Puntos de vista

EXTREME COLOR VARIATION IN THE PEREGRINE FALCON (*FALCO PEREGRINUS*) IN PATAGONIA

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Abstract.- From fieldwork begun in 1979 and continuing intermittently until the present, we show the range in variation in pigmentation of Peregrine Falcons (*Falco peregrinus*) native to the Patagonian region of South America. This variation nearly equals the full range in Peregrine Falcon color variation for all races worldwide. The pallid morph is paler than any other peregrine, and in extreme southern Patagonia, most dark or normal morph adults are as pale or paler than extremely pale arctic peregrines from northern Asia and North America. In the forests of the southern Andes Mountains, there are richly colored (i.e., with deep red-brown ventral background pigmentation) falcons that approach or equal the darkest peregrines anywhere. Some juvenile peregrines are more deeply red-brown ventrally than any other juveniles worldwide. Most important, we introduce the hypothesis that non-pallid adult color variants are largely segregated by habitat type. By inference, this suggests that adjacent ecotypes may represent different subspecies.

Keywords: *color morph,* Falco peregrinus*, Patagonia, Peregrine Falcon, polymorphism.*

Resumen.- VARIACIÓN EXTREMA DE COLORACIÓN EN EL HALCÓN PEREGRINO (*FALCO PEREGRINUS*) EN LA PATAGONIA. A partir de salidas de campo iniciadas en 1979 y continuadas de forma intermitente hasta la actualidad, presentamos el rango de variación en la pigmentación de Halcón Peregrino (*Falco peregrinus*) de la Patagonia, Sudamérica. Esta variación es casi idéntica al rango completo de variación en color observado en otras razas de Halcón Peregrino a lo largo de su distribución global. Comparado con otros halcones peregrinos, el morfo pálido es el más claro de todos. En el extremo sur de la Patagonia, la mayoría de los halcones peregrinos adultos de morfo oscuro o normal son igual o más pálidos que los peregrinos árticos más pálidos del norte de Asia y Norteamérica. En las zonas boscosas del sur de los Andes, los halcones peregrinos poseen una coloración intensa (por ejemplo, presentan ventralmente pigmentación de fondo castaño-rojiza oscuro) y se aproximan o igualan a los peregrinos más oscuros de otras regiones. Igualmente, algunos ejemplares juveniles de Halcón Peregrino en la Patagonia presentan ventralmente una coloración castaño-rojiza intensa más notoria que la observada en ejemplares jóvenes provenientes de otras regiones. Finalmente, presentamos la hipótesis de que los halcones peregrinos adultos de morfo no pálido están en gran medida segregados por el tipo de hábitat. Por ende, se sugiere qué ecotipos adyacentes de halcones peregrinos pueden representar diferentes subespecies.

Palabras clave: Falco peregrinus*, Halcón peregrino, morfo, Patagonia, polimorfismo*

Received 14 September 2020, accepted 22 October 2020

Color polymorphism is a common phenomenon in raptors (Brown and Amadon 1968) and is particularly prevalent in many species of Accipitridae and Strigidae (Galeotti et al. 2003). It is present to a lesser extent within Falconidae. Besides the forest falcons of the genus *Micrastur*, only a few species in the genus *Falco* show clear examples of color polymorphism. These include the Gyrfalcon (*Falco rusticolus*), Brown Falcon (*F. berigora*), and Eleonora's Falcon (*F. eleonorae*) (Cade 1982). With the determination that the Pallid Falcon (formerly known as *F. kreyenborgi*) is a pale morph of the Peregrine Falcon (*F. peregrinus*) (Ellis and Peres Garat 1983), we now know that the peregrine is also color polymorphic. Further, with the realization that the Peregrine Falcon has the broadest worldwide distribution not only of any raptor (White et al. 2013a) but of any bird, it should be of no surprise that it is also highly color variable. In Patagonia, peregrines occupy at least five different and extensive biomes (Fig. 1; Cabrera 1976, Burkart et al. 1999, Coronato et al. 2008), so it should be expected that five very different ecotypes (or color variants) would also be present. This manuscript is a first attempt to see if it is possible to classify color variants by the following

biomes: (1) the cold, wet, relatively flat, Patagonian Grassland Biome of interior Tierra del Fuego through southern Santa Cruz province, Argentina; (2) north of this, the warm Patagonian Steppe Biome which extends from the foothills of the Andes Mountains to the sea; (3) the Mar Argentino or Atlantic Coast Biome, a narrow strip along that sea; (4) the forested slopes of the Andes Mountains which constitute a mixture of three or more woodland types in two biomes (Fig. 1); (5) the coast of the Pacific Ocean and the associated plethora of forested islands and islets, again in the two forest biomes; and (6) the cold South Atlantic Biome on the Malvinas Islands.

With the publication of the encyclopedic monograph on peregrines of the world (White et al. 2013a), much of the color variation, worldwide, was clarified. That book is also an exhaustive history of the discovery and taxonomic affinities of each race. Most pertinent here, it also describes and discusses some, but not all, adult and juvenile plumages for southern South America. In this article, we illustrate and discuss the wide range in plumage variation observed in Patagonian Peregrine Falcons (i.e., those breeding south of 40° S) in Argentina and Chile including near-shore islands and the Malvinas Islands. Our observations are based on fieldwork conducted intermittently from 1979 to 2011, birds reared or bred in captivity, birds found dead, and photographs taken by the authors and others (Figs. 2 to 10). Although we collected observations over this extended period, our manuscript is a retrospective study based on the gradual realization (over 30 years) that some color variants were absent from some regions but were the common form in others.

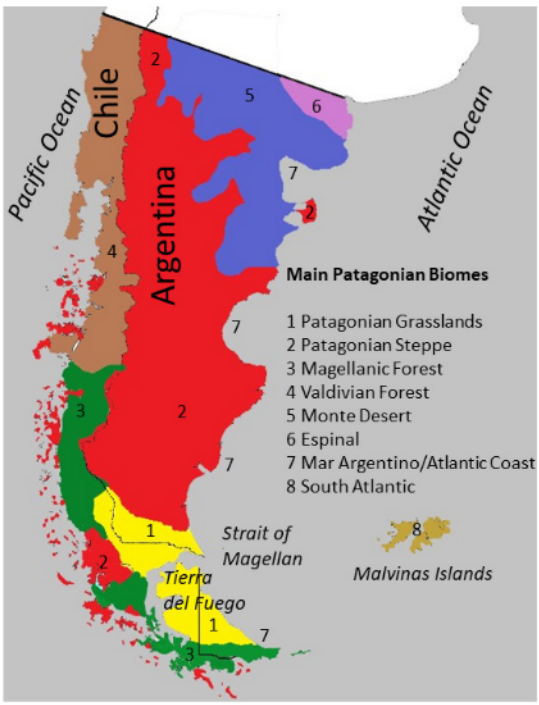

Figure 1. Patagonian biomes of southern Chile and Argentina (Note: Northern limit of Patagonia is arbitrary).

Figure 2. Extreme examples of color variation in juvenile Patagonian Peregrine Falcons. The dark male is from the Valdivian Forest Biome of the Andes Mountains; the pallid female is from Patagonian Grassland Biome. It is normal for pallid birds like this to have pale claws and bills. The Andean male was sooty black dorsally except for dark bluish-gray tail bars. Photo: David H. Ellis.

THE PHOTOGRAPHIC RECORD

Pallid juveniles are illustrated in figures 2 and 4, pallid adults in figure 3, normal (or dark) adults in figure 6, and normal-morph juveniles in figures 2 and 7. Previously published photographic series illustrating peregrines from Patagonia are: Ellis and Peres Garat (1983), Ellis (1985), Rogers (2002), Adreani (2009), Ellis et al. (2010), White et al. (2013a), De Lucca (2014), and De Lucca et al. (2015).

GENERAL RULES IN COLOR VARIATION AMONG PEREGRINE FALCONS BY AGE AND SEX

In describing plumages and, even though individual variation results in some exceptions, the fo-

Figure 3. Pallid morph adults. (a) Adult female, dorsal view, showing that gray bars lack the bluish cast of normal morph adults. Note pale yellow wash on head, not seen on male pallid adults. Also, the pale bars extend full length of the mantle rather than turn darker on the upper mantle as in normal morph adults. (b) Adult male (pale sheen on lower back and inner wing is due to reflection of sun). (c) Adult female, ventral view, showing the limited amount of barring on the flank and under wing coverts. (d) Adult female pallid. This bird has darker bars on the mantle than in Fig. 2a, but like 2a, the pale bars continue conspicuous over mantle (the bird's upper back) to neck. Photos: (a, b, d) David H. Ellis; (c) R. Wayne Nelson.

Figure 4. Pallid juveniles. (a) This recently fledged juvenile represents the commonly seen dorsal pattern of conspicuous pale edges and bars. (b) A darker pallid fledgling. (c) The darkest tail extreme. (d) Ventral view of the commonly seen pallid plumage; remiges are still growing, hence, the rounded wing tips. Photos: (a, b, d) David H. Ellis; (c) Miguel D. Saggese.

Figure 5. The falcon most like the pallid juvenile is not a peregrine but a juvenile, pale morph, Saker (*Falco cherrug*). The head and tail of this fledgling from Mongolia are much like pallid birds. However, the dorsum in general shows much fewer pale bars and narrower pale feather edges. Photo: David H. Ellis.

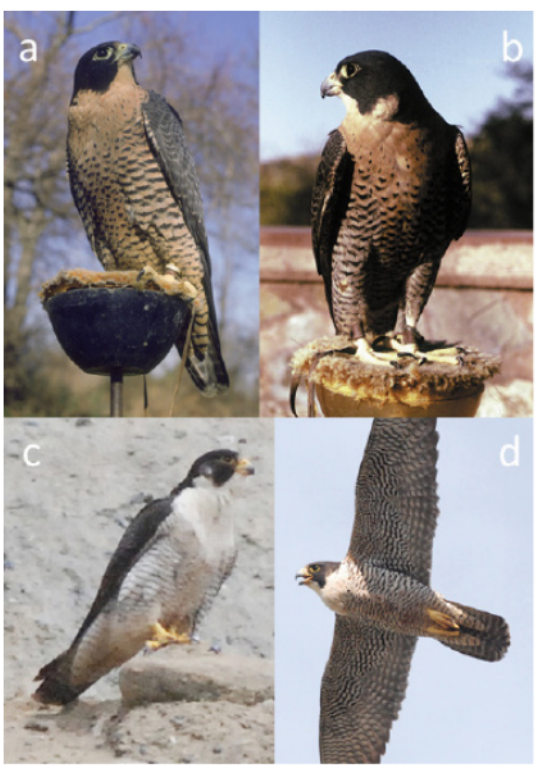

Figure 6. Normal or dark morph (i.e., not pallid morph) adults. (a) Heavily pigmented adult female taken as a nestling by loggers from the Andes Mountains. (b) Extremely dark adult male (sibling of 6a), Andes Mountains. This is the same bird as in Fig. 2. Note that flank barring grades from rust to gray. (c) White-breasted plumage of an adult male, southeastern Patagonia. Note that dark bars on the ventrum are much paler than in 6d. (d) This is the full expression of ventral barring but with a white background color common in southern Patagonia. This degree of barring closely matches the female from the Andes Mountains in 6a. Photos: (a, b) David H. Ellis; (c, d) R. Wayne Nelson.

llowing rules apply generally to peregrine coloration (and to a lesser degree to coloration in other falcons) worldwide [see also Ratcliffe (1980): 340, Zuberogoitia et al. (2009), and Chapter IV in White et al. (2013a)].

1. Ventrally, the dark marks on adult bodies are spots on breast and mid belly and bars on flank, crus, and undertail. If breast spotting is very limited, some or all marks can be juvenile-like streaks.

2. Darker adults are more spotted on the breast and more barred (and therefore less spotted) immediately below the breast along the midline and proceeding caudally.

Figure 7. Normal (or dark) morph juveniles. (a) These nestlings have deep reddish background color ventrally; eyrie was on the Atlantic Ocean Coast. (b) Many dark juveniles are dorsally deep chocolate brown with little pale on feather edges and few bars showing on the back and folded wing; captive-reared female. (c) Normal morph fledglings in mid Patagonia. Male (at right) is grayer dorsally than female.(d) This extremely pale yearling male is believed to represent the progeny of white-breasted adults (Fig. 6c-d). Photos: (a-c) David H. Ellis; (d) Pablo Adreani.

Figure 8. Ventral (a) and dorsal (b) view of an adult female Peregrine Falcon, mixed-morph. The head is darker than for any pure pallid adult. The white tail tip is also a pallid trait. Most unusual, the inner 5 or 6 antebrachial remiges are pallid on the right wing, while all others are normal morph. Photos: R. Wayne Nelson.

3. Within races, juveniles are darker and browner than adults. Their bodies are streaked below except for flank, crus, and undertail which are barred to a limited degree. The longer feathers on the flank and crus are often tipped with dark arrowheads or chevrons. Juveniles also have a

Figure 9. Adult Peregrine Falcon wintering near the west end of the Strait of Magellan. We have seen no other falcons so heavily spotted on the breast and so heavily barred on the abdomen as this falcon. Worldwide, no other peregrine has ventral dark bars so much wider than adjacent pale bars. Photo: Ricardo Ordóñez Henriquez.

Figure 10. (a) A very pale adult female Peregrine Falcon at its breeding ledge in tundra habitat along Hudson Bay, subarctic Canada. (b) Differences from South American pallid birds include a darker dorsum and (c) the lack of yellowish wash on the face (seen on some adult female pallids). Underwing barring is much reduced compared to normal tundra falcons, but nearly identical to pallid adults (Fig. 3c). Pale tail bars appear somewhat narrower than in pallid adults. Photos: Alastair Franke.

darker and browner ventral background color compared to adults.

4. Dorsally, adult females average browner; males grayer (bluer). This is true also for juveniles, but to a lesser degree.

5. In ventral background color, adult females average browner; males whiter.

6. Females generally have a less extensive black cap than males.

7. Females generally have more extensive dark marks on the breast than males.

8. The extent of black on the head is, for most populations/variants, proportional to the darkness of the plumage overall (White et al. 2013:11).

9. Recently grown feathers in adults and juveniles bleach considerably through time [Fig. 133 in White et al. (2013a)]. Bleaching is most conspicuous for background color (Ellis 2006). For example, the buff background color on the head and belly of fledgling Pallid Falcons has bleached to white before onset of molt.

By and large, regional (and racial) trends seem to follow Bergmann's Rule and Gloger's Rule (White and Boyce 1988).

WINTERING NORTH AMERICAN ADULTS: A COMPLICATING FACTOR

In reporting color variation in Patagonian peregrines, our task was complicated by the possibility of confusing resident falcons with wintering birds from the North American Arctic and sub-Arctic (*F. p. tundrius*). Thus, all of the birds we illustrate here were adults or young at breeding sites in Patagonia or captive birds with parents from breeding sites in Patagonia; the three exceptions to this rule are labeled. In fact, we have seen pale-colored falcons (i.e., presumed *F. p. tundrius*) wintering north of Patagonia, but we never with certainty identified any tundra peregrines in Patagonia. In Patagonia, the white-breasted adult color-variant (Figs. 6c and 6d) is the one most likely to be confused with a tundra peregrine, so we made sure we report here only those white-breasted adults that were actively breeding in Patagonia.

EXPLANATION OF THE PALLID FALCON

In Patagonia, there are two general morphs: normal and pallid (Fig. 2). The taxonomic affinities of the rare Pallid Falcon (formerly *F. kreyenborgi*, known as Tierra del Fuego Falcon or Kleinschmidt's Falcon) were clarified nearly 40 years ago (Ellis et al. 1981, Ellis and Peres Garat 1983, McNutt 1984). From observations of mixed (pallid x normal) pairs and pallid young in eyries with normal adults came the conclusion that pallid birds were not a separate species but rather that they were a very pale morph of the Patagonian Peregrine Falcon. At present all peregrines in South America, including the recessive pallid morph, are assigned the trinomial, *F. p. cassini*.

COLOR VARIATION IN AUSTRAL PEREGRINE FALCONS

Pallid adults

Illustrated in figure 3, pallid adults are the palest of all peregrines. For them, the pale dorsal barring common to all peregrines is more conspicuous and more extensive, and the dark ventral barring is least extensive. Ventral barring is so sparse as to be termed "scattered or vestigial". Also, unlike other pale peregrines, in pallid adults (and juveniles), the eye is not completely encircled with dark feathers. Further, the pale tail tip most conspicuous in juvenile peregrines (even in the darkest races: Fig. 7b) is extensive in adult pallids (Fig. 3), perhaps more so than in any other race. It is also noteworthy that the bluish tint to the dorsum common to adult peregrines around the world (particularly males) is absent in pallid birds.

Pallid juveniles

Concerning the uniqueness of juvenile Pallid Falcons (Fig. 4), White et al. (2013a:227) made the statement: "*pale juveniles, nearly of the patterning and coloring of juvenile pallid* cassini*, are found in other races such as* tundrius*,* calidus *and southern* pealei". Significantly, these authors illustrate juveniles of these three northern races, but we assert that none approach the paleness of pallid juveniles. We agree that the head markings approach pallid young, but even the palest young of these other races we have seen in photographs from around the world are much more conspicuously streaked ventrally [Cade et al. (1988: plate 44); the palest ventrum of non-pallid juveniles is probably *F. p. radama*, White et al. (2013a:249)] than

pallid young. All have darker tails and darker heads, with dark coloring completely surrounding the eye. Also, no juveniles we have seen are as heavily barred in pale dorsally as pallid young (Fig. 4a). Strangely, pale-morph juvenile Saker Falcons (*F. cherrug*; Fig. 5) come closest to the pallid juvenile in color.

Normal (or dark-morph) adults

Considerable variation is seen in normal-morph adults across Patagonia. The darkest birds we have seen in the wild and among museum specimens are exemplified by the male in figure 6b. Such birds are found in the forests of the Andes Mountains. In the Patagonian Steppe Biome, adults are typically like figure 6a, but their ventral background color is much paler than the warm brown seen in that adult female from the Andes. A third adult variant is common only in the cold, wet, wide-open Patagonian Grassland Biome of southern Patagonia and along adjacent portions of the Atlantic Coast (Mar Argentino Biome) (Fig. 1). Here falcons have a pure white ventral background color (Fig. 6c, d). Such birds either show conspicuous barring below (Fig. 6d) or faint barring (Fig. 6c). The whitest birds have no breast marks and very few markings along the ventral midline.

Many of these very white, normal-morph adults are heavily capped in black while at the same time they have a white ventral background color. In figure 6c, the head is not fully capped in black, but the ventrum is close to the pale extreme. Adreani (2009) remarked on the peculiarity of these dark-headed, white-breasted, birds. Such birds seem to be an exception to the following rule in color variation: "In Peregrines the size of the dark area [on the head] is generally proportional to the darkness of the entire falcon" (White et al. 2013a:11). A final, but distinctive, adult variant, represented by only one bird, will be discussed later.

Normal (or dark-morph) juveniles

Normal-morph juveniles are shown in figures 2 and 7. The juvenile male from the Valdivian Forest of the southern Andes Mountains (Fig. 2, left) is perhaps as dark as any young peregrine worldwide. Another variety is exemplified by the nest mates with orange-rust ventral background color (Fig. 7a) seen occasionally along the Atlantic Coast. The young in figure 7c are typical of the Patagonian Steppe Biome. The male yearling in Fig. 7d is an extremely light normal morph juvenile from the Patagonian Grassland Biome in Tierra del Fuego. It will likely molt into an adult like in Fig. 6c-d). In Patagonia, all but pallid young are very dark dorsally (Fig. 7b).

Juvenile pallid-normal intermediates

Pallid-normal intermediates are occasionally seen in the zones where full pallids occur (Ellis 1985, White et al. 2013a). The simple monogenic explanation that each pallid bird is homozygous recessive for the pallid trait is complicated by the presence of these oddly colored birds. Two likely explanations for the intermediates are that the pallid gene (or gene cluster *sensu* McNutt 1984) is unstable and that a somatic back mutation to the normal (more heavily pigmented form) occasionally occurs. Co-dominance may also apply. At present, we do not know.

We have seen two juveniles (Fig. 4b) with darker markings than what seems to be the norm and two large nestlings for which the background color was darker than in figure 4. The darkest juvenile tail markings we have seen are illustrated in figure 4c. This bird was typically pallid on the head and ventrum. Pale juveniles are exemplified by the male in figure 4d, but we have seen photos of one juvenile for which the tail was as pale as the Saker tail in figure 5.

Mixed-morph adults

Two examples of mixed-morph adults follow. In November 1980, an adult male pallid bird was found attending a cliff with a normal-morph adult female in northwestern Santa Cruz Province, Argentina (Ellis et al. 1981). The male was unique in that, low on the right side of its breast, it had an asymmetrically placed patch of about 20 light gray feathers. Although the bird was photographed at a distance, fine details of the markings in its plumage were seen (and drawn) through a telescope. From many observations of this tiercel in flight and perched, no other aberrant markings were noted.

The second example of a mixed-morph bird was an adult female at an eyrie in eastern Santa Cruz Province, Argentina (Fig. 8). The uniqueness of its plumage led us to conclude that it was the same bird in both 2010 and 2011. This bird was paired with a normal male and produced young in both years. It was classed as pallid because the dark and white zones on its head were sized and located much as for adult pallids (Fig. 3). Further, its plumage was a chimerical patchwork of normal and pallid areas. Its singular plu-

mage consisted of pallid zones as follows: (1) lesser coverts of the underwing, (2) on the right wing, five or six of the inner secondary remiges and their coverts, and (3) most of the mantle. Fewer pallid feathers were on the left wing compared to the right wing. Half pallid areas included the head, and perhaps belly and under and upper tail coverts. Rectrices also showed abnormally pale tips for a normal-morph adult.

Mixed-morph individuals are occasionally found among Gyrfalcons (Brown and Amadon 1968:833, Potapov and Sale 2005). In the instance of the odd adult pallid male, the dark patch was asymmetrically placed on the right side of the breast. On the adult female, the normal patches appear nearly bilaterally symmetrical, however, the abrupt transition between pallid and normal secondaries on the right wing (Fig. 8) is remarkable.

COLOR VARIATION AND GEOGRAPHIC RACES

A century of confusion surrounding the origin and use of the name *cassini* and its synonyms was reviewed by Anderson et al. (1988) and White et al. (2013a). In brief, Sharpe's (1873) description of *Falco cassini* ostensibly was based on an adult female, an adult male, and a juvenile, but no specimen identification numbers are mentioned, so there are no type specimens to revisit. However, various authors claim to have identified one type, an adult male (Anderson et al. 1988). Second, Sharpe's (1873) adults were so vaguely described that we are left to guess that the adults were probably the buff-ventrally type common on the Patagonian steppe. The juvenile is described as ferruginous below, so was probably like the nestlings in figure 7a. With vague descriptions and no type specimens identified, it would be easy to conclude that *cassini* is an invalid subspecies name. Similar confusion has been noted for some other races of the peregrine (White et al. 2013a).

How does the range in variation presented here relate to geographic races? Of course, formal taxonomic designations of subspecies will require plumage descriptions, values for the frequency of each color variant in each biome/region, and physical measurements of a sample of specimens. Attempts to relate genomic variation to races (e.g., White et al. 2013b, Mengoni et al. 2018) have so far failed but should succeed when more of the genome is examined. However, the continent of South America is so large, habitat types are so varied, and peregrine pigmentation types are so diverse, that we believe several races could be described.

Long ago, Preston (1980) demonstrated that light and dark morph Red-tailed Hawks (*Buteo jamaicensis*) perched and hunted differently. Raptors of various colors may hunt different prey assemblages and/or hunt at different times of the day as was recently shown definitively by Tate and Amar (2017) for the Black Sparrow Hawk (*Accipiter melanoleucus*). Here we suggest that the five different pigmentation types of normal morph peregrines in Patagonia occupy different biomes.

Concerning trends in biome use, the most obvious is for the white-breasted form (Fig. 6c, d) to be common across the cold Patagonian Grasslands Biome (Fig. 1). Inasmuch as this is likely the most southerly distributed peregrine in the world, this group could appropriately be called the Austral (i.e., southern) race (*F. p. australis*). Adult and juvenile plumages in this region are far different from Sharpe's (1873) description. Our records show that, in the Patagonian Steppe Biome, white-breasted adults are extremely rare north of Santa Cruz Province, Argentina.

The second most obvious trend is that the darkest and reddest adults (Fig. 6a, 6b) and juveniles (Fig. 2) were from the forested slopes of the southern Andes Mountains. If birds there are consistently darker than birds from the open steppe habitats, they may form a separate deme, an Andean race, *F. p. andensis*. Their northern limit is unknown.

Across the vast Patagonian Steppe and Argentine Monte Biomes (Fig. 1), including the central and northern portions of Santa Cruz Province, Argentina, and northward to 40°S, adults show the full pattern of ventral barring (Fig. 6d) and warm buff below (approximately midway between the Andean female in figure 6a and the pale variant in figure 6d). Birds of this form nest east even to the Atlantic Coast. If the name *cassini* is retained, these birds should carry that name or better yet a unique geographic name *patagonensis* or *patagonicus*. Proceeding south toward the Strait of Magellan, the brownish background color lightens, then disappears (Adreani 2009, pers. obs.); the northern limit of this variant is unknown (but see White et al. 2013a:220-224).

A seeming anomaly in pigmentation (i.e., an exception to Gloger's Rule) occurs in the sunny clime

along the Atlantic Coast. Some young falcons there are very dark red-brown ventrally [Fig. 7a and photo 16 in De Lucca (2014)]. Also, some coastal fledglings appear nearly as black dorsally as some Andean young [Figs. 2, 7b, photo 9 in De Lucca et al. (2015)]. Elsewhere, the peregrines that are the reddest ventrally and blackest dorsally are tropical races (*F. p. peregrinator*, *F. p. nesiotes*, and *F. p. ernesti*) and, as stated above, birds from the Andean forests. We are therefore left to wonder if the dark-backed, red-bellied young of the Atlantic Coast are linked by some avenue of gene flow to some other population, perhaps the dark deme in the Andes Mountains to the west.

Pertinent to the discussion of races, pallid adults have never been reported from the Andes but are present in the open habitats east of the Andes Mountains from southern Tierra del Fuego to north-eastern Patagonia. The complete absence of pallid birds from the Malvinas Islands, South Atlantic Biome, suggests that there is very little or no gene flow between continental Patagonia and these islands (separated by ca 300 km of ocean). Further, the Malvinas Islands birds, juveniles and adults, seem to lack variability in plumage coloration, again suggesting low gene flow with mainland Patagonia (where color varies greatly in various habitats). Taken together, these factors may justify the designation of a separate Malvinas race. Adults and juveniles there are like the typical steppe-inhabiting birds from central and northern Patagonia, and unlike the white-breasted form which is common on the mainland nearest to the Malvinas Islands. Although we never have seen Malvinas birds ourselves, many photos can be seen on the internet.

Our primary focus in this manuscript was to document the range in color variation in Patagonian peregrines for comparison with other peregrines around the world. A much more complex treatment of regional variation of plumage traits worldwide was given by White and Boyce (1988). In Table 1, we see that Patagonian birds display the full range in variation in head coloration except for the red-naped form (four races, Fig. 9 in White et al. 2013a). In addition, pale/white nuchal ocelli (eye spots on the nape) were seen on one white-breasted adult female in central Patagonia [Fig. 2 in Ellis (1985)]. Such spots are largely ignored in the literature, but various races have them [12 figures in White et al. (2013a)]. They are most evident in pallid birds (Figs. 3, 4, 10).

The other color trait not found in Patagonia (Table 1) is the pale orange ventral background color seen in adults of two or three races [Fig. 4 in White et al. (2013a)]. Also, the deep red-brown to deep gray in belly coloration seen in adult Indonesian and Fujian peregrines [see Fig. 4, 115, 130, 131 in White et al. (2013a)] may not be equaled even by the darkest Andean birds, but the match is very close [compare figure 6b with *F. p. nesiotes* and *F. p. cassini* in figure 4 in White et al. (2013a)].

Some peregrine races that are otherwise very dark have colorful but unspotted breasts. Wide variation in breast spotting is also evident in Patagonian birds. Worldwide, the darkest extreme in breast spotting is found in adults from the Aleutian Islands, *F. p. pealei* [see Plate 31 in Ratcliffe (1980), and Plate 67 in Cade et al. (1988)], with some birds having black spots that cover ca. 40% of the breast. Aleutian adults also have wide dark bars on the belly and flank that are as wide as adjacent pale bars. No other race displays spotting and barring to this degree. Or does it? A hint that even this extreme may be found in Patagonia is figure 9, a winter photograph by R. Ordóñez, southwestern Patagonia. The presence of this bird, with its breast spotted like an Aleutian Peregrine and broader dark bars ventrally than even Aleutian birds, suggests the possibility that a separate race of peregrines resides in the cold, wet, windy marine habitat along the southwestern coast of Chile.

If a *pealei*-like race exists, it will be yet another example of Patagonian wildlife closely matching, species by species, animals from the Pacific Northwest (Oregon to Alaska). Other examples of raptors that exemplify this, the Paired Habitats: Similar Inhabitants Hypothesis (i.e., the close resemblance of conspecific or congeneric animal demes that occupy similar, but widely separated, habitats/niches), are Chilean Hawk (*Accipiter chilensis*)/Cooper's Hawk (*A. cooperii*), Rufous-tailed Hawk (*Buteo ventralis*)/Red-tailed Hawk (*B. jamaicensis*), and Magellanic Horned Owl (*Bubo magellanicus*)/Great Horned Owl (*B. virginianus*). Further, as discussed earlier, the white-breasted, black-capped peregrines from the Tierra del Fuego region may be closely matched by dark-headed tundra birds in Keewatin, Canada (Court et al. 1988) and common in Greenland (White et al. 2002:5). It is germane that some marine mammals and even some marine arthropods of the southern tip of South America closely match cold climate species of North America.

Among juveniles, the race with the darkest head and darkest ventral plumage is also the Aleutian Peregrine [Figs. 73, 74 in White et al. (2013a)]. Future expeditions may show if Aleutian-like adults (Fig. 9) produce Aleutian-like young.

Concerning mantle pigmentation (Table 1), Patagonian birds represent nearly the full spectrum of color variation in peregrines. The black-backed races include some birds from Madagascar, Australia, and Tasmania [e.g., Fig. 86 in White et al. (2013a)], and most birds from Indonesia and other islands in the southwestern Pacific Ocean. Many of these falcons are almost without visible barring on the back and folded wings. The darkest Andean birds we have seen [Figs. 2 and 6b; see also Fig. 4 in White et al. (2013a)] approach this. Juveniles that dorsally are deep chocolate brown are seen across the Patagonian steppe (Fig. 7b). In the Andes Mountains (Fig. 2), some are even darker. Further, the darkest young seen in northeastern Patagonia (see photo 9 in De Lucca et al. 2015) may equal, in dorsal pigmentation, young anywhere.

NORTH AMERICAN "PALLID" FALCONS

Before leaving the topic of Patagonian plumage variants, we must mention two extremely pale adult Arctic birds. Both approach the pallid morph in paleness. One was reported by Gordon Court, nesting near Rankin Inlet, Nunavut (northern Hudson Bay), Canada (Fig. 10). The other was captured by Mark Prostor at 42° S in Chile. The bird from Chile was instrumented and followed by GPS north to coastal Belize before its signal was lost (White et al. 2013a), thus confirming that it was not a Patagonian nesting bird. Although White et al. (2013a) termed both birds leucistic (meaning aberrantly pale), they were so similar to pallid adults that they deserve detailed treatment here.

From the head and ventral surface of the Canadian bird (Fig. 10), it would be easy to believe it was a typical pallid adult. The only noticeable difference is that in pallid adults, the pale gray barring so prominent on the dorsum (e.g., Fig. 3a), appears darker on the Canadian pallid-like adult (Fig. 10). Pale bars on the inner webs of adult pallid rectrices also seem wider than on the Canadian adult. That said, the falcon's head is pallid and it has only vestiges of barring on abdomen and lesser coverts of the underwing and would therefore have been classed as pallid if seen in Patagonia. This finding of the pallid-like adult in northern Canada is, we believe, unprecedented. How is it to be explained? Temple (1988) reports that ca. 4% of falcons released in the eastern USA (to reestablish peregrines there) were of South American stock. Could this bird be the progeny of released birds? We do not know.

The second bird was surely a northern breeding falcon because, after capture, it migrated north at least as far as Belize (locations via satellite radio). However, only tundra birds (no other North American falcons) are believed to winter this far south. Although this bird was very pale [photo in White et al. (2013a:135) and photo series from Mark Prostor], it differed from pallid adults in having a full pattern of dark ventral barring and spotting on underwing and abdomen just as for normal-morph adults of many races (midway between figures 6c and 6d) and unlike pallid adults (Figs. 3c, 3d). It also lacked the pale dorsal barring found in pallid birds. Further, dark encircled the eye on the tundra bird, while in pallid adults (including the Canadian bird) the dark ring is interrupted (Fig. 3 and Fig.10). Because of a juvenile rectrix retained in this bird's plumage in the photo series we have seen, we concluded that, as a juvenile, its tail had much narrower pale bars than on the darkest juvenile pallid tail we have seen (Fig. 4c). All of this points to this bird being an extremely pale tundra bird, but clearly not pallid.

CONCLUDING REMARKS

Falcons across Patagonia are so variable in coloration that individuals can be found that represent nearly the full range of color variation in peregrines worldwide. White et al. (2013a) credits the Black Shaheen (*F. p. peregrinator*) with perhaps showing the greatest range in color variation of all races, but Patagonian birds (of the pallid morph) exceed the paleness of any other peregrine race, and dark Patagonian birds equal, or nearly equal, the darkness of all races. However, two color traits remain undocumented in Patagonia. These are the adult red-naped and the adult pale orange-bellied forms (Table 1). In this report we illustrated two juvenile variants (red-bellied, Fig. 7a, and pale-bellied, Fig. 7d) and one adult color variant (Fig.9, like the Aleutian Island peregrines) which were not known when White et al. published in 2013 (White et al. 2013a). We also showed how pallid adults compare with the palest tundra peregrines from North America. Finally, we illustrate variation within the pallid morph and a mixed-morph adult.

The identification of five different peregrine color variants in Patagonia and the observation that each

Table 1. Conspicuous color traits of adult Peregrine Falcons worldwide and the occurrence of these traits in normal-morph adults in Patagonia. Frequency classes: Very common = 61–100% of normal morphs; Common = 6–60%; Rare = 1–5%; Absent = 0%.

Body part	Description	Zone/race showing trait	Occurrence in Patagonia	Frequency in patagonia
Head				
	Hooded in black	Various races	+	Common
	Narrow malar stripe	Arctic, subarctic (circumpolar)	–	Absent
	White nuchal ocelli (eye spots)	Arctic, subarctic (circumpolar)	+	Rare
	Red-brown nape	Four races (see Fig. 9 in White et al. 2013a)	–	Absent
Ventral Background Color				
	White	Arctic, subarctic, (circumpolar)	+	Common in south
	Buff to pale brown	Mediterranean Sea, various	+	Common on steppe
	Orange	Central Asia, India, China	–	Absent
	Medium red-brown	Southern Asia islands	+	Common
	Deep red-brown to gray	Islands of the southwestern Pacific	+	Andes only
Ventral Barring and Spotting				
	Breast unspotted	Arctic, subarctic (circumpolar)	+	Common in south
	Breast with small spots	Various races	+	Common
	Breast with bold spots	Aleutian Islands	+	Rare in southwest
	Belly and flank narrowly barred (background pale)	Arctic and subarctic	+	Common in south
	Belly and flank narrowly barred (background very dark)	Islands of the southwestern Pacific	+	Andes only
	Belly and flank conspicuously barred (background buff)	Various races	+	Common
	Belly and flank broadly barred	Aleutian Islands	+	Rare in southwest (see Fig. 9)
Mantle				
	Black, unbarred	Islands of the southwestern Pacific	+	Rare
	Dark gray, obscurely barred	Various	+	Common
	Medium gray, distinctly barred	Arctic, subarctic (circumpolar)	+	Common

seems to be associated with a different biome highlights the need for further research on the ecological determinants and genetic mechanisms involved in this phenomenon. The close resemblance of two Patagonian peregrine color types with two variants occupying matching habitats in North America provides a unique opportunity to further explore the Paired Habitats: Similar Inhabitants Hypothesis, which is a special case of convergent evolution wherein one wide-spread taxon produces similar phenotypes in similar, but widely separated, habitat types. Further research is needed to better document the areas occupied by each plumage variant, to determine racial affinities, and, where warranted, to describe subspecies.

What is the primary lesson from observing the extensive color variation of Patagonian peregrines? How should we interpret the observation that we only

once saw a white-breasted adult, characteristic of the Patagonian Grassland Biome, breeding in the Patagonian Steppe Biome? How could it be that we never saw even one of the deeply pigmented Andean forest tiercels (Fig. 6b) breeding in the immediately adjacent Patagonian Steppe? These observations strongly suggest that color variants segregate by biome type. Yet, the only races worldwide that are known to do so are island races where gene flow with other races is inhibited by oceans. Future research will determine to what extent Patagonian color variants are restricted to any particular biome/habitat.

ACKNOWLEDGEMENTS

We express our deep appreciation to the various people and organizations that financed and facilitated our travels through the decades. First is the family of Charles de Ganay who loaned us vehicles in 1981 and 2010 and who financed much of our work in 1981, 2009, and 2010. Safari Club International paid travel expenses in 1979. National Geographic Society provided photographic film in various years and travel expenses in 1981. The US Air Force helped finance fieldwork in 1980. We are especially grateful to the Western University of Health Sciences; Fundación de Historia Natural Félix de Azara; I. Tizard, Schubot Exotic Bird Center; Texas A&M University; J. Blanco, Eagle Conservation Alliance; L. Joyner, Lafeber Vet; and Administración de Parques Nacionales for supporting our work with Patagonian raptors between 2008 and 2011 in multiple ways. Others who have hosted and helped include Peter Simpson, the Amorós family, the Peyjavek family, and the many landowners who allowed our passage. Coinvestigators/field assistants through the years include Rich Glinski, Terry Roundy, Bud Anderson, Brian Millsap, Jim Fackler, Isabel Caballero, Ana Trejo, Joan Morrison, Maite Amorós, Santiago Imberti, Agustin Quaglia, and Catherine Ellis (who also helped immensely on manuscript preparation). Pablo Adreani, Gordon Court, Ricardo Ordóñez Henríquez, Roman Montero, Eduardo R. De Lucca, Alan Henry, Roman Montero, Claudio Del Fabro, Agustin Anzoategui, Christian Gonzales, Santiago Imberti, Mark Prostor, and Cristina Wilner have our deep appreciation for sharing their photographs. The Wildlife Secretaries of Rio Negro, Chubut, Santa Cruz, and Tierra del Fuego provinces, Argentina, supported our studies on raptors in Patagonia. Finally, we thank Santiago Imberti, Stella M. Galarza, Mauricio del Valle, Eduardo Pavez, Patricia Capllonch, Isabel Caballero, Alora Nelson, Adrian Giacchino, Sonia Cadierno, Carlos Amorós, and Gastón Peyjavek for supporting our research in various ways. Correspondence with one reviewer, Iñigo Zuberogoitia, helped us refine our thinking on peregrine variation worldwide.

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