Taxonomic status of Bay-winged Hawk Parabuteo (unicinctus) unicinctus and Harris's Hawk P. (u.) harrisi, with documentation of delayed plumage maturation in Bay-winged Hawk

Authors: Clark, William S., and Seipke, Sergio H.

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Taxonomic status of Bay-winged Hawk *Parabuteo* (*unicinctus*) *unicinctus* and Harris's Hawk *P.* (*u.*) *harrisi*, with documentation of delayed plumage maturation in Bay-winged Hawk

by William S. Clark & Sergio H. Seipke

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Summary.—The two main populations of *Parabuteo unicinctus* have long been treated as subspecies of the same species: Harris's Hawk *P. u. harrisi* in the southern USA to Costa Rica, and Bay-winged Hawk *P. u. unicinctus* in South America. However, they differ considerably in their morphology, number of plumages, and behavioural ecology. Adult Harris's Hawk differs in multiple plumage characters from adult Bay-winged Hawk, and differences are even more marked in juvenile plumage. Harris's Hawk has two age-related plumages but Bay-winged Hawk shows delayed plumage maturation and has four such plumages. Harris's Hawk breeds and hunts cooperatively, whereas Bay-winged Hawk nests only in pairs, and hunts individually. There are no valid records of Harris's Hawk in South America. We believe that the differences in adult and juvenile plumages, the number of immature plumages, and differences in breeding and hunting mean that Harris's Hawk and Bay-winged Hawk are best treated as separate species.

The two main populations of *Parabuteo unicinctus* have long been treated as subspecies of the same species: Harris's Hawk *P. u. harrisi* (Audubon 1837) of North and Middle America, and Bay-winged Hawk *P. u. unicinctus* (Temminck 1824) of South America. All of the major world bird checklists (e.g., Dickinson & Remsen 2013, del Hoyo & Collar 2014, Clements *et al*. 2022, Gill *et al*. 2023) treat them as conspecific. However, in this paper we document and review evidence that these taxa differ considerably in plumages and behavioural ecology, and, as such, merit consideration as separate species. In particular, the immature plumages of Bay-winged Hawk are not well understood.

Harris's Hawk and Bay-winged Hawk differ diagnostically in adult and juvenile plumages (Clark & Wheeler 2001, Pallinger & Menq 2022). Furthermore, due to delayed plumage maturation, Bay-winged Hawk has four age-related plumages; its Basic II and Basic III have not been well understood but are described fully herein. Basic II and Basic III plumages of Bay-winged Hawk are similar to that of juvenile Harris's Hawk, but are easily distinguished by the presence of flight feather moult, or wave moult fronts. Harris's Hawk regularly hunts and breeds cooperatively (Bednarz 1987, Bednarz & Ligon 1988, Bednarz 1995, Coulson & Coulson 2013, Dwyer & Bednarz 2020), whereas these behaviours have not been reported in Bay-winged Hawk (e.g., Jiménez & Jaksić 1993), although Coulson & Coulson (2012) presented anecdotal accounts to suggest that they may occasionally hunt communally. No published reports of cooperative breeding or hunting in Bay-winged Hawk were found (e.g., Jiménez & Jaksić 1993). The only published comparative DNA studies of these taxa, Riesing *et al*. (2003) and Raposo do Amaral *et al*. (2009), reported a small difference between two samples from Brazil of Bay-winged Hawk and one from the USA of Harris's Hawk. Herein we discuss the many differences between these two taxa, which we believe are sufficient to consider them as species.

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Methods

We have observed, studied and taken more than 100 photographs of both taxa in the field and have examined 119 specimens of *P. unicinctus* from throughout the range in 14 museums: Carnegie Museum of Natural History, Pittsburgh, PA (CM); Cleveland Museum of Natural History, Cleveland, OH (CMNH); Natural History Museum of Los Angeles County, Los Angeles, CA (LACM); Moore Lab of Zoology, Occidental College, Los Angeles, CA (MLZ); Museum of Comparative Zoology, Cambridge, MA (MCZ); Museum of Zoology, University of Michigan, Ann Arbor, MI (UMMZ); National Museum of Natural History, Smithsonian Institution, Washington DC (USNM); Museo de la Plata, La Plata (MLP); Museo de la Estación Biológica de Rancho Grande, Maracay (MEBRG); Museo de las Aves de Patagonia, El Bolsón; Colección Ornitológica Phelps, Caracas (COP); Louisiana Museum of Natural History, Baton Rouge, LA (LSUMNS); Santa Barbara Museum of Natural History, Santa Barbara, CA (SBMNH); and Western Foundation of Vertebrate Zoology, Camarillo, CA (WFVZ) (Table 1). We compared juvenile and adult plumages between both taxa, using primarily the 119 specimens, augmented by >100 photographs of in-hand Harris's Hawks and >10 photographs of Bay-winged Hawks. We also compared photographs of both taxa online at the websites: WikiAves (www.wikiaves.com.br), Macaulay Library (https://www.macaulaylibrary.org) and iNaturalist (https://uk.inaturalist.org/). We compared Basic II and Basic III plumages of Bay-winged Hawk vs. juvenile Harris's Hawk. We searched the literature for reports of cooperative hunting and cooperative breeding, and discuss the DNA evidence to date. We use the moult and plumage terminology proposed by Clark & Pyle (2015).

TABLE 1
Number of specimens of Bay-winged Hawk *Parabuteo unicinctus* by age class examined at 14 museums listed in Methods (which see for acronyms) and collected in all parts of South America.

Museum/Age	Juvenile	Basic II	Basic III	Adult	Total
CM	2	2		2	6
CMNH				1	1
COP	1			1	2
El Bolsón	3				3
LACM	15	1		2	18
LSUMNS	2	3		1	6
MCZ	7	1		2	10
MLP	10	8			18
MLZ	1	1			2
MEBRG	1	1		1	3
SBMNH	1				1
UMMZ	12	5		3	20
USNM	10	5		3	18
WFVZ	8	2	1		11
Totals	73	29	1	16	119

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Results

Adult plumage.—Definitive Basic (adult) plumages of these taxa are similar, but all adults differ in several traits, namely throat markings, colour and markings on the undersides of the remiges, markings on the belly and breast, markings on the leg feathers, and extent of white at the base and tips of the rectrices (Figs. 1–2). *Throat markings.* All adult *harrisi* have an unmarked dark throat, whereas adult *unicinctus* almost always shows a variable amount of white streaking on the dark throat (Fig. 1). *Underside of remiges*. All adult *harrisi* have unmarked dark undersides to the remiges (Fig. 2b), whereas all adult *unicinctus* have whitish primaries with narrow dark bands and black tips on the outer ones, but many adult *unicinctus* have whitish secondaries with narrow dark bands (Fig. 2a), though some have darker secondaries with some narrow white bands (e.g., https://www.wikiaves.com/4185104). All adult *unicinctus* have a broad darker subterminal band on the secondaries

Figure 1a. Adult Bay-winged Hawk *Parabuteo u. unicinctus* at Carnegie Museum, Pittsburgh (CM P94603, Bolivia, August 1922; top in both images) vs. adult Harris's Hawk *P. u. harrisi* (CM P165789, Texas, December 1913; below); note differences in throat, underparts and tarsal markings (W. S. Clark)

Figure 2a. Adult Bay-winged Hawk *Parabuteo u. unicinctus* (left, Venezuela, June 2006); vs. 2b. adult Harris's Hawk *P. u. harrisi* (right, Texas, April 2014); note differences in the colour and markings on the undersides of the remiges, and width of the white base and terminal tail-band (W. S. Clark)

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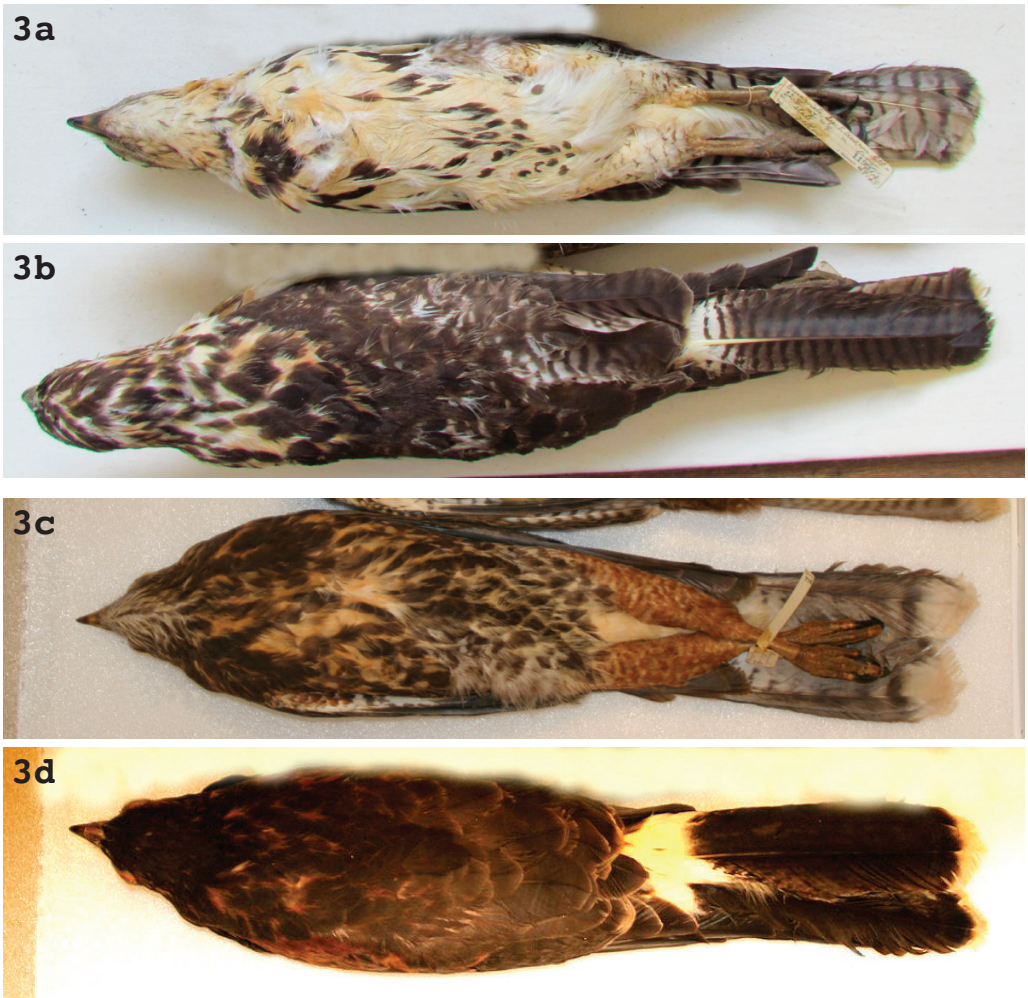

Figure 3a–b. Juvenile Bay-winged Hawk *Parabuteo u. unicinctus* specimen at the Carnegie Museum (CM P119975; Bolivia, June 1927); vs. 3c–d. juvenile Harris's Hawk *P. u. harrisi* specimen at Museum of Comparative Zoology (MCZ 314440; Texas, December 1909); note differences in the throat, extent of dark on the underparts and upperparts, tarsal markings, and width of the tail-bands (W. S. Clark)

(Fig. 2a). *Underwing-coverts*. Uniformly rufous lesser and median underwing-coverts, and plain black greater underwing-coverts are characters of all *harrisi*. Uniformly rufous lesser and median underwing-coverts and barred greater underwing-coverts are shown by most *unicinctus*, but some are all rufous. *Pattern on underparts*. All adult *harrisi* have unmarked dark underparts, whereas almost all adult *unicinctus* show a variable number of white markings on otherwise dark underparts, especially the belly (Fig. 1). *Markings on leg feathers*. All adult *harrisi* have unmarked rufous tarsal feathers, whereas in adult *unicinctus* they can be rufous or rufous with some pale barring (Fig. 1). *Rectrices*. All adult *harrisi* show a broad white base and tips to the uppertail. All adult *unicinctus* show less white on the base and narrower white tips to the same feathers (Fig. 2). More photographs of adult Bay-winged Hawk can be seen at https://www.wikiaves.com.br/4777890 and https://www.wikiaves.com.br/785274; for adult Harris's Hawk see https://macaulaylibrary.org/asset/477195211 and https://macaulaylibrary.org/asset/475940421.

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Figure 4a. Juvenile Harris's Hawk *Parabuteo unicinctus harrisi* (left, Texas, December 2005) (W. S. Clark); vs. 4b. juvenile Bay-winged Hawk *P. u. unicinctus* in flight (right, Argentina, June 2019 (© Gustavo Sebastian Cabanne); note difference in markings on underparts and underwing-coverts.

Figure 5a. Juvenile Bay-winged Hawk *Parabuteo u. unicinctus* (left, Ecuador, August 2010) (© Roger Ahlman); 5b. juvenile Harris's Hawk *P. u. harrisi* (right, Texas, December 2010) (W. S. Clark); note differences in markings on underparts, head and tarsal feathers.

Juvenile plumage.—Juvenile plumages of the two taxa are consistently and markedly different in multiple characters. *Underparts*. All juvenile *unicinctus* have buffy underparts with narrow dark streaking (Fig. 3a), whereas juvenile *harrisi* have dark underparts with white to buffy markings (Fig. 3c). *Undertail*. Juvenile *unicinctus* has the undertail whitish with narrow dark bands (Fig. 3a), whereas juvenile *harrisi* has a medium grey undertail with fewer and broader dark bands (Fig. 3c). *Upperparts*. Juvenile *unicinctus* has buffy markings on the upper back (Figs. 3b, 5a), not shown by any juvenile *harrisi* (Figs. 3d, 5b). Rufous markings on the upperwing-coverts are visible in juvenile *harrisi* (Figs. 3d, 5b), but the rufous area is smaller and less visible in *unicinctus* (Figs. 3b, 5a). *Underwings*. Underwing-coverts are mostly rufous on *harrisi* but mottled buffy and dark brown in *unicinctus*

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Figure 6. Basic II Bay-winged Hawks *Parabuteo u. unicinctus* in flight feather moult (National Museum of Natural History, Smithsonian Institution) (left: ventral; right: dorsal; four from Paraguay and one from Chile); note similarity to juvenile Harris's Hawks *P. u. harrisi* in Fig. 3c–d (W. S. Clark)

TABLE 2
Plumage characters of Basic II and Basic III Bay-winged Hawks *Parabuteo u. unicinctus*. Based on 29 Basic II specimens and two Basic II specimens.

Character/Age	**Basic II**	**Basic III**
Head	Pale cheeks and supercilium	Like adult, or with pale cheeks or eyeline
Throat	Buffy, narrow dark streaks	Whitish streaks
Underparts	Blotched dark brown, buffy areas	Dark brown, some whitish on belly; no buffy
Tarsus feathers	Buffy and rufous barring	Rufous or barred buffy and rufous
Underwing-coverts	Buffy and rufous mix, rufous barring	Mostly rufous, but buffy barring on 'wrists'
Underside to remiges	Primaries like juveniles; single moult wave, and secondaries longer forming ragged rear edge to wing	Like adult; two waves of primary moult
Undertail	Like juveniles, but broader subterminal band; can also be adult-like	Like adult, some whitish on outer feathers
Upperwings	Buffy wing-coverts	Rufous wing-coverts

(Fig. 4). More photographs of juvenile Bay-winged Hawk can be seen at https://www.wikiaves.com.br/3524655, https://www.wikiaves.com.br/807065, https://www.wikiaves.com.br/2664694, and https://www.wikiaves.com.br/1211468; for juvenile Harris's Hawk see: https://macaulaylibrary.org/asset/477177731, https://macaulaylibrary.org/asset/473920961, and https://macaulaylibrary.org/asset/478452121.

Basic II and Basic III plumages.—Only *unicinctus* has intermediate annual plumages between juvenile and adult plumages, taking three years to attain adult plumage. Basic II and III specimens of *unicinctus* are all quite different from juvenile specimens of the same taxon, appearing more like juvenile *harrisi* (Fig. 6). The characters associated with these intermediate plumages are shown in Table 2, determined from 29 specimens of Basic II *unicinctus* from all parts of South America and >100 photographs. They differ from *harrisi*

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Figure 7. Basic III Bay-winged Hawk *Parabuteo u. unicinctus* at Western Foundation of Vertebrate Zoology, which showed two waves of primary moult (WFVZ 46385; Chile, August 1937) (top: ventral; below: dorsal); note similarity to Harris's Hawks *P. u. harrisi* in Fig. 3c–d (W. S. Clark)

mainly by showing moult in the inner primaries. Photographs of Basic II *unicinctus* in flight showing primary and body moult can be seen at: https://www.wikiaves.com.br/692648 (p1 and r1 new and underparts show extensive molt); https://www.wikiaves.com.br/4784500 (p7 growing and pp1–6 new, as are many rectrices, with extensive body moult in the underparts); https://www.wikiaves.com.br/1090880 (pp1–6 and many tail feathers new; underparts in extensive moult); and https://www.wikiaves.com.br/3878012 (p7 growing and pp1–6 plus some secondaries and rectrices are new; underparts in extensive moult). We found one specimen of *unicinctus* in Basic III plumage (WFVZ 46385, from Chile); it showed two waves of primary moult and an adult-like undertail (e.g., Fig. 7). Photographs of Basic III *unicinctus* in flight showing two waves of primary moult can be seen at: https://www.wikiaves.com.br/2906986 (new p9 and p1, thus two waves of primary moult; tail almost adult-like); https://www.wikiaves.com.br/1984344 (new p9 and p1; tail almost adult-like); https://www.wikiaves.com.br/3492276 (new p10 and p1; tail almost adult-like); https://macaulaylibrary.org/asset/471713411 (new p10 and p6; tail almost adult-like); and https://www.ecoregistros.org/site/imagen.php?id=130229 (new p8 and p1; tail has many new feathers). A photograph of a Basic III male that was mated with a breeding adult female was taken by M. Juhant near Buenos Aires, Argentina, and showed the characters of this age as listed in Table 2. Harris's Hawk undergoing the second pre-basic moult show flight feather replacement similar to Basic II and III Bay-winged Hawks, but can be distinguished by their new dark (vs. whitish in Bay-winged Hawk) remiges and new adult rectrices. A photograph showing a Harris's Hawk in second pre-basic moult with new dark remiges and rectrices can be seen at https://macaulaylibrary.org/asset/475156091. The only references to mention Basic II and Basic III *unicinctus* plumages we found were Coulson & Coulson (2012), which has a brief description, and the recently published Pallinger & Menq (2022), which described only Basic II plumage.

We found no specimens or photographs exhibiting characters of both taxa. There are mentions of presumed juvenile Harris's Hawks in northern South America (Blake 1977, Coulson & Coulson 2012), but these probably involved Basic II and Basic III Bay-winged Hawks, which as described above possess a similar appearance.

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Behavioural ecology.—Harris's Hawk is a cooperative breeder, with nest helpers and polygamy, as well as cooperative hunting, reported regularly (Bednarz 1987, Bednarz & Ligon 1988, Coulson & Coulson 2013, Clark 2017, Dwyer & Bednarz 2020). We found only one record of a helper at a Bay-winged Hawk nest. M. Juhant (pers. comm.) saw two Basic III breeding Bay-winged Hawks with a juvenile-plumaged helper and chicks in a nest around Buenos Aires. Likewise, we found no reports of Bay-winged Hawk hunting cooperatively (e.g., Jiménez & Jaksić 1993). The two cases of trios reported by Salvador (2012) at 13 nests monitored were most likely cases of polygyny. The female of one trio that laid and incubated the eggs was in Basic II plumage, and the helper female was in adult plumage. Some references report Harris's Hawk as occurring in western South America (e.g., Blake 1977, Ortiz-Crespo 1986), but these are most likely due to sightings and specimens of the previously undescribed Basic II and Basic III plumages of Bay-winged Hawk. All specimens from this region are Bay-winged Hawks. Researchers in Ecuador have seen only Bay-winged Hawk in the field (J. Bednarz pers. comm., P. Bloom pers. comm.).

Coulson & Coulson (2013) found reports of cooperative hunting only in Harris's Hawk and only in North America; they found no records of such behaviour in Harris's Hawk in Middle America and in Bay-winged Hawk in South America. The lack of records of this behaviour from Middle America could be an artefact of fewer observers there. We believe that the lack of records from South America suggests that Bay-winged Hawk does not hunt, or rarely hunts, cooperatively.

DNA studies.—Only two molecular studies have included these taxa, Riesing *et al*. (2003) and Raposo do Amaral *et al*. (2009). The former screened two mitochondrial markers and stated 'Interestingly, intraspecific variability of *Parabuteo unicinctus* is not detected in the five specimens of our study, although the samples investigated cover much of the species' distribution in North and South America. This finding indicates a rapid and recent expansion from South America.' However, their figs. 2–4 show only three specimens. Raposo do Amaral *et al*. (2009) used sequences of mitochondrial DNA and one nuclear intron; they reported a small difference between two samples of *unicinctus* and one of *harrisi*. Lerner *et al*. (2008) sampled only *P. u. harrisi* in their molecular phylogeny of the buteonines.

Discussion

Main findings.—This study documents multiple differences between Harris's and Bay-winged Hawks in both adult plumage (six differences, including two fully diagnosable) and juvenile plumage (five diagnosable differences). In addition, we document a difference between them in plumage maturation: Bay-winged Hawk has four different plumages whereas Harris's has only two. Furthermore, our review of the behavioural and ecological evidence reveals that Harris's Hawk regularly hunts and breeds cooperatively, behaviours not reported for Bay-winged Hawk.

Taxonomic interpretation.—Modern views of species consider them as lineages (segments of population lineages; Mayden 1997, de Queiroz 1999, 2007). This concept is operationalised via integrative taxonomy (Padial *et al*. 2010, Sangster 2018). As described by Sangster (2018) and Wei *et al*. (2022), integrative taxonomy has several main tenets: (i) any type of data is potentially relevant to document differences between species, (ii) different types of evidence are complementary and can highlight different aspects of the speciation process, (iii) taxonomists should try to obtain as many lines of independent data as possible, (iv) data should be integrated to fully understand the evolutionary history of the relevant taxa, and (v) taxonomic evaluations should be revisited when novel data become available.

We used multiple, independent lines of evidence to address the taxonomic status of Harris's and Bay-winged Hawks. The many differences in adult and juvenile plumages

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strongly suggest that Harris's and Bay-winged Hawks each have a unique evolutionary history and are separate lineages. We believe that the differences in number of immature plumages are genetically based and corroborate the evolutionary distinctiveness of these taxa. In any case, we are unaware of any other single species of Accipitridae that has populations with different numbers of annual plumages. Cooperative hunting and breeding by Harris's Hawk and their absence in Bay-winged Hawk may be considered a further indication that the two taxa represent distinct lineages.

The Biological Species Concept (e.g., Mayr 1982, Johnson *et al*. 1999) does not address well how to categorise allopatric taxa as either species or subspecies, as its basis is that populations do not fuse into a single species when they come into contact (Mayr 1982: 285). Morphological differences between adult Harris's and Bay-winged Hawks may help reduce interbreeding if the two taxa were to come into contact. Even if pairing is successful, we suspect eggs would be infertile given differences in plumage maturation, probably reflecting considerable physiological differences between the taxa.

DNA evidence.—Clearly, further molecular comparisons of these taxa are called for, especially whole-genome sampling. The small difference identified between Harris's and Bay-winged Hawks may be interpreted by some as evidence against species rank. However, shallow genetic divergences between species are not unusual in Accipitriformes. For example, several widely accepted allopatric or parapatric species pairs show very low mitochondrial divergence, indicating recent separation or, in some cases, recent gene flow. These include Sanford's Sea Eagle *Haliaeetus sanfordi* / White-bellied Sea Eagle *H. leucogaster* (Wink *et al*. 1996), Himalayan Griffon *Gyps himalayensis* / Eurasian Griffon *G. fulvus* (Johnson *et al*. 2006), Galapagos Hawk *Buteo galapagoensis* / Swainson's Hawk *B. swainsoni* (Bollmer *et al*. 2006, Raposo do Amaral *et al*. 2009), Common Buzzard *B. buteo* / Long-legged Buzzard *B. rufinus* (Raposo do Amaral *et al*. 2009), Eurasian Sparrowhawk *Accipiter nisus* / Rufous-breasted Sparrowhawk *A. rufiventris* (Breman *et al*. 2013) and Eastern Marsh Harrier *Circus spilonotus* / Swamp Harrier *C. approximans* (Oatley *et al*. 2015).

English names.—Many authorities use the name Harris's Hawk for both subspecies of *P. unicinctus* (e.g., Dickinson & Remsen 2013, Gill *et al*. 2023). Clements *et al*. (2022) use Harris's Hawk for the species but Bay-winged Hawk for the subspecies *P. u. unicinctus*. Meyer de Schauensee (1970) used Bay-winged Hawk, with Harris's Hawk in parentheses. Ferguson-Lees & Christie (2001) and del Hoyo & Collar (2014) called the northern taxon (*harrisi*) Harris's Hawk and South American *unicinctus* Bay-winged Hawk, a convention we have followed herein.

Delayed plumage maturation.—Basic II and Basic III plumages of Bay-winged Hawk are not fully described in any raptor handbook, in any South American field guide or handbook, except Coulson & Coulson (2012), who briefly described Basic II and IIII plumages, and a new Brazilian raptor guide (Pallinger & Menq 2022), which described only Basic II plumage, under the vague term 'subadulto.' Delayed plumage maturation in Bay-winged Hawk is shared with three other buteonines in their South American ranges: White-tailed Hawk *Geranoaetus albicaudatus*, Variable Hawk *G. polyosoma* and Black-chested Buzzard *G. melanoleucus*. On the other hand, other buteonines in Harris's Hawk's range in Middle and North America lack delayed maturation, except White-tailed Hawk, which also occurs in South America.

The only accurate field guide illustrations of Bay-winged Hawk plumages we found are in Schulenberg *et al*. (2007), however Basic II and Basic III plumages were neither shown nor described. Ridgely & Greenfield (2001) illustrated adult Bay-winged Hawk with the dark remiges of Harris's Hawk. Brown & Amadon (1989) showed adult Harris's Hawk and juvenile Bay-winged Hawk, but did not indicate the taxon in either case. Del Hoyo *et al*.

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(1994) depicted adults of both taxa, but did not describe differences in juvenile plumages or the Basic II and Basic III plumages of Bay-winged Hawk. Robbins *et al*. (1966) depicted juvenile Harris's Hawk as a typical juvenile Bay-winged Hawk, with whitish underparts narrowly streaked dark and pale undertail with narrow dark bands. All other field guides to North and Middle America have illustrated Harris's Hawk plumages correctly (e.g., Howell & Webb 1995, Angehr & Dean 2010, Clark & Schmitt 2017).

It is not clear that the differences in presence or absence of cooperative hunting or breeding possess any taxonomic value. These could just be an adaptation to prey and habitat differences. As none of the other 320+ diurnal raptors has subspecies with different numbers of immature plumages, this character in itself very strongly hints at their speciation. If they were to hybridise, how many plumages would the offspring have, one, two, or three? Ferguson-Lees & Christie (2001) concluded their account of these taxa with 'the two might be better treated as allospecies', despite being unaware of the Basic II and Basic III plumages of Bay-winged Hawk. We agree that they should be considered as separate species for the reasons presented herein.

Distribution.—Some authorities (e.g., Dickinson & Remsen 2013, Clements *et al*. 2022) have mistakenly listed Harris's Hawk for north-west South America. These records probably involved Basic II or Basic III Bay-winged Hawks, as all authorities were unaware of these plumages and field observers would be unable to separate them from juvenile Harris's Hawk.

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Addresses: William S. Clark, 2301 South White House Circle, Harlingen, TX 78550, USA, e-mail: raptours@earthlink.net. Sergio H. Seipke, Venezuela 686, Eldorado, Misiones (3380), Argentina.

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