzards' residence and abundance, and (b) to have a representative sample of all morphs present at a site at any given time.

Farquhar (1998) also linked variations in wing length with the altitude of the collection site, which he obtained from the labels on skins and bibliographical sources. However, that information may not be reliable given that many collectors may have been unable to calculate exact altitudes. Moreover, the abrupt relief of the Andes means that altitudes vary greatly over very short distances. On occasions, localities on the skin labels may not match the

exact site of collection but may refer to the residence of a commissioner who received skins from a collector and then sent them to museums, as in the case of the type specimen of the Gurney's Buzzard (Cabot & de Vries 2005). At times, the locality on skin labels also does not match to the species habitat or lie outside its range (Buitrón-Jurado *et al.* 2010). Moreover, a single name may in fact refer to two different geographical locations. For example, Chimborazo, Cotopaxi, and Tungurahua are all either a volcano or a province in Ecuador. Likewise, a name may refer to a large region or province but also be the name of the capital city. This is the case of Valdivia and the mountainous regions of Arica and Antofagasta.

Assigning an altitude to a collection locality referring to a whole volcano with a wide altitudinal range is also questionable since both buzzard species may be present at different elevations: the Variable Buzzard at the base (Buitrón-Jurado *et al.* 2010) and Gurney's Buzzard nearer the summit (Cabot *et al.* 2010).

Alarm calls

Farquhar (1998) used only a few samples of alarm calls (four individuals) to distinguish Variable from Gurney's Buzzards. He recorded calls emitted when buzzards mobbed intruders and thus those calls possibly did not associate with mating. Farquhar represented vocalizations in sonograms of the four individuals he presumed were females from three different localities and concluded without any quantitative analysis that these alarm calls were similar. This contrasts with our results obtained from Farquhar's own sonograms, which show that birds of different geographical origins have different vocalizations. Several other authors have also reported differences in the vocalizations of the Variable and Gurney's Buzzard (Brown & Amadon 1968, Fjeldså & Krabbe 1990, Walker 2002, Pavez 2004). Unfortunately, Farquhar missed the opportunity to conduct a major comparative analysis based on the frequencies and intensities of the calls.

An overlook at the genetic evidence

Although Riesing *et al.* (2003) concluded that both species are conspecific based on the very little divergence between their respective mitochondrial DNA base sequences, they fail to remark that there is a direct correspondence between the degree of variation of the base sequences and phenotypic differences (morphological, ecological, and biological), which is obvious. Furthermore, the exclusive use of a phylogenetic tool (mitochondrial DNA) for classificatory purposes is insufficient. In eventual future phylogenetic studies of South American buzzards, researchers should follow Kruckenhauser *et al.* (2004), who included phenotypic characters to distinguish close species of the genus

Buteo. Despite similar results with Riesing *et al.* (2003), Lerner *et al.* (2005) treated the Variable and Gurney's Buzzard as different species given that the great similarity between their mitochondrial DNA sequences is not incompatible with a recent speciation process that has not yet left its molecular mark (Cabot & de Vries 2010c).

Conclusions

In sum, Farquhar (1998) provided weak evidence for defending the conspecificity of the Variable and Gurney's Buzzard. The scarce genetic evidence is not sufficiently convincing to consider categorically both species conspecifics. Therefore, the Variable and Gurney's Buzzard ought to remain defined as two biologically distinct species, as affirmed by Cabot & de Vries (2003).

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