THE CRYPTIC OCCIPITAL SPOT IN THE ACCIPITRIDAE (FALCONIFORMES)

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ABSTRACT.—The heretofore undescribed cryptic white occipital spot is shown to be a conservative familial trait of the accipitrid Falconiformes. Excluding the "naked-headed" vultures and the pale-headed forms, only two genera of the 55 accipitrids surveyed (*Pithecophaga* and *Harpyopsis*) were found to lack the triangular occipital spot. Differential spot trends occur in the New and Old World Accipitridae and variation in the spot is detailed. The spot while functioning as an appeasement signal also serves to inhibit an adversary behaviorally during agonistic encounters. An additional deflective function is suggested to constitute an antipredatory mechanism. Taxonomic and systematic aspects pertaining to the occipital spot are discussed.—*Department of Biological Sciences and The Museum, Texas Tech University, Lubbock, Texas 79409, and Moore Laboratory of Zoology, Occidental College, Los Angeles, California 90041. Present address of both authors: Museum of Vertebrate Zoology, University of California, Berkeley, California 94720.* Accepted 1 October 1975.

SEVERAL years ago we noted a cryptic white spot in the capital tract of a captive Red-tailed Hawk (*Buteo jamaicensis*). Although there have been ptilological studies of many falconiform birds (Chandler 1914, Compton 1938), a search of the literature uncovered only a few brief statements regarding nape or occiput feathers with white bases (e.g. Friedmann 1950: 167; Brown and Amadon 1968: 39). Our initial observation prompted further investigation, culminating in this review of the occurrence of a concealed white spot in raptorial birds and a discussion of its behavioral and taxonomic significance.

We examined both living and museum specimens of 65 genera representing the five families in the order Falconiformes to assess the occurrence and general morphology of the spot. Because of similarities between the falconiform and strigiform birds, we also examined representatives of several genera of owls for presence of this character.[1] It was soon evident that the cryptic white occipital spot occurs only in the Accipitridae.

DESCRIPTION OF THE OCCIPITAL SPOT

The typical accipitrid spot lies in the occipital region of the capital tract and is approximately triangular in shape (Fig. 1). The spot is composed of numerous bicolored contour feathers. The basal two-thirds of a spot feather is snow-white; the distal portion is often slightly darker and longer than surrounding cephalic feathers. The terminal darkening of the feathers appears to accentuate the whiteness of the basal portion during crest erection and conceals the white when the cephalic feathers are in the normal relaxed position (Fig. 2). A clear demarcation occurs between the white bases of spot feathers and the darker bases of nonspot feathers (Fig. 3). The microscopic structure of the feathers comprising the spot shows no differentiation from that of the general cephalic contour feathers. The relative size and general

[1] *Non-accipitrid species examined.*—Cathartidae: *Cathartes aura*, and *Sarcoramphus papa*; Pandionidae: *Pandion haliaetus*; Sagittariidae: *Sagittarius serpentarius*; Falconidae: *Daptrius americanus*, *Phalcoboenus megalopterus, Polyborus plancus, Herpetotheres cachinnan, Micrastur semitorquatus,* and *Falco sparverius*; Strigidae: *Bubo virginianus, Speotyto cunicularia, Athene noctua, Asio flammeus,* and *Otus asio*; Tytonidae: *Tyto alba.*

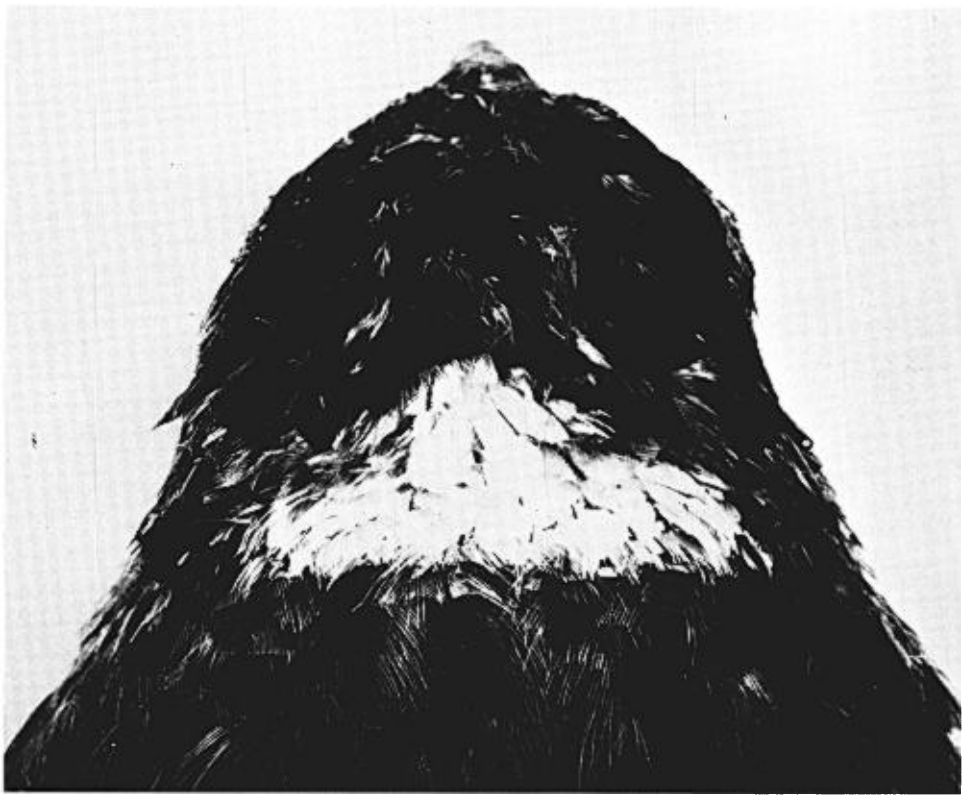

Fig. 1. Cooper's Hawk (AMNH 470458) showing the occipital spot. Distal one-third of all contour feathers in the coronal, occipital, and cervical regions have been excised.

morphology of the white spot was found to vary intergenerically (Table 1). The spot is present and appears identical in both sexes. Age variation, when present, is detailed in Table 2.

SURVEY OF GENERA

Of the 64 recognized genera of accipitrids (Brown and Amadon 1968), 55 were surveyed (Table 2). It was noted that New World accipitrids have generally bold

TABLE 1

ANALYSIS OF THE SPOT INDEX IN 10 NEW WORLD ACCIPITRID GENERA[1]

Species	N	Mean	Range	SE of Mean
Ictinia misisippiensis	7	1.10	0.4–2.3	0.25
Rostrhamus sociabilis plumbeus	7	2.39	0.7–3.5	0.47
Haliaeetus leucocephalus (juv.)	7	9.16	8.3–10.1	0.24
Circus cyaneus hudsonius	20	2.48	1.0–3.6	0.15
Geranospiza caerulescens nigra	6	5.88	4.4–7.2	0.42
Accipiter cooperii	20	2.08	1.1–3.2	0.12
Buteogallus a. anthracinus	13	3.80	2.6–6.3	0.33
Parabuteo unicinctus harrisi	10	1.84	1.1–2.8	0.15
Buteo jamaicensis calurus	18	2.51	1.4–4.3	0.19
Aquila chrysaetos canadensis	18	6.37	2.8–10.3	0.46

[1] Spot index = area of spot/interorbital width of head. Spot area computed as one-half length times greatest width. This index relates spot area to head size. A larger mean value for spot index indicates a relatively larger occipital spot.

Fig. 2. Red-tailed Hawk showing the terminal darkening of the occipital spot feathers.

definitive spots while many Old World species exhibit poorly developed, possibly vestigial spots. Of the New World taxa examined, all had occipital spots except *Leucopternis* and the cosmopolitan *Elanus*. These two genera have pale heads in adult plumage, perhaps explaining the absence of the spot (see below). Four other genera, *Elanoides, Busarellus, Harpia,* and the cosmopolitan *Haliaeetus* have the spot in only the dark-headed juvenile plumage; the spot is not apparent on the pale-colored head of the adults.

Size and shape of the occipital spot varies considerably among Old World species. Notable deviations from the typical spot are summarized below. Several genera possess indistinct occipital spots (*Henicopernis, Lophoictinia, Circaetus, Terathopius, Dryotriorchis, Polyboroides,* and *Megatriorchis*). Two other

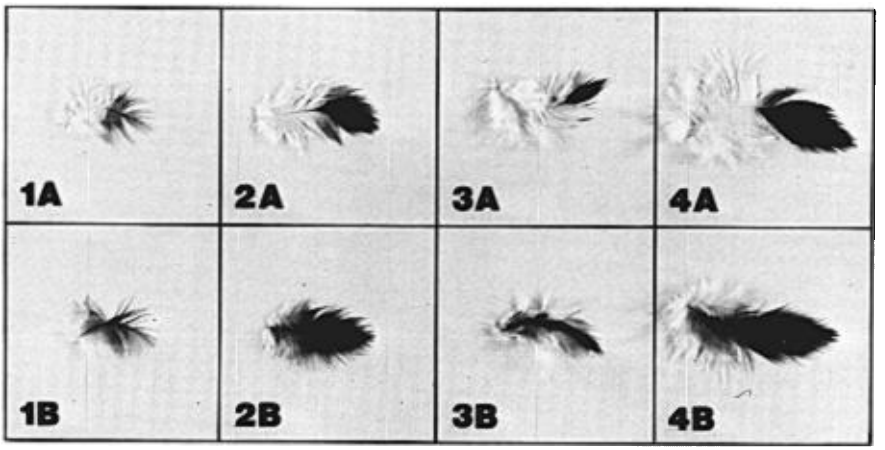

Fig. 3. Contour feathers of the capital tract of four genera of accipitrid birds: A, feather from within the occipital spot region; B, feather about the periphery of the occipital spot. 1, *Ictinia misisippiensis*; 2, *Circus cyaneus*; 3, *Accipiter cooperii*; 4, *Buteo jamaicensis*.

TABLE 2

VARIATION IN THE OCCIPITAL SPOT OF ACCIPITRIDAE[1]

Species	Class[2] 1	2	3	4	5	6
Aviceda cuculloides	O	–	–	–	–	–
Leptodon cayanensis	N	–	–	–	–	–
Chondrohierax urcinatus	N	–	–	–	–	–
Henicopernis longicauda	–	–	O	–	–	–
Pernis celebensis	O	–	–	–	–	–
Elanoides forficatus	–	N	–	–	–	–
Machaerhamphus alcinus	O	–	–	–	–	–
Gampsonyx swainsonii	N	–	–	–	–	–
Elanus leucurus	–	–	–	C	–	–
Chelictinia riocourii	O	–	–	–	–	–
Rostrhamus sociabilis	N	–	–	–	–	–
Harpagus bidentatus	N	–	–	–	–	–
Ictinia misisippiensis	N	–	–	–	–	–
Lophoictinia isura	–	–	O	–	–	–
Hamirostra melanosternon	O	–	–	–	–	–
Milvus migrans	O	–	–	–	–	–
Haliastur indus	–	–	–	O	–	–
Haliaeetus leucocephalus	–	C	–	–	–	–
Gypohierax angolensis	–	O	–	–	–	–
Gypaetus barbatus	–	–	–	O	–	–
Necrosyrtes monachus	–	–	–	–	–	O
Gyps fulvus	–	–	–	–	–	O
Aegypius monachus	–	–	–	–	–	O
Circaetus gallicus	–	–	O	–	–	–
Terathopius ecaudatus	–	–	O	–	–	–
Spilornis cheela	O	–	–	–	–	–
Dryotriorchis spectabillus	–	–	O	–	–	–
Polyboroides typicus	–	–	O	–	–	–
Geranospiza caerulescens	N	–	–	–	–	–
Circus cyaneus	C	–	–	–	–	–
Melierax metabates	O	–	–	–	–	–
Megatriorchis doriae	–	–	O	–	–	–
Erythortriorchis radiatus	O	–	–	–	–	–
Accipiter cooperii	C	–	–	–	–	–
Urotriorchis macrourus	O	–	–	–	–	–
Butastur indicus	O	–	–	–	–	–
Leucopternis albicollis	–	–	–	N	–	–
Buteogallus anthracinus	N	–	–	–	–	–
Heterospizias meridionalis	N	–	–	–	–	–
Busarellus nigricollis	–	N	–	–	–	–
Geranoaetus melanoleucus	N	–	–	–	–	–
Parabuteo unicinctus	N	–	–	–	–	–
Buteo jamaicensis	C	–	–	–	–	–
Morphnus guianensis	N	–	–	–	–	–
Harpia harpyja	–	N	–	–	–	–
Harpyopsis novaeguinae	–	–	–	–	O	–
Pithecophaga jefferyi	–	–	–	–	O	–
Aquila chrysaetos	C	–	–	–	–	–
Hieraaetus morphnoides	O	–	–	–	–	–
Spizastur melanoleucus	N	–	–	–	–	–
Lophaetus occipitalis	O	–	–	–	–	–
Spizaetus ornatus	C	–	–	–	–	–
Stephanoaetus coronatus	O	–	–	–	–	–
Oroaetus isidor	N	–	–	–	–	–
Polemaetus bellicosus	O	–	–	–	–	–
Total per Class:	34	5	7	4	2	3
New World genera per Class:	14	3	0	1	0	0
Percent New World genera per category:	77.7	16.7	0	5.6	0	0
Old World genera per Class:	15	1	7	2	2	3
Percent Old World genera per category:	50.0	3.3	23.3	6.7	6.7	10.0

[1] Symbols: O = Old World genera (N = 30), N = New World genera (N = 18), C = cosmopolitan genera (N = 7).

[2] Class 1, spot present in both adult and juvenile plumages; 2, spot present in only the juvenile plumage and adult plumage exhibiting a pale head; 3, indistinct spot present; 4, no spot seen in any plumage, but pale head present; 5, no spot seen; 6, naked head present.

Fig. 4. The Ornate Hawk-Eagle (*Spizaetus ornatus*), among others, shows the white occipital spot each time the crest is erected.

genera, *Haliastur* and *Gypaetus*, have no spot in any plumage, but these genera have pale-colored heads in the adult plumage similar to that of the New World *Leucopternis*. *Gypohierax* has the spot in only the dark-headed juvenile plumage, the white head of the adult exhibiting no apparent spot. The three vulturine genera examined, *Necrosyrtes*, *Gyps* and *Aegypius*, being "naked-headed," lacked the occipital spot. Lastly two Old World genera of accipitrids, *Harpyopsis* and *Pithecophaga,* lacked the spot.

Functional Significance

Signaling organs are not uncommon among birds and a student of avian ethology will rarely dismiss as functionless such a bold plumage marking as the accipitrid spot. As the spot is highly organized with extreme contrast of colors and can be displayed and concealed at will, we proposed, *a priori,* that the spot functions as a

Fig. 5. Female Cooper's Hawk displaying the occipital region upon the male's arrival at the nest. Sunlight may enhance the spot in this photograph. (Photograph courtesy of Helen Snyder.)

social signal associated with crest erection. All evidence gathered to date supports this proposal.

Accipitrid hawks are noted for their ability to raise the feathers of the occipital and nape regions in behavioral situations. As discussed by Morris (1956), crest erection is a display that occurs primarily in agonistic and sexual contexts. Feather erection in an agonistic context serves in part to enhance the apparent size of the bird (Brown and Amadon 1968: 90). We found that crest erection also serves to display the occipital spot (Fig. 4). Innumerable observations of captive and wild birds support the hypothesis that most accipitrid birds, indeed, display the spot during cephalic feather erection.

We have assessed the behavioral interactions of accipitrid birds viewed by us, our colleagues, and those described in the literature and we conclude that the spot functions primarily (1) in agonistic contexts and (2) in deflection (Cott 1940). As the white spot occurs in the occipital region, hawks necessarily must assume particular postures to exhibit it. Three postures of the displaying bird are pertinent to this discussion: (1) bowing, (2) facing away, and (3) sleeping.

Function in an agonistic context.—Accipitrid birds are morphologically suited for predation and are generally aggressive and asocial. Agonistic encounters leading to physical contact between rapacious birds would likely result in injury or death to one or more individuals involved. Such encounters between conspecifics would be highly maladaptive and selection would logically favor a character that would reduce physi-

Fig. 6. During agonistic encounters, the spot of the Red-tailed Hawk is exposed to the rear and may function in deflection.

cal aggression. The accipitrid spot appears to be such a character. Helen Snyder (pers. comm.) working with Cooper's Hawks (*Accipiter cooperii*) reports that showing the back of the head, and concomitant display of the white spot, cause immediate behavioral inhibition on the part of the aggressor in this species. The red patch at the back of the head of young Water Rails, *Rallus aquaticus* (Lorenz 1952: 195), and the cryptic white of the White-necked Raven, *Corvus cryptoleucus* (Johnston 1958) are reported to be signal organs with this function.

The spot is rendered visible during possessional conflicts. While eating in our presence, Red-tailed Hawks displayed the spot while mantling over their food. In such instances the birds erected their crests while bowing deeply and rotating in semicircles. The side-to-side movements resulted in a frontal display of the spot to us, the antagonists. M. Alan Jenkins (pers. comm.) has observed this same display in an imprinted Goshawk (*Accipiter gentilis*) and confirms our observations. Konig (1974) presents several illustrations of accipitrid vultures bowing in situations of an agonistic nature. It is possible that the bowing behavioral pattern of the vultures is in itself a display, having been emancipated from the ancestral stimulus wherein the white spot of the occiput was displayed. Regardless of its significance, the bowing behavior patterns in accipitrid vultures illustrates the conservative nature of such displays of the back of the head within the Accipitridae.

Numerous observations have been assessed wherein the back of the head and particularly the white spot are displayed during sexual encounters of both wild and

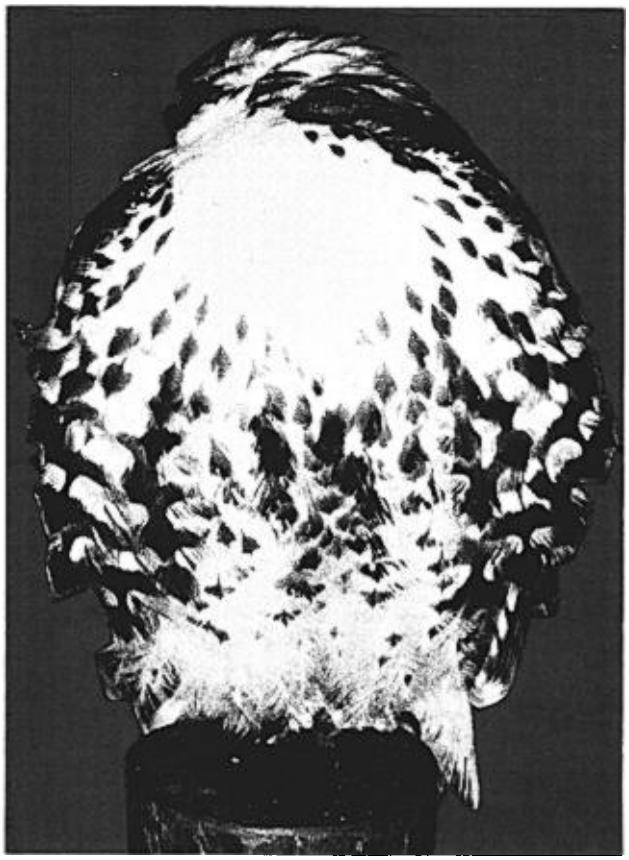

Fig. 7. Sleeping Red-tailed Hawk exhibiting the deflective facial disc.

human-imprinted birds. Hamerstrom and Hamerstrom (1972) report that during a sexual display, the male Red-tailed Hawk faces away. It is interesting to note that the bird "faced away" as he would be properly positioned to exhibit the spot. Frances Hamerstrom (pers. comm.) describes a captive female Red-tailed Hawk that flattened low in the nest and displayed the white occipital spot each time the male approached the nest. Helen Snyder (pers. comm.) similarly reports that the wild female Cooper's Hawk, when brooding eggs, erects the crest upon the male's arrival at the nest (Fig. 5). It seems apparent that the frontal stare is a signal of aggression, which is apparently appeased by the display of the spot. Such an appeasement gesture would logically precede any transfer of food from male to female at the nest site. Lastly the spot appears to be a significant social signal among nestlings of *A. cooperii*. Snyder further reports a strong back-turning response during conflict between siblings of this species and states that during this sort of struggle over prey, the crest is erected and the back of the head shows white in both sexes.

Function in a deflective context.—Besides the apparent voluntary display of the spot in an agonistic situation, the spot appears to serve a dual role by functioning also as a deflective character. The spot functions in deflection (Cott 1940), as it would tend to confuse and misdirect the attack of a predator, by misrepresenting the prey (the hawk). The white occipital spot, viewed from behind when the crest is erected

(Fig. 6) or when the bird is asleep, appears to engender a cephalic illuminance that seems to convey awareness to an observer.

Significantly it appears that hawks are preyed upon by nocturnal predators, particularly owls (Hamerstrom and Hamerstrom 1951, Craighead and Craighead 1956, Orians and Kuhlman 1956, Luttich et al. 1971). Accipitrid birds, like many other avian species, rotate their heads and nestle their faces deep in the interscapular feathers to assume a sleeping posture; only the occipital region of the head is visible. Ptiloerection is concomitant with this posture. Assuming such a posture, an accipitrid bird conspicuously exhibits the cryptic white spot (Fig. 7). In perspective, this cephalic illuminance seems to form a facial disc on the sleeping bird. We suggest that the accipitrid spot, like the ocelli of the American Kestrel (*Falco sparverius*), represents a facial disc that psychologically deters the attack of a predator by destroying the element of surprise (Balgooyen 1975). Admittedly the theory would be difficult to test under any conditions. Nonetheless we have noted such facial discs on other unrelated species of sleeping birds (e.g. Chestnut-backed Chickadee, *Parus rufescens*; American Kestrel) and they are probably of widespread occurrence as a deflective character reducing predation.

Variations in the Occipital Spot

Although most accipitrid birds have the distinct occipital spot, several genera show rather indistinct spots or lack the spot entirely (Table 2). At an early point in our study we suspected that the spot and the crest might serve similar functions: a bird with a large crest might have a reduced spot and vice versa, but we found no correlation between spot size and length of crest feathers in the 55 genera surveyed.

Within this family many genera have the cephalic feathers paler in color than the general body feathers; this is best seen in the Bald Eagle (*Haliaeetus leucocephalus*). As this occipital spot functions in behavioral interactions, it is possible that the pale-colored head represents an extreme enlargement of this character, possibly serving as a supernormal stimulus. By this reasoning, the pale or white head would tend to inhibit an adversary behaviorally. This explanation is particularly applicable to the Bald Eagle inasmuch as it is a piratic species that systematically attacks and robs the Osprey (*Pandion haliaetus*) of its prey and is also known to pursue vultures and force them to disgorge (Bent 1937). Among accipitrid birds, the Bald Eagle seems behaviorally unique as it engages in a disproportionate amount of agonistic encounters.

Carlquist (1965) notes that predators are generally scarce on islands. If the occipital spot is indeed a deflective character serving to protect the diurnal hawk from nocturnal predation, one would expect this character to be absent or vestigial on island species. As mentioned above, two genera, *Pithecophaga* and *Harpyopsis* lack the occipital spot. Besides being among the largest of all accipitrid birds and perhaps less prone to nocturnal predation, *Pithecophaga* and *Harpyopsis* are completely restricted to island distributions, the Phillipines and New Guinea respectively. Furthermore *Henicopernis* and *Megatriorchis*, which are restricted to New Guinea, have indistinct spots that lend credence to the above theory. The one other genus restricted to an island distribution, *Eutriorchis,* was not examined. Balgooyen (1975) aptly noted that the deflection face of the continental races of the American Kestrel is absent in the subspecies inhabiting the Isle of Pines and Cuba. Probably the deflective facial disc lost its selective value and atrophied as a consequence of the reduced

predation pressure on these island genera. This explanation is in concord with that of Balgooyen.

The relatively social Bateleur (*Terathopius*) also has an indistinct occipital spot, and it exhibits a bizarre nape-back patch (Grossman and Hamlet 1964: 360, photograph) that is light in color and, although not cryptic, is possibly commensurate to the occipital spot. This nape patch, like the white head variation, may also function as a supernormal stimulus.

TAXONOMIC AND SYSTEMATIC ASPECTS

We have shown the cryptic occipital spot to be, almost without exception, a familial trait of the accipitrid Falconiformes. Albeit slight, the taxonomic significance of the spot as a diagnostic character of the family is undeniable. Systematic implications derived from one character alone are at once tenuous, but a character that shows consistency throughout diverse taxa merits high taxonomic weight (Mayr 1969: 220–221). The white occipital spot is present in the kites, which show evidence of having retained many primitive familial characters (Brown and Amadon 1968: 19). Presence in the kites and a general widespread occurrence in the family suggests the spot to be a primitive and conservative character probably present in the ancestral stock. Moreover the persistence of the spot through the numerous ecological shifts associated with the diverse life styles of the accipitrid hawks further supports its primitive and conservative nature. It follows that the absence of the occipital spot in the Falconidae and other falconiform families is of significance when one considers the evolutionary origin of the order. The spot's presence in the ancestors of the Accipitridae and absence in the falconid ancestry suggests that attainment of the major adaptive zone of the predatory existence was polyphyletic. This phyletic distinction is further evidenced by anatomical and behavioral data (Hudson 1948, Jollie 1953, Starck and Barnikol 1954, Brown and Amadon 1968). The white occipital spot serves to support the premise that the five falconiform families are not closely related and have converged toward the predatory existence.

Although this family has radiated into a number of divergent taxa, recognized as several natural groups on the basis of morphological, behavioral, and other features (Brown and Amadon 1968), we could identify no group-specific size or shape of the occipital spot (Table 1). The spot's conservative nature within the family makes it probably of little aid to the taxonomist. The similarities between the cephalic plumage patterns of the Bald Eagle and the Vulturine Fish Eagle (*Gypohierax angolensis*), with particular regard to the spot, do however corroborate the presumed close relationship between these groups (Brown and Amadon 1968). Undoubtedly the large number of island endemics and overall greater diversity of Old World taxa explain the variation in the spot in Old World forms as compared with New World forms.

Note added in galley proof.—Subsequent to the completion of this paper, Dean Amadon and John Bull of the American Museum of Natural History examined for us two specimens of the Madagascar Serpent Eagle (*Eutriorchis astur*). Like certain other accipitrid genera entirely restricted to island distributions, *Eutriorchis* lacks an occipital spot.

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