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ON THE UNIQUENESS OF COLOR PATTERNS IN RAPTOR FEATHERS

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Abstract.—For this study, I compared sequentially molted feathers for a few captive raptors from year to year and symmetrically matched feathers (left/right pairs) for many raptors to see if color patterns of sequential feather pairs were identical or if symmetrical pairs were mirror-image identical. Feather pairs were found to be identical only when without color pattern (e.g., the all-white rectrices of Bald Eagles [*Haliaeetus leucocephalus*]). Complex patterns were not closely matched, but some simple patterns were sometimes closely matched, although not identical. Previous claims that complex color patterns in feather pairs are fingerprint-identical (and therefore that molted feathers from wild raptors can be used to identify breeding adults from year to year with certainty) were found to be untrue: each feather is unique. Although it is unwise to be certain of bird of origin using normal feathers, abnormal feathers can often be so used.

Key Words: Aquila chrysaetos; *Golden Eagle*; *color pattern*; *feather*; *molt*; *plumage*; *symmetry*.

SOBRE EL CARÁCTER ÚNICO DE LOS PATRONES DE COLOR DE LAS PLUMAS DE LAS RAPACES

Resumen.—En este estudio, comparé plumas mudadas secuencialmente de año a año en algunas rapaces en cautiverio y plumas asociadas simétricamente (pares izquierda/derecha) de varias especies de aves rapaces, para determinar si los patrones de color de pares de plumas secuenciales eran idénticos y si los pares de plumas simétricas eran imágenes especulares. Las plumas de los pares resultaron ser idénticas sólo cuando carecían de patrones de color (e.g., las rectrices completamente blancas de *Haliaeetus leucocephalus*). Los patrones más complejos no coincidieron exactamente, pero algunos patrones más simples sí, aunque no de forma idéntica. Encontré que la aseveración previa de que las plumas pareadas son idénticas como huellas digitales (y, por lo tanto, que las plumas mudadas por las rapaces silvestres pueden usarse para identificar adultos reproductivos año a año con certeza) no es verdadera: cada pluma es única. Aunque es poco recomendable estar seguro acerca de la identidad del ave de la cual se originó una pluma normal, esto sí es frecuentemente posible con plumas anormales.

[Traducción del equipo editorial]

Naturalists, falconers, and aviculturalists have long known that some individual birds can be identified by peculiarities in physical features. The most distinctive birds are those with gross abnormalities (e.g., Seton-Thompson [1898] wrote about White Spot, the American Crow [*Corvus brachyrhynchos*]). Identification of falcons by persistent patterns in toe scales also seems secure (Smith et al. 1993). Much less likely, Dixon (1937) claimed the ability to identify wild female Golden Eagles (*Aquila chrysaetos*) by the peculiarities of color patterns on eggs. Concerning normal plumage, various authors have claimed that it was possible to identify adult Peregrine Falcons (*Falco peregrinus*) at the eyrie from year to year by comparing the amount of light and dark coloration on the head (Nelson 1988; Craig and Enderson 2004), and Rymon (1993) claimed to be able to identify Ospreys (*Pandion haliaetus*) at the nest with certainty by comparing head and body plumage from year to year.

That individual remiges and rectrices of adult raptors are grossly similar in pattern to their replacements in subsequent plumages is self-evident (except where injuries, advanced age, etc., impinge). Also, symmetrically matched feathers are normally much alike, as is consistent with the rules governing bilateral symmetry (see reviews of asymmetry in Neville 1976; Møller and Swaddle 1997).

In recent decades, some authors have further claimed that wild breeding accipiters could be individually identified through the years from molted feathers (Opdam and Müskens 1976). However,

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Table 1. Species examined for feather pattern congruency and showing conspicuous dissimilarity in color patterns for right and left matched pairs of feathers.

SPECIES	*N*	AGE	RESULTS OF COMPARISON
Diurnal raptors			
Oriental Honey-buzzard (*Pernis ptilorhynchus*)	1	Ad	Dissimilar
Northern Harrier (*Circus cyaneus*)	2	Ad, Juv	Dissimilar
Sharp-shinned Hawk (*Accipiter striatus*)	4	Ad	Dissimilar
Cooper's Hawk (*A. cooperii*)	1	Ad	Dissimilar
Northern Goshawk (*A. gentilis*)	1	Ad	Dissimilar
White Hawk (*Leucopternis albicollis*)	1	Ad	Dissimilar
Great Black-Hawk (*Buteogallus urubitinga*)	1	Juv	Very dissimilar
Harris's Hawk (*Parabuteo unicinctus*)	2	Ad, Juv	Dissimilar
Black-chested Buzzard-Eagle (*Geranoaetus melanoleucus*)	1	subAd	Very dissimilar
Red-shouldered Hawk (*Buteo lineatus*)	1	Ad	Dissimilar
Swainson's Hawk (*B. swainsoni*)	1	Ad	Dissimilar
Red-backed Hawk (*B. polyosoma*)	1	Imm	Dissimilar
Red-tailed Hawk (*B. jamaicensis*)	4	Ad, Juv	Dissimilar
Upland Buzzard (*B. hemilasius*)	5	Ad	Dissimilar
Ferruginous Hawk (*B. regalis*)	1	Ad	Dissimilar
Rough-legged Hawk (*B. lagopus*)	4	Ad, Juv	Dissimilar
American Kestrel (*Falco sparverius*)	2	Ad	Dissimilar
Gyrfalcon (*F. rusticolus*)	7	Ad	Dissimilar
Saker Falcon (*F. cherrug*)	2	Ad, Juv	Dissimilar
Owls			
Western Screech-Owl (*Megascops kennicottii*)	1	?	Dissimilar
Great Horned Owl (*Bubo virginianus*)	4	?	Dissimilar
Spotted Eagle-Owl (*B. africanus*)	1	?	Dissimilar
Burrowing Owl (*Athene cunicularia*)	1	?	Dissimilar
Barred Owl (*Strix varia*)	1	?	Dissimilar
Non-raptors			
Ruffed Grouse (*Bonasa umbellus*)	2	Ad	Dissimilar
Whimbrel (*Numenius phaeopus*)	1	Juv	Dissimilar
Common Poorwill (*Phalaenoptilus nuttallii*)	4	?	Dissimilar
Red-naped Sapsucker (*Sphyrapicus nuchalis*)	2	?	Dissimilar
Cactus Wren (*Campylorhynchus brunneicapillus*)	1	?	Dissimilar
Rock Wren (*Salpinctes obsoletus*)	1	?	Dissimilar

Table 2. Species showing extreme similarity, but not congruence in color patterns for right and left matched pairs of feathers. For each species, color patterns were not complex.

SPECIES	*N*	AGE	RESULTS OF COMPARISON
Diurnal raptors			
Osprey (*Pandion haliaetus*)	1	?	Similar
Gabar Goshawk (*Melierax gabar*)	1	?	Similar
Bald Eagle (*Haliaeetus leucocephalus*)	1	Ad	No pattern
American Kestrel (*Falco sparverius*)	1	Ad	Similar
Merlin (*F. columbarius*)	1	Ad	Similar
Non-raptors			
Mourning Dove (*Zenaida macroura*)	1	Ad	Very similar
Long-tailed Meadowlark (*Sturnella loyca*)	1	?	Very similar

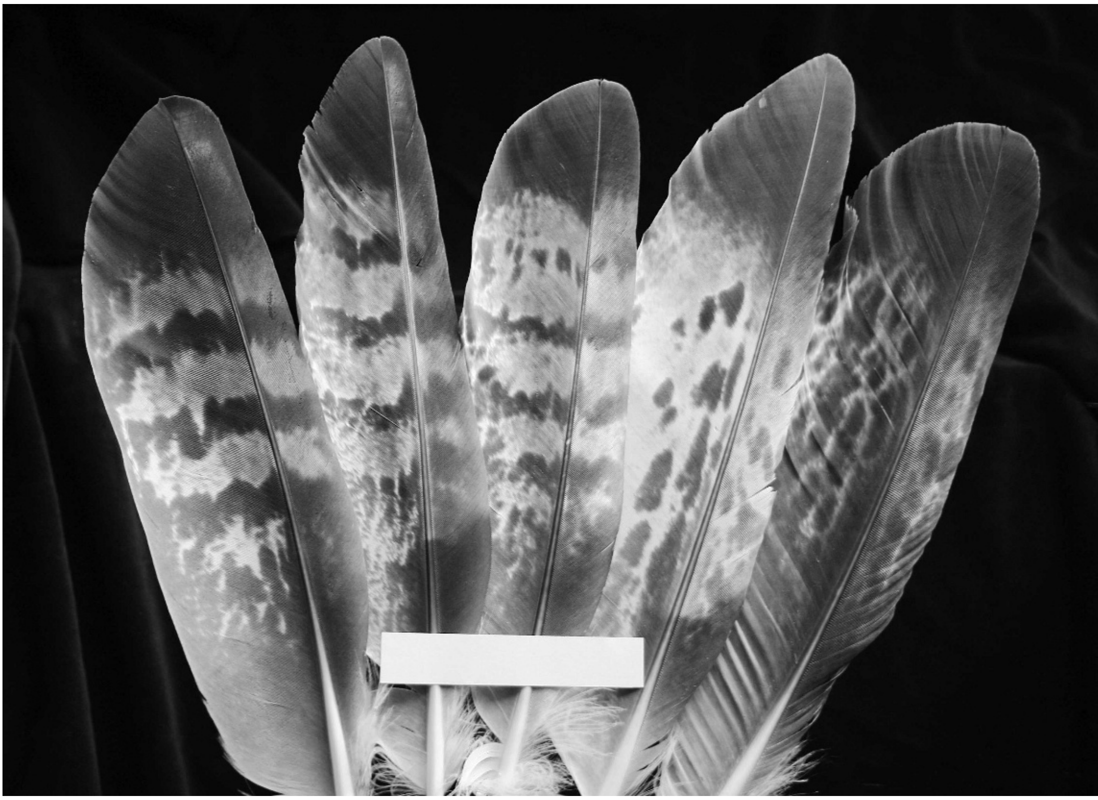

Figure 1. Wide variation in color pattern is common in primaries from adult Golden Eagles. All are molted from birds on territory, left to right: L2 (northwestern Siberia), L3 (Scotland), L1 (Scotland), L3 (northeastern Siberia), L1 (central Mongolia). (Bar is 10 cm long.)

they interjected a caution that ''small differences in feathers of subsequent moults may occur.'' Ziesemer (1983) used year-to-year consistency in feather patterns to identify Goshawks (*Accipiter gentilis*) at the nest. Bortolotti and Honeyman (1985) identified some Bald Eagles (*Haliaeetus leucocephalus*) by spotting on otherwise immaculate feathers. Newton (1986) claimed that the details of feather patterns from year to year ''gave a means of identification analagous to human fingerprints.'' He also asserted that ''any particular feather in one wing had the same pattern as its counterpart in the other wing.'' More recently, Struwe-Juhl and Schmidt (2002) used feather length and rectrix color pattern to identify individual breeding White-tailed Eagles (*H. albicilla*) from year to year within a small local population. They cautioned, however, that closely related females had similar color patterns, thus limiting usefulness of the technique. It is noteworthy that, in the feather series illustrating all of the above studies, no sequential feathers were identical.

In those studies, researchers suggest that feather pattern identification could be useful for other species having complex color patterns. The implication is that it would be more difficult to use the technique on feathers with very simple patterns (e.g., it would serve poorly for the black and white rectrices of adult Pallas's Fish-Eagles [*H. leucoryphus*] and be totally useless for the all-white rectrices of adult Bald Eagles). Conversely, it should work best for species with the most complex patterns, such as the Golden Eagle.

In this study, I focus on melanin-based patterns (Roulin et al. 2008) easily visible to humans. For an expanded review of the influence of color on sexual selection see Hill and McGraw (2006a, 2006b). Color saturation of individual feathers not only varies between individuals but is also condition dependent

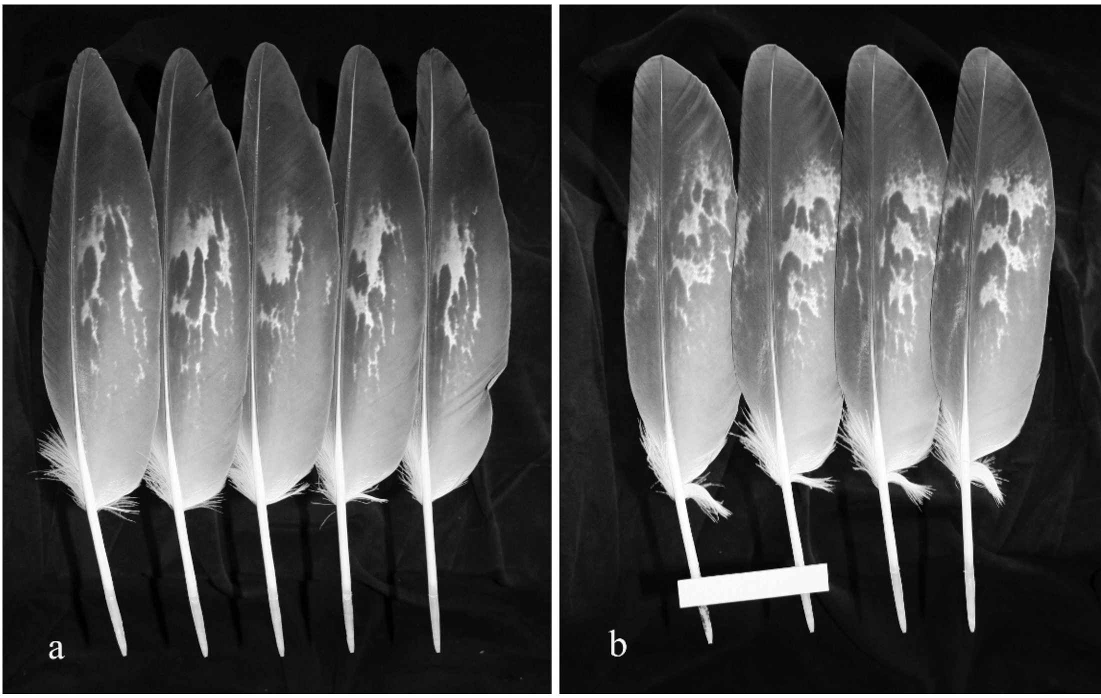

Figure 2. Sequential series of adult Golden Eagle primaries. All are from a captive female from Montana. (a) R4, molt year (from left to right) was 1987, 1989, 1991, 1993, and 1995. (b) R2, molt year (from left to right) was 1999, 1995, 1993, 1989. All patterns are unique. (Bar is 10 cm long: a and b are not to the same scale.)

(Wiebe and Bortolotti 2002), so caution must be employed in plumage comparisons.

Here, I examine seven questions. First, for normal feathers: (1) Are the color patterns produced by the corresponding follicles by all birds in a population unique? (2) Is the color pattern produced by one follicle for an individual adult bird identical from year to year? (3) Are symmetrical pairs of feathers on the wing and tail of an individual mirror image identical? (4) If color patterns are not identical but only similar, can we be certain that one bird produced any two feathers?

Second, for two types of abnormal feathers: (5) Are color patterns in abnormally pigmented feathers identical from year to year? (6) Are misshapen feathers identical from year to year? (7) If abnormal feathers are not identical from year to year, can we be certain that they are from the same bird?

For perfect surety in identification of individual birds by color patterns in normal feathers produced by the same follicle in succeeding generations, two conditions must be met: first, no two individuals in a population can have identical feather patterns. Second, the pattern in a feather produced one year must be identical to the pattern in succeeding years. Only if both conditions are met, can an observer state positively that two feathers were from the same bird.

METHODS

I collected feathers from a female Golden Eagle held in captivity long term, beginning when it was ca. 24 yr old and concluding at its death around age 44 yr. Details of the eagle's handling are in Ellis and Kéry (2004). I also collected feathers from a second captive Golden Eagle over a 3-yr period, beginning when the bird was in juvenile plumage. Molted feathers from three captive adult Peregrine Falcons (two females, one male) were also used, but only for 4 yr each. Feathers from many other raptors (and a few non-raptors) were also inspected for this study (Table 1, 2).

For this study, I considered that identical feathers have bars, streaks, dots, and spots that match in size, shape, and location. In the ornithological literature, bars are broad, dark lines roughly perpendicular to the rachis (Fig. 1, left three remiges are barred). Streaks parallel the rachis as exemplified in the

Figure 3. Long-term variation in adult Golden Eagle rectrices. (a) L1 molted (left to right) in 1988, 1989, 1991, 1993, and 2002. (b) R2 molted (left to right) in 1989, 1993, 1995, and 1999. Although each feather is clearly unique, the rightmost feather at each locus is divergent from the general pattern. (Not to scale.)

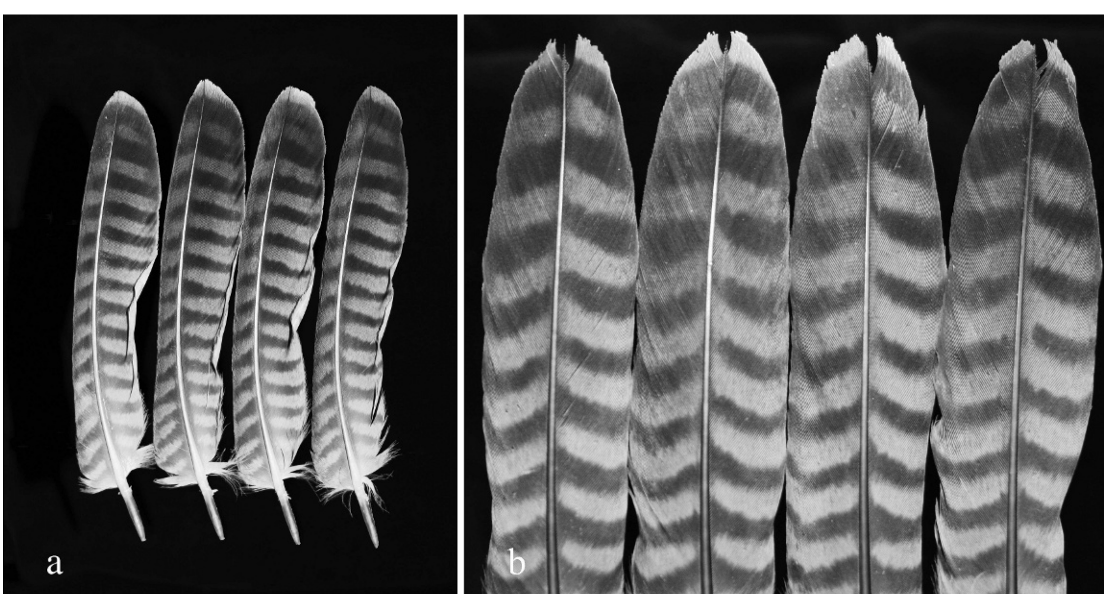

Figure 4. Sequential series of rectrices from an adult male Peregrine Falcon. Feathers in each series show general similarity, but note that even gross features vary through time. For example, (a) the number of transverse bars changes on the outer web of rectrix R6 (from left to right, 1982 [15 bars], 1983 [15], 1984 [14], and 1985 [14½]), and (b) the fifth dark bar from the tip through time became non-continuous to the rachis on rectrix R1 (from left to right, 1982, 1983, 1984, and 1985). Also, subtle details of the width and outline of each bar in each photograph are different from year to year. (Not to scale.)

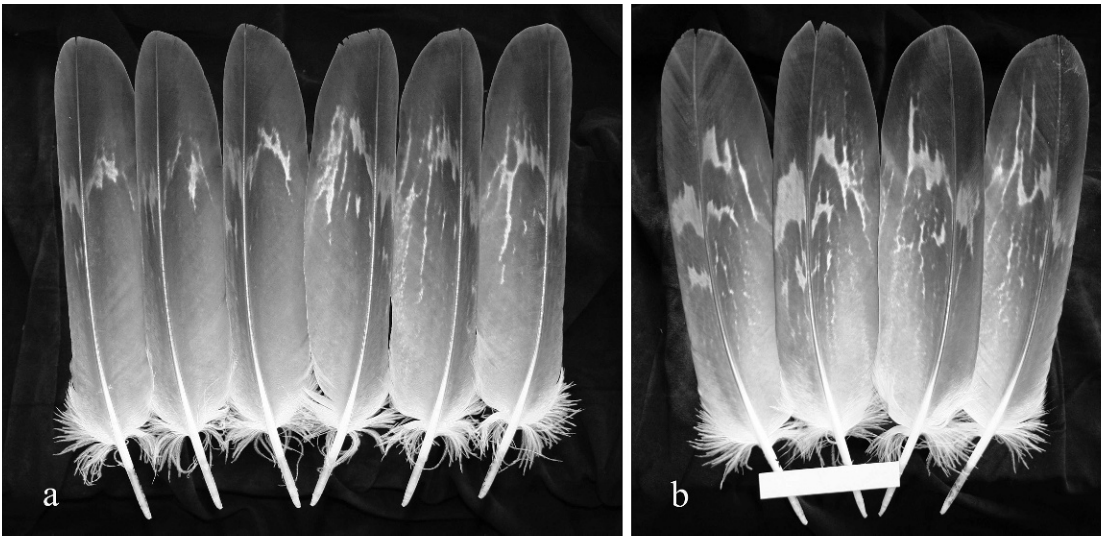

Figure 5. Symmetrical pairs and sequential series of rectrices from an adult female Golden Eagle. (a) L6 and R6: (from left to right) molt year 1991, 1989, 1987, 1987, 1989, and 1991. (b) L5 and R5 rectrices: (left to right) molt year 1996, 1992, 1992, and 1996. Differences in color pattern between left and right are so great, especially for L6 and R6, that such feathers, if collected in the wild, would likely lead to the conclusion that two birds had produced them. (Bar is 10 cm: a and b are not to same scale.)

marks closest to the rachis on the inner web of the feather second from right. Dots (smaller) and spots are round, are usually darker than the background color, and can best be seen in the right two feathers in Fig. 1. Blotches are irregularly shaped large marks. Blotches and streaks intergrade on the inner webs of the right two feathers in Fig. 1. Variation in color saturation due to fraying, bleaching, condition-dependent growth, soiling, and fault bars were not considered.

Feathers from the same follicle in different years are hereafter referred to as ''sequential pairs'' (or ''sequential series'' if consisting of three or more feathers). Feathers from matched follicles on opposite sides of the body are here termed ''symmetrical pairs'' (or ''symmetrical series'' if three or more). ''Feather pairs'' refers to either or both. Consistent with standard practice, rectrices are numbered from the center (L1 and R1) outward. Primary remiges are numbered from the wrist outward (the most distal are L10 and R10); secondaries from the wrist inward (the most distal are L1 and R1).

Comparisons of symmetrical pairs of feathers using museum specimens were difficult (because the wings and tail are typically folded) except for outer primaries and outer and central rectrices. No attempt was made to quantify or codify color pattern differences. Rather, I present numerous photos to illustrate coloration trends.

Because of the need to photograph feathers separate from the bird, most of the photographs that accompany this text were, except for molted feathers from the two eagles and three falcons, taken from feather bag series from museum specimens or from feathers plucked from dead birds. Most photos were taken in the shade, above a black velvet background, with digital cameras, and in flash/portrait mode.

RESULTS AND DISCUSSION

I addressed questions of identification by feather patterns most completely using Golden Eagles. In the darkest individuals, light areas in wing (Fig. 1: rightmost feather) and tail (Ellis and Lish 2006:6) are restricted. In pale individuals, light areas in some feathers are much more extensive than dark (Fig. 1: second from right). Some adults show evenly sized and evenly spaced barring (Fig. 1: left two feathers), whereas in others, barring is replaced by blotches and/or streaks (Fig. 1: right two feathers), or even variegation/vermiculation (Fig. 1: seen most clearly in the pale zone on the basal half of the inner web of second feather from left).

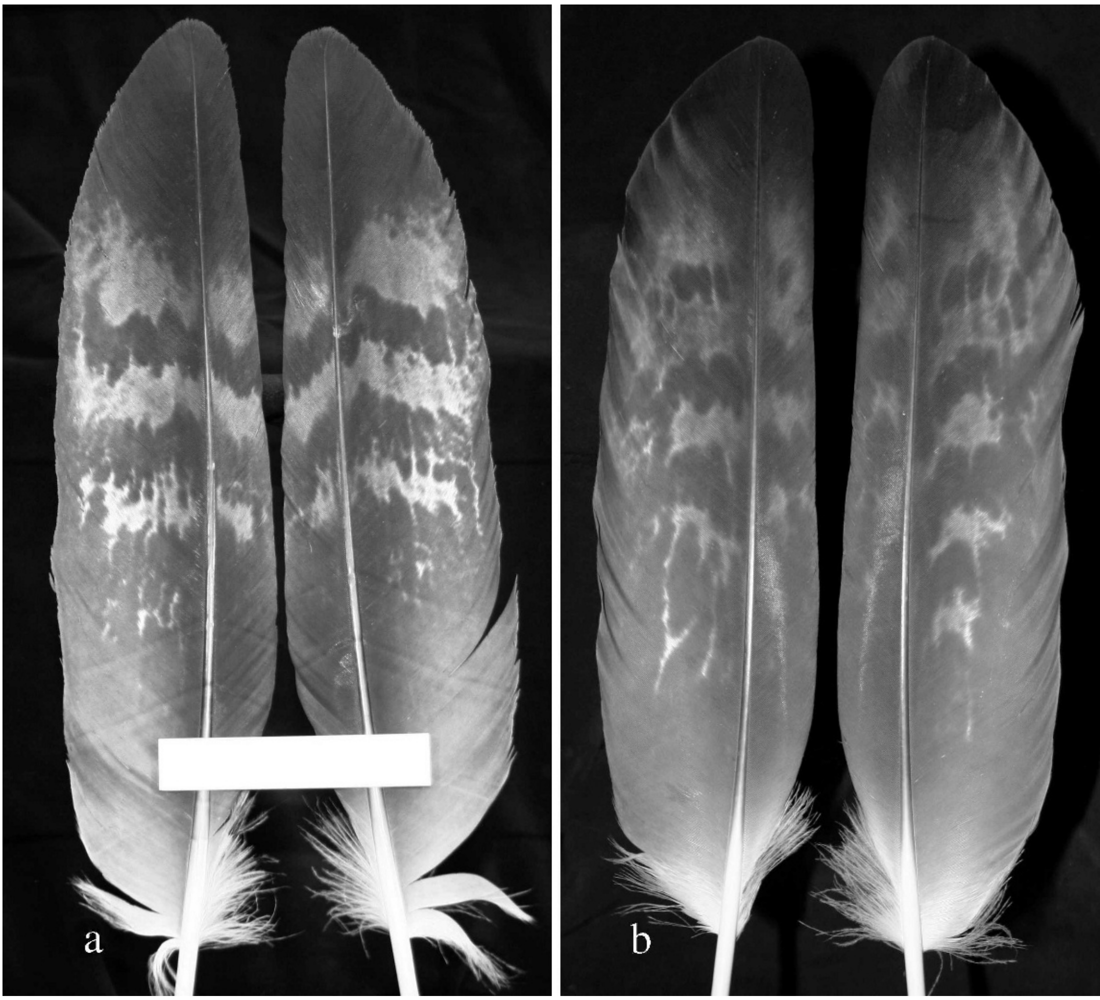

Figure 6. Closely matching symmetrical pairs of molted primaries (scale varies) from two Golden Eagles: (a) L3 and R3 molted by a wild breeding adult female from western Mongolia, an extreme example (at least for complex patterns) of mirror-image similarity. (Bar is 10 cm long.) (b) Third generation primaries L2 and R2 from a captive female from Montana (not the same bird as in other figures) show only general similarity in pattern.

Differences in Color Patterns in Sequential Feathers. In Figure 2, feathers selected from sequential series of Golden Eagle primaries, representing two loci, show general similarity, but each individual feather pattern is clearly unique. Further, two loci for the tail also differ greatly (Fig. 3). Some feathers are sufficiently different from others in their series (e.g., the primaries on the far left in Fig. 2 and the rectrices on the far right in Fig. 3) that if found in the wild it would be easy to conclude that they came from different eagles.

In a species with regular barring, a Peregrine Falcon (Fig. 4), color patterns are grossly similar. However, on closer inspection, even coarse features such as the number and width of the dark bars on the outer web at rectrice R6 (Fig. 4a) vary from year to year. The offset in spacing of the bars on the inner and outer webs also changes through time. Fine details of the boundaries between light and dark bars are everywhere different from year to year.

In Figure 4b, there is a temporal trend toward interruption of the fifth bar (from the tip) on the inner web. In the 1982 R1 (a first-generation adult

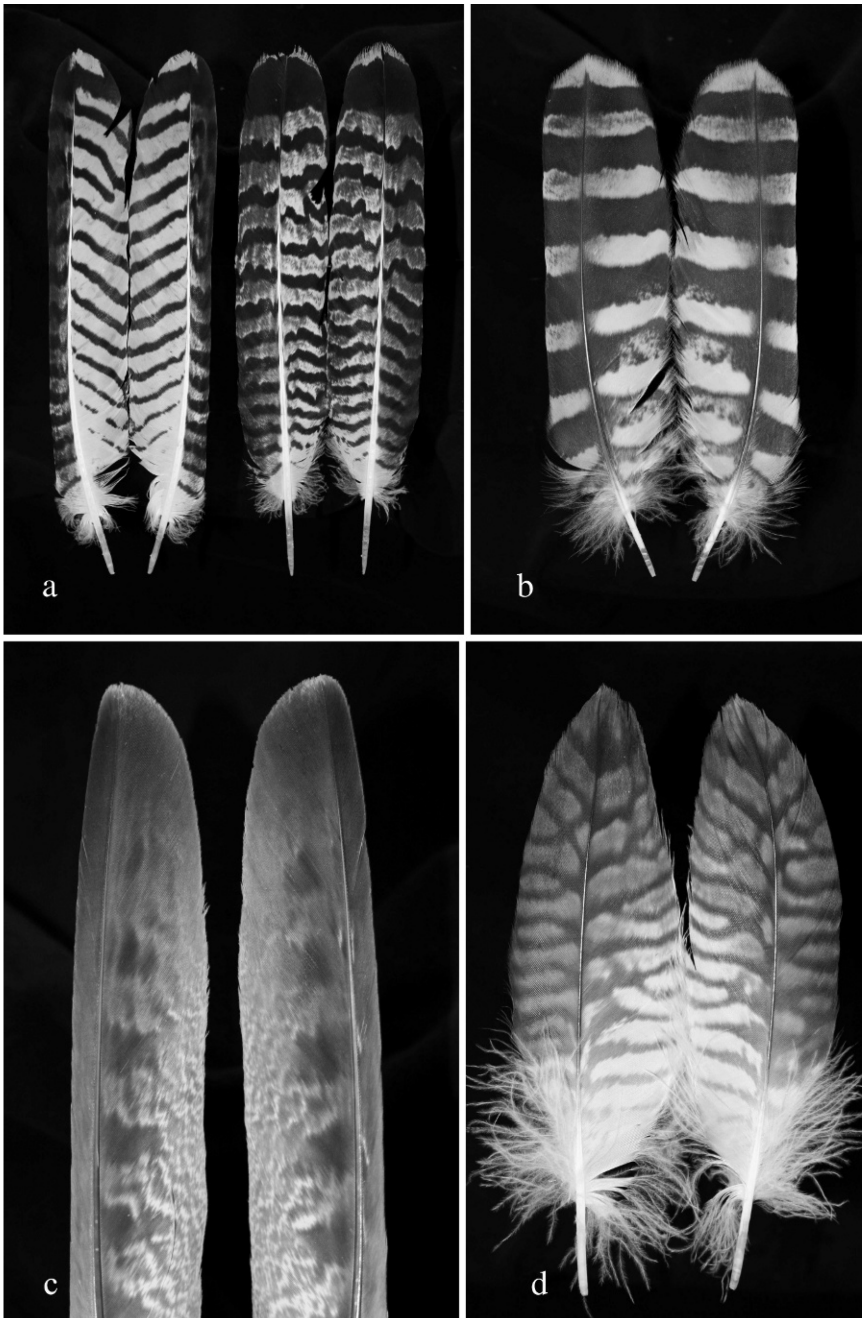

Figure 7. Rectrices from four species (scale varies) show a broad spectrum of variability between symmetrical pairs. (a) Rectrices L6 and R6 and L1 and R1 from a juvenile Great Black-Hawk (*Buteogallus urubitinga*; shot in Guatemala) show that complex, bold patterns are only generally similar, with great differences evident in boundaries of bars. (b) These Spotted Eagle-Owl (*Bubo africanus*; roadkill from South Africa) rectrices show that relatively simple patterns can be closely matched. Note, however, that on the inner webs of the basal four bars, the patterns become complex and divergent. (c) Rectrices L6 and R6 from a Northern Goshawk (*Accipiter gentilis*; North America, no data). (d) Perhaps the rarest of all

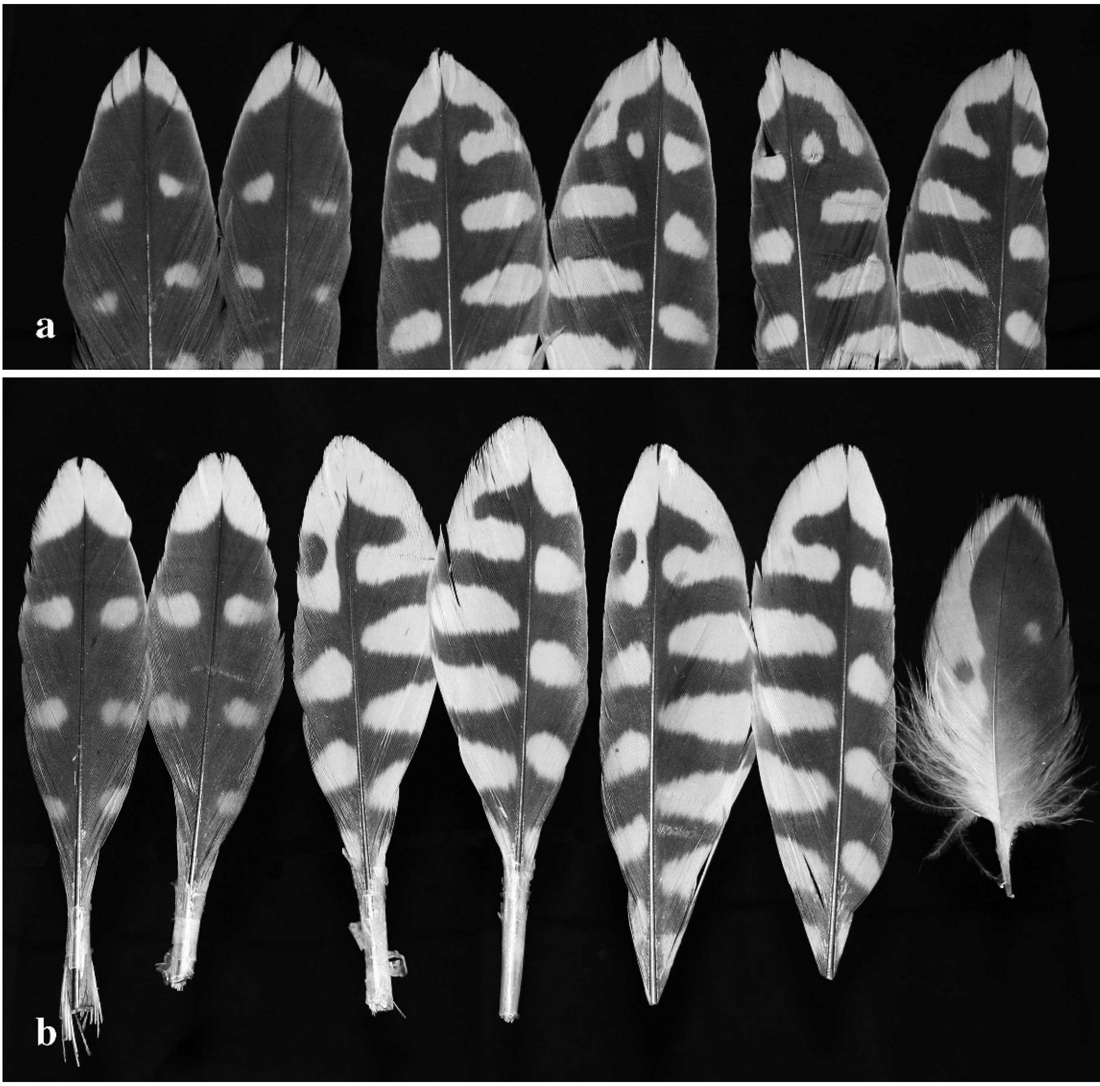

Figure 8. Symmetrical pairs from the tails of two juvenile Saker Falcons (*Falco cherrug*; both from Mongolia) show that considerable divergence is the norm even in simple patterns. (a) Note that matching dots on centrals (left pair in a and b) vary greatly in size and shape. Proceeding right, both pairs have a pale dot on one feather which is unmatched on its mate. (b) Here, dark dots on some feathers are bars on their mates. The covert (rightmost feather) illustrates pattern reversal in light and dark zones. (Not to scale.)

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patterns, anastomosing dark bars, is exemplified by these matched tertiaries from an immature Red-backed Hawk (southern Patagonia, Argentina, roadkill or shot). Patterns in a, c, and d are extremely complex, generally similar, but with extreme divergence in detail.

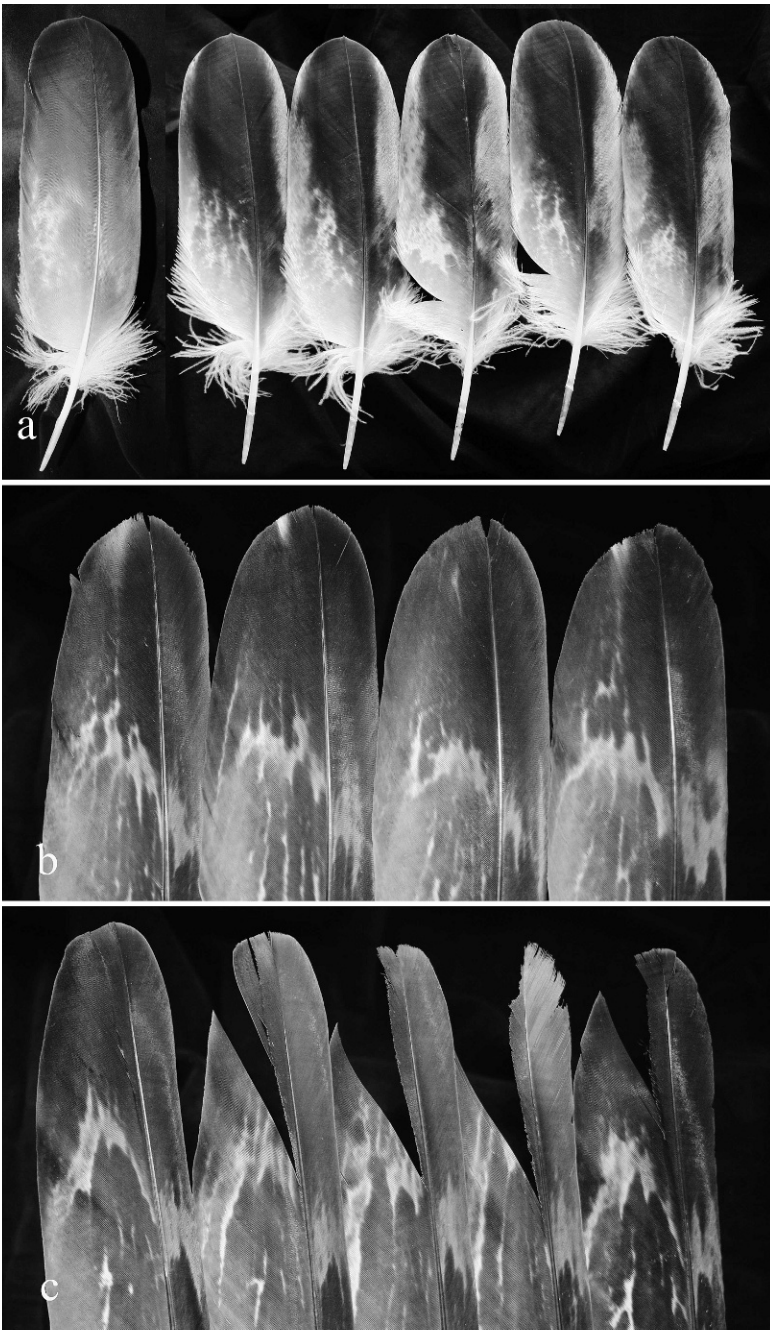

Figure 9. Three abnormalities in Golden Eagle flight feathers. (a) Grossly aberrant color patterns in secondary L11. The left-most feather is a normal secondary from a different locus on the same eagle. The pale feathers (from left to right) were molted in 1993, 1995, 1998, 2001, and 2003. The dark blotching in the basal zones on the inner webs is more variable through time than seen in normal feathers. (b) This minor aberration, a pale-to-white spot at or near the tip of rectrix L5 changed greatly in size, color saturation, and even location through time. Molt years are (left to right) 1986, 1994, 1998, and 1999. (c) A gross physical abnormality of rectrix L6 first appeared as a few weakened barbs in 1993. The ''cut'' spread over half of the inner web in 1995, then continued to be conspicuous thereafter. Molt dates (left to right)

Figure 10. Closely matched patterns in left/right symmetrical pairs with relatively simple color patterns for three species of raptors. (a) Sharp-shinned Hawk (*Accipiter striatus*; U.S.A., no data) primaries L8 and R8 show general symmetry, but fine details are everywhere not mirror-image congruent. (b) Central rectrices of a Burrowing Owl (*Athene cunicularia*; roadkill, Utah) show great similarity, but on closer inspection, pale dots are divergent in shape, size, and location. (c) Rectrices R5 and L5 for an adult male American Kestrel (roadkill, Nevada) show great left/right symmetry, perhaps as much as for any raptor, but note that even in this extremely simple pattern, the subtle details are everywhere only approximately matched. (Not to scale.)

feather), the bar is continuous to the rachis; year by year there is a graded transition until 1985, when this bar stops short of the rachis. Lesser differences for other features are also readily visible.

Differences in Mirror-image Color Patterns of Symmetrical Feathers. Figure 5 illustrates these differences for a Golden Eagle at two tail loci. In Figure 6, two wing loci are shown. In none of the comparisons are patterns of matched feathers even approximately congruent. In Figure 5a, it could easily be concluded that each of the left feathers came from a different bird than those from the right side of the tail.

Two pairs of eagle primaries in Figure 6 show great similarity in general pattern, but fine details at the borders between light and dark areas differ. Differences are great enough in Figure 6b that it would be easy to conclude that the feathers came from different birds.

Comparisons for non-eagles (Fig. 7, 8) illustrate the same general trends: symmetrical pairs are often very similar but not identical. Extremely complex patterns are less closely matched in symmetrical pairs (Fig. 7a, 7c, 7d). The owl feathers (Fig. 7b) have relatively simple patterns that are more alike

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are 1995, 1997, 1999, 2001, and 2002. Feathers with such abnormalities as in a and c, if found molted through the years, would lead to the certain conclusion that all came from one bird; not so the abnormality in b. (Not to scale.)

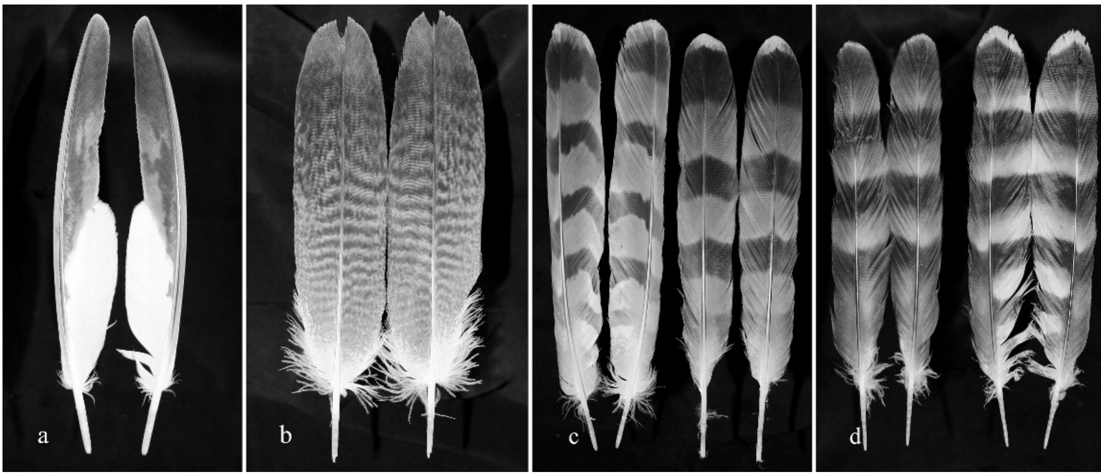

Figure 11. Left/right asymmetry in simple to complex color patterns in four raptors. (a) The very dark patterns in the gray zones of primaries L1 and R1 are not even closely matched on this adult male Northern Harrier (*Circus cyaneus*; roadkill, Wyoming). (b) Pale zones can be washed and/or flecked and dark bars can be multiplied in number but reduced in width as seen on the rectrices (L1 and R1) of this subadult Black-chested Buzzard-Eagle (Patagonia, Argentina, no other data). (c) Two symmetrical pairs of rectrices (L5 and R5 [at left] and L1 and R1: Cooper's Hawk [*A. cooperii*] roadkill, Maryland) illustrate that some feather pairs (L1 and R1) closely match while others (L5 and R5) are divergent. (d) Symmetrical pairs (L1 and R1, and L3 and R3) from a Gabar Goshawk (South Africa, roadkill) are probably as closely matched as for any other conspicuously patterned raptor. Comparisons between c and d show that patterns with diffuse boundaries are more difficult to distinguish and therefore easier to claim as mirror-image identical. Inasmuch as central rectrices are very alike on both species, lateral rectrices provide a better choice when searching for distinguishing marks for either species. (Not to scale.)

than feather pairs with complex patterns, but even for the owl, the patterns are not mirror-image identical. The relatively simple patterns of juvenile Saker Falcon (F. *cherrug*) rectrices (Fig. 8) are clearly divergent when symmetrical pairs are compared. In five comparisons, a spot on one feather is matched with a bar on its mate.

Differences in Abnormally Pigmented or Deformed Feathers. Sequential series for three feather loci (Fig. 9) from the same captive adult female Golden Eagle show that aberrant feathers are also each unique. However, the abnormal secondaries (Fig. 9a) are so different from normal feathers that it would be possible to state with near-absolute certainty that each feather is from the same eagle even if the feathers were found in the wild.

Figure 9b demonstrates a caveat: less severe color abnormalities, such as the pale-to-white spot at the tip of rectrix L5, can transform, disappear, and even reappear from year to year. Such variability would provide unconvincing evidence for identification of the bird if the feathers were collected in the field.

The third abnormality, a physical flaw on the inner web of rectrix L6 (Fig. 9c), resulted in a weakness in all barbs on the distal portion of the inner vane severe enough to sometimes result in portions of the vane falling free. Finding a series of feathers with this or a similarly severe abnormality would provide convincing evidence of identity.

Overview of Color Pattern Comparisons. Preliminary observations (above) from a few species may be further refined by examining symmetric pairs from a broader array of species (Fig. 10, 11, 12). In addition, 24 species of Falconiformes, five owls, and eight non-raptors were evaluated (Table 1, 2). Although differences within feather pairs were evident for all, the patterns for the male American Kestrel (*Falco sparverius*; Fig. 10c) and for two small accipiters (Fig. 11c R1 and L1; Fig. 11d) are very alike. From the Gabar Goshawk (*Melierax gabar*) feathers (Fig. 11d), it is easy to see how Newton (1986) could conclude that symmetrically matched feathers were mirror-image identical. However, that species exhibits simple bars with diffuse boundaries between light and dark areas, whereas feathers from

Table 3. Trends in color pattern congruency/similarity in sequential pairs and symmetrical pairs of feathers of raptorial birds.

Axiom	Sub-axiom	Reference Figures
1. Simple patterns are often closely duplicated.		
	a. Straight or smoothly curving boundaries can be approximately duplicated	4, 10c, 11c, 11d, 12a
	b. Diffuse and low-contrast boundaries are often closely duplicated	11c (L1 and Rl), 11d
	c. Centers of uniformly pigmented areas are commonly closely duplicated	All figures
	d. Peculiarities in shape of small spots, blotches, and bars are often perpetuated but not exactly matched	8, 10b, 10c
2. Extremely complex patterns are not closely duplicated.		
	a. Complex boundaries of uniformly pigmented areas are not closely duplicated	7, 10a, 11a, 11c (L6 and R6), 12b
	b. Sharply contrasting boundaries are not closely duplicated	10a, 11c (L6 and R6)
	c. Extensive patches of vermiculation, flecks, or spots are often very similar in general value and hue, but the size, shape, and distribution of dark marks are not closely matched	3b, 7c, 12c
	d. Narrow, tortuous boundaries are not closely duplicated	6a, 7c, 10a
	e. Narrow, tortuous bars are not closely duplicated	7a, 7c, 11b, 12b
3. For abnormally pigmented feathers, variability in color pattern is greater than for normal feathers.		9

species with complex patterns and sharp boundaries are clearly unique (Fig. 10a).

Some additional generalizations are: first, broad zones with uniform pigmentation (e.g., Fig. 11c, 11d) on one feather are closely matched on its symmetric mate. Second, boundary lines where pale and dark zones meet are, if jagged, poorly matched (Fig. 10a, 11a). However, straight and smoothly curving boundaries are often closely approximated in paired feathers (Fig. 11c, L1 and R1), especially when the boundaries between light and dark zones are diffuse and/or have little contrast (Fig. 11d). Where boundaries are distinct, they are more visibly different in shape (Fig. 7a, 8, 10a).

Third, dark markings in extensive pale zones (Fig. 7c, 12a) are not closely matched (Table 3, Axiom 2c) even though the general appearance of the zones under comparison are typically very alike in hue and brightness. For all species inspected so far (raptor and non-raptor) which have very narrow, tortuous, transverse bars (Fig. 12b), such bars are widely disparate in matched pairs (Table 3, Axiom 2e).

Applying the principles of Ancestral-state Reconstruction (Cunningham et al. 1998, Cunningham 1999), the ancestral color pattern for the wings and tails of raptorial birds consisted of alternating bands of broad uniformly dark bars and broad uniformly light bars (e.g., Fig. 4, 7b, 8, 11c, 11d). It appears that the amount of difference between paired feathers is generally proportional to the degree to which the species' feather pattern has diverged from the juvenile or ancestral pattern. Good examples are seen in Figures 3b, 7c, 7d, 11a, 11b. Exceptions to this rule include species with extreme pattern reduction for purposes of social signaling (e.g., the Bald Eagle [solid white tail] and the adult Black-chested Buzzard-Eagle [*Geranoaetus melanoleucus*; solid black tail]).

Deviation from the ancestral form can take several directions. Light bars may be flecked with dark as in Figures 11b and 12c. Bars may be replaced by streaks as seen to a small degree in the right feather in Figure 12c (also Fig. 1, 3, 5). Bars may be narrowed and multiplied as in the subadult Black-chested Buzzard-Eagle (Fig. 11b). Bars can be widened and reduced in number, as in many species of raptors for which tail pattern signals age, status, or gender (Fig. 12a). Extreme deviation from the coarsely barred pattern can yield vermiculation as in some feathers of the Great Horned Owl (*Bubo virginianus*; Fig. 12d) and many caprimulgids, or anastomosing dark bars as in the Red-backed Hawk (*Buteo polyosoma*; Fig. 7d).

Positive Identification of Individual Birds. Although most individual raptors cannot be identified with certainty from color patterns in normal feathers, under some circumstances, individual birds can be identified even in the wild. The pale secondary remige in Figure 9a could be diagnostic, and an adult female Golden Eagle in Montana (see Ellis 1979:43) was readily identifiable long-term, even

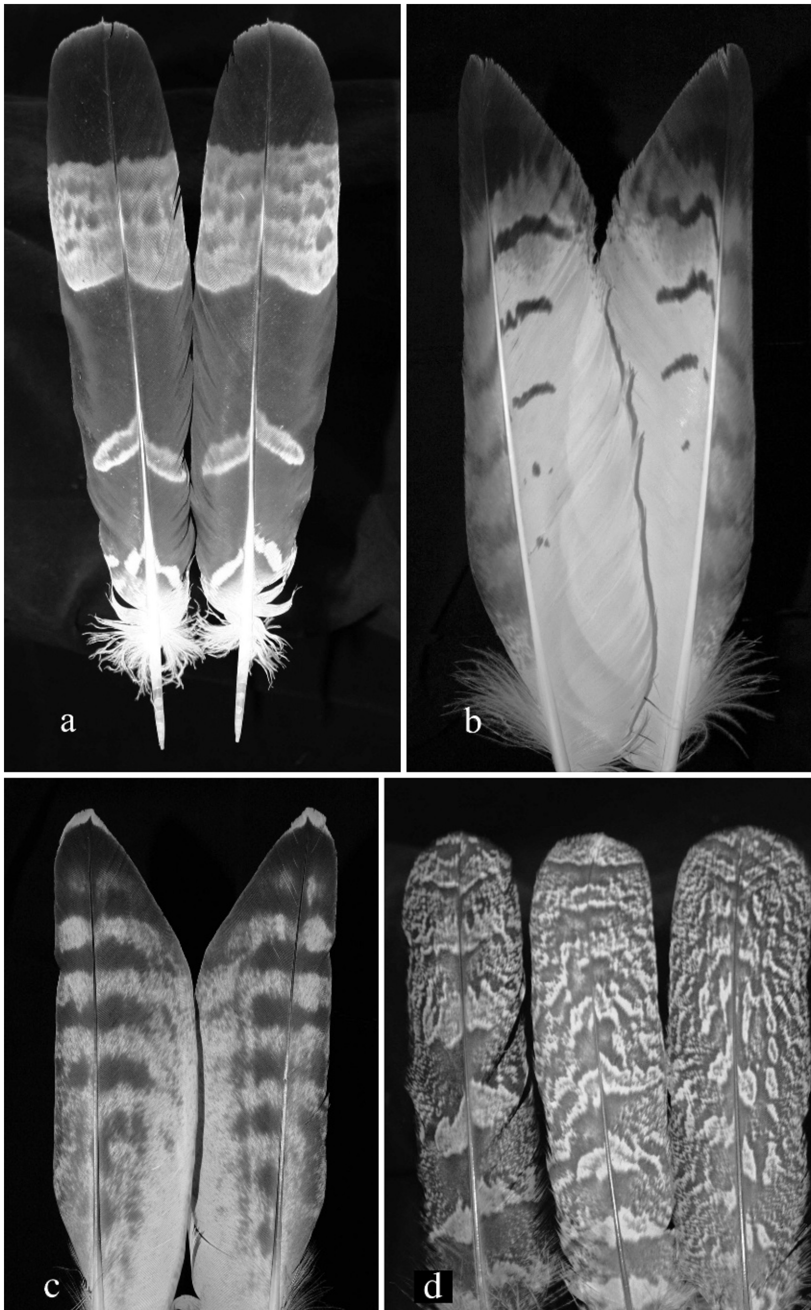

Figure 12. Departure from the ''ancestral pattern'' of broad, light and dark, alternating, transverse bars. (a) As for many raptors with broad pale zones in the tail, the pale areas in these central rectrices of the Oriental Honey-buzzard (*Pernis ptilorhynchus*; southeastern Mongolia, mammalian predation) are marked with indistinct spots, blotches, and bars. The general patterns thus created are often very similar, but details are poorly duplicated side to side. (b) Details of the very narrow bars on this symmetrical pair of primaries (L3 and R3) in the Upland Buzzard (*B. hemilasius*; central Mongolia, electrocution) are very different. (c) Pale zones can be flecked with dark and dark bars can become interrupted and transformed into streaks as in these primaries (L3 and R3, Gyrfalcon [*F. rusticolus*], molted from a captive

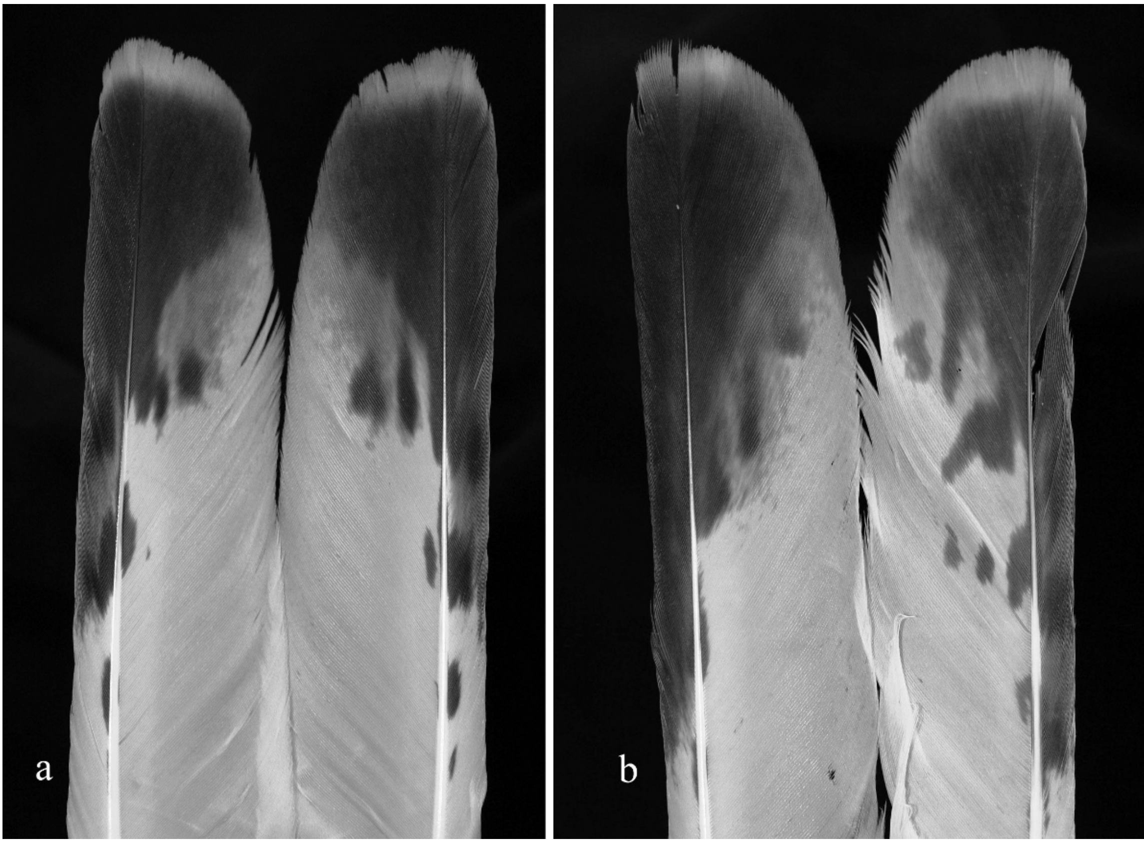

Figure 13. Rectrices (L6 and R6) from three Rough-legged Hawks (*B. lagopus*; U.S.A., no other data) illustrate the difficulties inherent in deciding bird of origin. (a) A symmetrical pair. (b) Feathers from two other hawks from a sample of only three birds of the same age, color morph, and sex class. If a feather in ''a'' was matched with a feather in ''b,'' would we be certain that they came from different birds? If feathers so similar can be found when only three birds are compared, how many even more similar matches can be found if many birds are compared? And if feathers from different birds so closely match, is it prudent to claim that any two feathers come from one bird? (Not to scale.)

in flight and often at great distances, because she had two adjacent rectrices permanently missing (R4 and R5). When the tail was fanned, R6 flared far beyond the normal position. Other abnormalities in other birds may be just as diagnostic.

A second method that could be used to identify an individual with certainty from year to year requires that the molt be incomplete (as in the Golden Eagle) or that the bird be photographed periodically through the molt. If an eagle were photographed with enough detail in one year and then rephotographed the following year, many of the exact same feathers (albeit more faded and worn) would be present and therefore the bird would be identifiable with certainty in the subsequent year (or in some cases years). Note, however, that this conclusion depends on each feather being unique.

Conclusions. From the many comparisons, three primary generalizations emerge. First, complex patterns are not identical for either sequential feathers

←

bird). (d) Strigid owls (rectrices L1 or R1 from Great Horned Owls, U.S.A.) and nightjars (Caprimulgidae) have some of the most complex color patterns in the bird world. Here dark and light bars are broken into streaks, dots, tortuous lines, and even vermiculation. (Not to scale.)

or symmetrical pairs. Second, simple patterns are more closely duplicated than complex patterns. Third, grossly abnormal feathers, while not identical from year to year, can be safely used to identify an individual. These generalizations, although true for the species so far studied and likely true for all species, must be considered tentative until each species of raptor is evaluated.

In closing, the hypothesis that individual raptors can be identified from year to year by normal feather patterns required that two conditions be met: (1) that feather pairs be identical and (2) that all individuals in a population differ. I found instead, for species with complex patterns and therefore great potential interindividual variation, that paired feathers were not identical (thus the first condition was not met). For species with simple patterns and therefore much less interindividual variation, there is greater similarity between feathers but also greater likelihood that another individual in the population has similar feathers (Fig. 13). Because of both conditions, certainty of identification is not possible.

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