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# THE SYSTEMATIC POSITION OF CERTAIN HAWKS IN THE GENUS *BUTEO*

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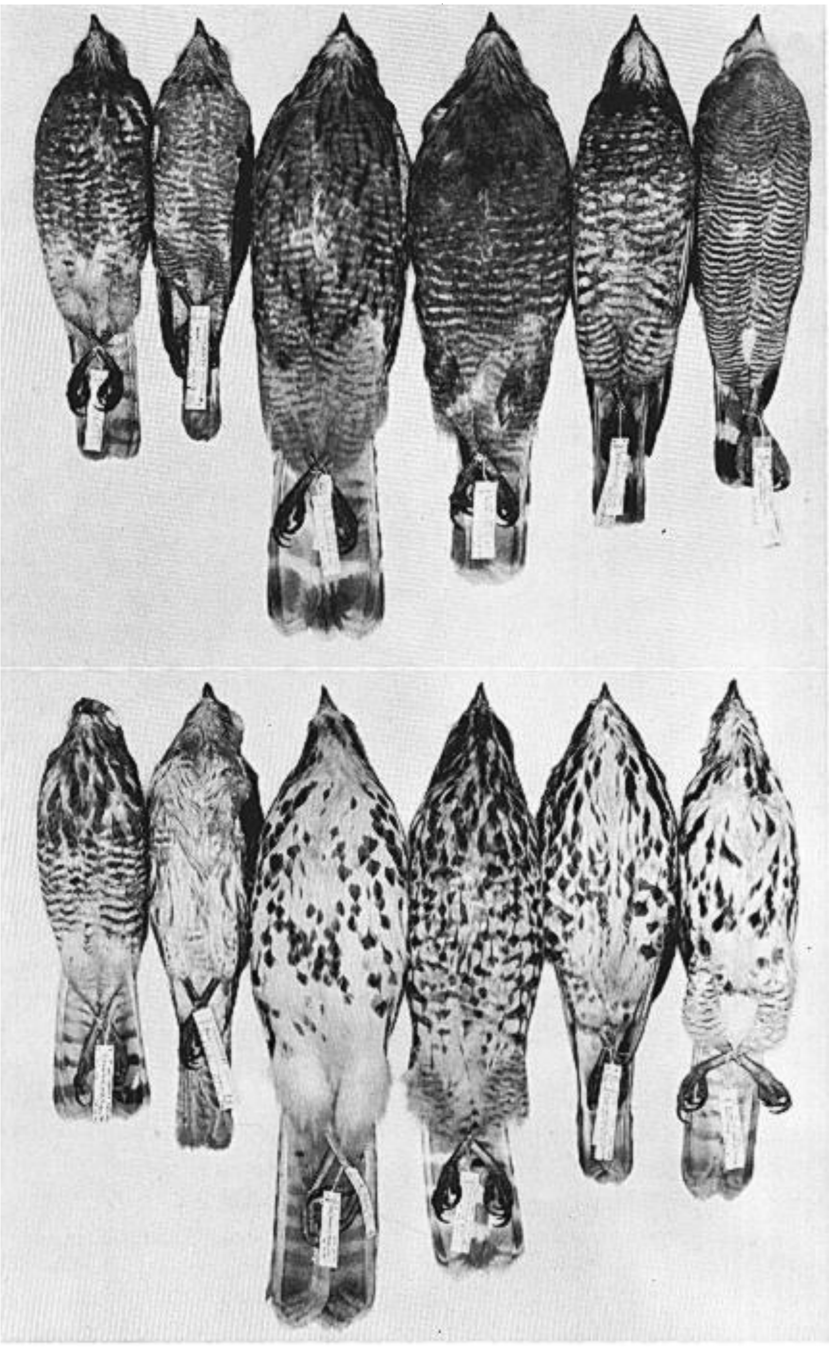
THE most recent authoritative work dealing with the North and Middle American Falconiformes states that the genus *Buteo* "is such a composite (that is, is so variable within its included subgenera) that any description of the genus as a whole would be largely a matter of exceptions in one or another subgenus of all the generic characters." In other words, the group "defies subdivision" (Friedmann, 1950: 212–213), and it is apparent that the existing subgeneric classification of North American forms is largely subjective.

The present report attempts to delineate what seems to be a natural unit of five New World species of *Buteo* based upon certain common features of plumage, proportions, distribution, and behavior. These species, hereafter referred to as the "woodland buteos," are the Roadside Hawk (*B. magnirostris*), Ridgway's Hawk (*B. ridgwayi*), Red-shouldered Hawk (*B. lineatus*), Broad-winged Hawk (*B. platypterus*), and Gray Hawk or Mexican Goshawk (*B. nitidus*).

## GEOGRAPHIC AND ECOLOGIC DISTRIBUTION

For purposes of discussion, the following synopsis of distribution of the woodland buteos is presented. Except where otherwise noted, statements regarding geographic range are based on the *Check-list of North American birds* (A.O.U., 1957) and on the *Distributional check-list of the birds of Mexico,* Part I (Friedmann *et al.*, 1950).

The Roadside Hawk occurs from Mexico to Argentina, with 16 races recognized by Hellmayr and Conover (1949) and also by Peters (1931). Mexican races prefer open country, second-growth woods, and forest edge (Blake, 1953). In the province of Bocas del Toro, Panama, Eisenmann (1957: 250) found it to be an "edge" species. In Surinam it lives along "forest edges and in open forests" (Haverschmidt, 1962: 156).



The monotypic Ridgway's Hawk is restricted to Hispaniola and surrounding islands in the Greater Antilles where it occupies woods and fairly open country in the lowlands (Bond, 1961).

The Red-shouldered Hawk occurs in two disjunct populations. The race *B. l. elegans* breeds from northern California south to northwestern Baja California. Four other races, *B. l. lineatus*, *B. l. alleni*, *B. l. extimus*, and *B. l. texanus*, occupy various portions of eastern North America from Minnesota and southern Quebec to central Mexico and the Florida Keys. This species inhabits moist woodlands such as are found along lowland rivers (Peterson, 1961; Grinnell and Miller, 1944; and Bent, 1937).

The Broad-winged Hawk is found from Alberta and Nova Scotia south to Texas, Florida, and the West Indies. Hellmayr and Conover (1949) and Friedmann (1950) both recognize six races of this species; Peters (1931) lists five. Mixed deciduous forests on hillsides adjacent to small clearings and swamps seem to constitute the favored habitat for the single continental race occurring in eastern North America (Burns, 1911).

The Gray Hawk is found from southern Arizona and southern Texas to eastern Bolivia and southern Brazil. Hellmayr and Conover (1949) recognize four races of this species, whereas Peters (1931) lists five. Bent (1937) reports the former breeding of this species in riparian woodland of mesquite, cottonwood, hackberry, and sycamore in southern Arizona. Populations in Mexico use open country and well-watered second-growth woods, according to Blake (1953). In Surinam, Haverschmidt (1962) reports that the species lives in the same habitat as the Roadside Hawk (see above).

## PLUMAGE PATTERN AND SEQUENCE

Although certain of the woodland buteos differ rather markedly in coloration, particularly with regard to the ventral body plumage of the adult, as far as the patterning and marking of the plumage is concerned, obvious basic similarities exist (Figure 1). It is not difficult to see how minor changes in the configuration of feather marks typical of one species could produce marks typical of another species in the group. This element of uniformity in feather patterning has led us to propose that the woodland buteos belong to a "common ontogenetic pattern system." The word "ontogenetic" is used because the development and definitive appearance of the patterning of both juvenal and adult plumages provides

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Figure 1. Ventral view of study skins of *Buteo*. (a) Above, from left to right, adults of *B. magnirostris griseocauda*, *B. ridgwayi*, *B. lineatus lineatus*, *B. l. elegans*, *B. platypterus platypterus*, and *B. nitidus micrus*. (b) Below, juveniles of *B. magnirostris petersi*, *B. ridgwayi*, *B. lineatus lineatus*, *B. l. elegans*, *B. platypterus platypterus*, and *B. nitidus maximus*.

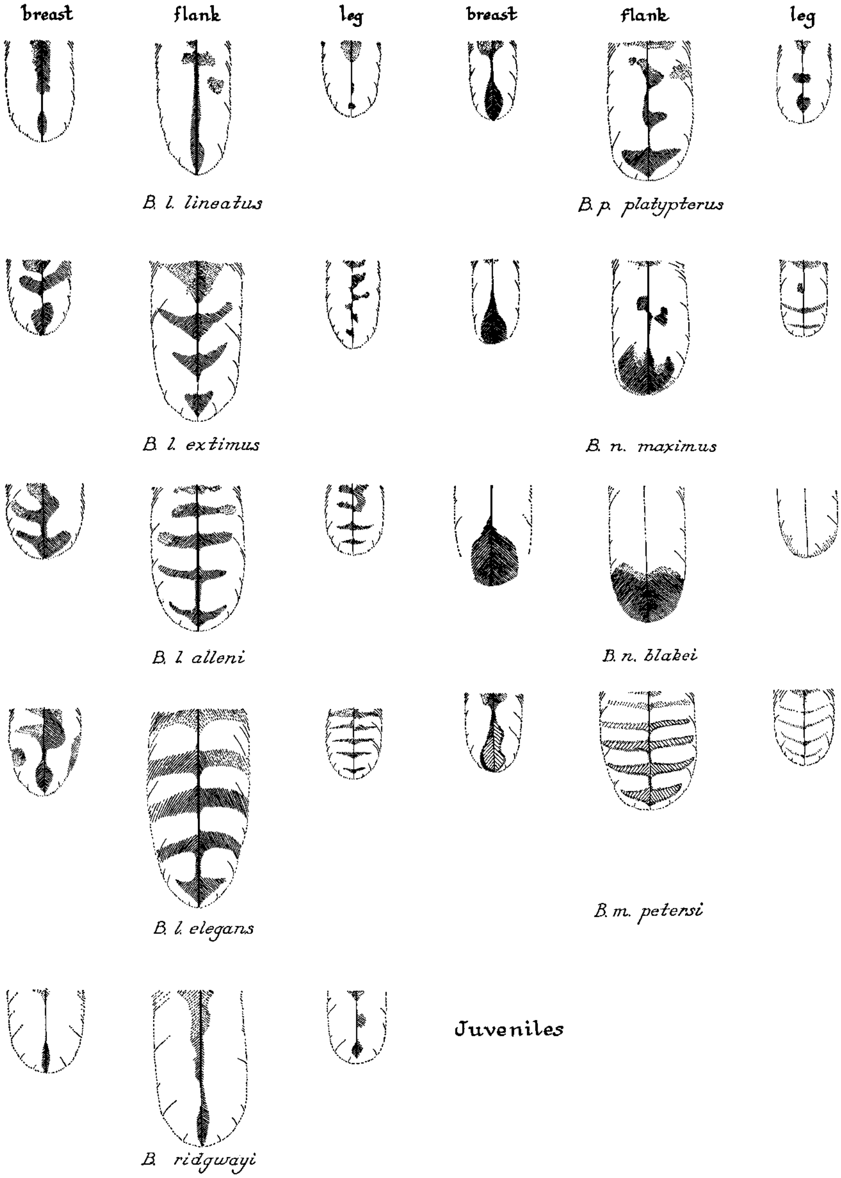

Figure 2. Patterns on major portions of selected ventral body feathers from juveniles of nine kinds of *Buteo*.

evidence that the woodland buteos may be closely related. Of prime importance in the woodland buteos is the configuration of the markings of the ventral body plumage and of the tail. In the following accounts of plumages the descriptive detail is provided that is necessary groundwork for a discussion of the theoretical basis of the ontogenetic pattern system described more fully on page 440. Certain erroneous statements in the literature concerning plumages are also corrected.

At the outset it should be stated that there seem to be only two distinctive plumages in each species, a juvenal plumage acquired by a postnatal molt and an adult plumage acquired by a complete molt one year after the postnatal molt. There is no evidence, to our knowledge, of a postjuvenal molt that provides a distinctive immature plumage in any of the woodland species.

### *Buteo magnirostris*

The Roadside Hawk. Friedmann has reviewed the plumages of 11 of the Mexican and Central American races of this extremely variable and complex species by comparing them with a detailed description of *B. m. griseocauda* of eastern and southern Mexico. These descriptions are adequate and need not be discussed in detail here. For our purposes we wish merely to comment on the manner in which the plumages of this species as a whole can be incorporated into the pattern system of the woodland buteos.

*Juvenal plumage.*—From an examination of Figures 2 and 4 it is readily apparent that individual feather patterns of the juvenal plumage of *B. magnirostris* are rather similar to comparable feathers of the other species of woodland buteo. One feature not noted in the other species concerns the presence of an abrupt transition between the tear-shaped streaks or irregular elongate marks on the breast feathers, to strong and even barring on the flank feathers. Thus, the more posterior feathers are at a more advanced ontogenetic stage in the system than are the breast feathers. The tail of the juvenile is rather intermediate in number and in contrast of bands, when the variety of tail patterns of all the woodland buteos is considered.

*Adult plumage.*—An interesting point concerning this plumage is that it is relatively unchanged from that of the juvenile. The major difference in pattern involves the tear-drop shaped streaks of the breast feathers, which in the adult plumage have gained lateral lobes, resulting in the formation of broad V's or broad arrowhead-shaped marks on these feathers that often suggest the development of irregular barring. In some races this somewhat splotched pattern is so extensive on individual breast feathers that the breast becomes solidly colored. The tail of the adult is slightly more advanced in the pattern system than that of the juvenile, with fewer, wider, and more contrasting dark bands.

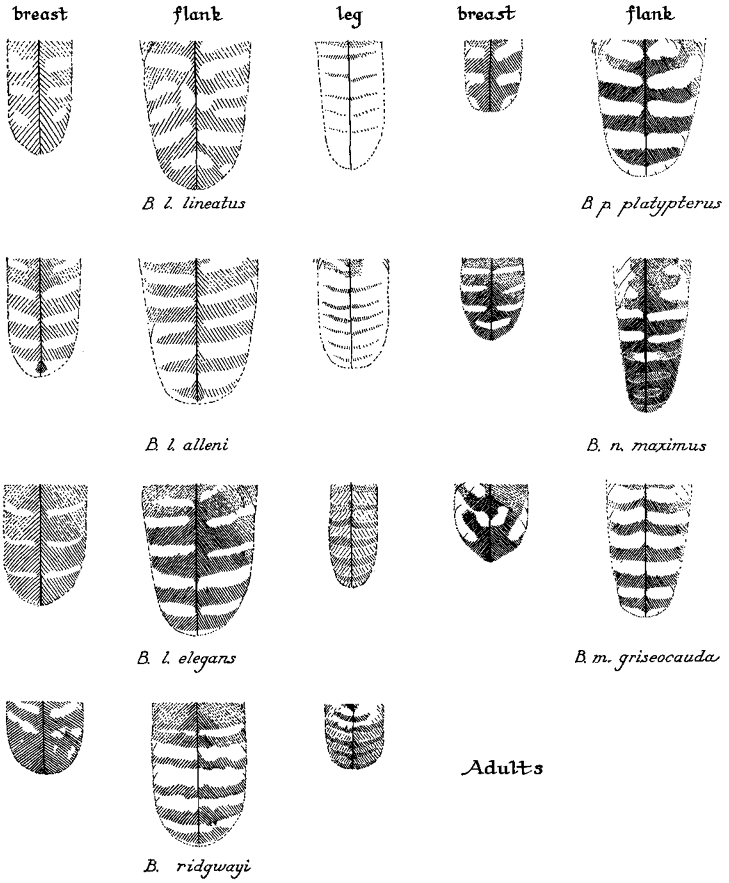

Figure 3. Patterns on major portions of selected ventral body feathers from adults of seven kinds of *Buteo.*

## *Buteo ridgwayi*

Friedmann (1950) has adequately characterized the plumages of the Ridgway's Hawk. The photographs and drawings in the present paper illustrate the markings necessary to show how *B. ridgwayi* fits into the plumage pattern system of the woodland buteos. It is apparent that the closest resemblance in both juvenal and adult markings of *B. ridgwayi* is with *B. lineatus.* This is shown clearly in Figures 2 and 3. The Ridgway's Hawk shows considerable variation in tail banding, in that the light bands on individual rectrices do not always fall evenly in line with the light bands of adjacent tail feathers.

### *Buteo lineatus*

*Juvenal plumage.*—In races of the Red-shouldered Hawk the markings on the breast, abdomen, flanks, and thighs consist variously of streaks, bars, or spots of irregular shapes that are actually the visible distal portions of more extensive patterns on the feathers that are concealed by overlying feathers. Figure 2 illustrates typical examples of patterns shown on major portions of selected ventral feathers for all races of *B. lineatus* except *B. l. texanus.*

Friedmann (1950: 287) described the juvenal plumage of *B. l. elegans* as being: "Similar to that of *B. l. lineatus,* but . . . with the underparts more abundantly spotted and streaked with fuscous, the spots smaller, but much more numerous, and extending over the lower abdomen . . . ." However, as can be seen from Figure 2, the numerous ventral marks of *B. l. elegans* are not usually "tear-shaped spots," as in *B. l. lineatus,* but are more typically marks of a triangular or diamond shape that may connect or blend with bars across the feathers. The range of variation shown by the breast feathers of *B. l. lineatus* is such that there is an approach by a few individuals to the pattern of *B. l. elegans* as shown in Figure 2; most examples of the former race, however, have elongate streaks on these feathers. The extreme in barring of the breast feathers in *B. l. elegans* displays a pattern similar to that of the flank feathers of that race. The degree of barring of the flanks commonly found in *B. l. elegans* is seldom encountered in *B. l. lineatus*; in the latter race the flank feathers often are merely streaked (Figure 2) or irregularly marked to form patterns like those of the breast feathers of *B. l. elegans.* Some *B. l. lineatus* have immaculate legs; the majority show tiny spots or irregular vermiculations on the feathers of these areas. The legs of *B. l. elegans* are marked very differently, always with conspicuous bars. *B. l. lineatus* and *B. l. elegans* represent the extremes in types of juvenal plumage pattern among races of the Red-shouldered Hawk.

The juvenile of *B. l. alleni* is described by Friedmann as being: "Similar to *B. l. lineatus* but smaller, the ventral spots smaller as a rule and somewhat more numerous . . . thighs only sparsely marked with dusky" (*op. cit.*, pp. 290–291). Whereas these differences certainly exist, it must be stressed that the ventral feather marks of *B. l. alleni* are typically shaped much more like those of *B. l. elegans* than like those of *B. l. lineatus* (Figure 2). In *B. l. alleni,* however, there are some individuals that approach the streaked ventral pattern of *B. l. lineatus,* as would be expected from the contiguity of their breeding ranges.

Friedmann further says (p. 289) that *B. l. texanus* also resembles *B. l. lineatus* in juvenal plumage but that the underparts of *B. l. texanus* are "more heavily spotted and with the spotting extending over the thighs."

Here again we must state that the ventral pattern of *B. l. texanus* (not illustrated) shows a much greater similarity to *B. l. alleni* and to *B. l. elegans* than to the nominate race, because of the emphasis on barring rather than streaking of the underparts.

The few specimens of *B. l. extimus* examined show a pattern type essentially intermediate between that of *B. l. lineatus* and *B. l. alleni* (Figure 2). This is of interest because *B. l. extimus*, breeding in southern Florida, is geographically separated from *B. l. lineatus* by the breeding range of *B. l. alleni.* Friedmann does not comment on the juvenal plumage of *B. l. extimus* other than to state that it is "similar to *B. l. alleni.*"

TABLE 1

OCCURRENCE OF TAIL PATTERNS IN JUVENILES OF *BUTEO LINEATUS*

| *Subspecies and region* | *Sex* | *Number of dark bands*[1] | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | *3½* | *4* | *4½* | *5* | *5½* | *6* | *6½* | *7* | *7½* | *8* | *8½* | *9* |
| *lineatus*[2] | ♂ | | | | 2 | 1 | 12 | 1 | 15 | – | 1 | – | – |
| | ♀ | | | | – | – | 7 | 2 | 19 | – | 3 | – | 1 |
| | ? | | | | – | – | 3 | – | 6 | – | 1 | – | – |
| *alleni*[3] | ♂ | | | 1 | 1 | – | 5 | 1 | 1 | | | | |
| | ♀ | | | – | 2 | 3 | 5 | – | – | | | | |
| *extimus* | ♂ | | | | 1 | 1 | – | – | – | | | | |
| (Florida) | ♀ | | | | – | – | 3 | – | 1 | | | | |
| *texanus* | ♂ | | | | 6 | 4 | 9 | – | 1 | – | – | | |
| (Texas) | ♀ | | | | 5 | 3 | 13 | – | – | – | 1 | | |
| *elegans* | ♂ | 4 | 5 | 1 | | | | | | | | | |
| (California) | ♀ | 1 | 3 | – | | | | | | | | | |

[1] Beyond upper tail coverts.

[2] Specimens from Ontario, New York, Pennsylvania, New Jersey, Connecticut, New Hampshire, Maryland, Illinois, Iowa, Missouri, Kansas, Indiana, Oklahoma, North Carolina, and South Carolina.

[3] Specimens from Arkansas, Louisiana, Mississippi, Florida, and Georgia.

A further difference in plumage pattern between certain races of *Buteo lineatus* concerns the banding of the tail. Friedmann did not mention the fact that conspicuous geographic variation exists, both in the number of tail bands and in the degree of contrast of the bands, in the juvenal plumage (Table 1). For example, the number of exposed (visible beyond tips of upper tail coverts) dark bands in *B. l. lineatus* of northeastern North America varies from five to nine; most specimens show six or seven. *Buteo l. alleni*, *B. l. texanus*, and *B. l. extimus* have an intermediate number of exposed dark bands, from four and one-half to seven (rarely eight); the typical individual shows five or six. Juvenile *B. l. elegans* of California usually have three and one-half or four dark bands exposed and thus illustrate a striking divergence from the other races, particularly *B. l. lineatus*. Furthermore, there is a progressive change in degree of contrast between the dark and intervening light tail bands that parallels the geographic change in number (and, hence, width) of bands. The greater the number of bands present, the less obvious is the contrast between the bands. Thus, whereas *B. l. lineatus* has a grayish brown tail crossed by "dusky chaetura drab bars" (Friedmann, 1950: 281), *B. l. elegans* possesses a tail that is banded alternately with grayish white and dark umber.

TABLE 2

OCCURRENCE OF TAIL PATTERNS IN ADULTS OF *BUTEO LINEATUS**

| *Subspecies and region* | *Sex* | *Number of dark bands*[1] | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | *2* | *2½* | *3* | *3½* | *4* | *4½* | *5* |
| *lineatus*[2] | ♂ | | – | 34 | 8 | 2 | – | – |
| | ♀ | | 1 | 9 | 4 | 14 | 1 | 1 |
| | ? | | – | 3 | – | 1 | – | – |
| *alleni*[3] | ♂ | | 1 | 25 | – | – | | |
| | ♀ | | – | 10 | 4 | 2 | | |
| *extimus* (Florida) | ♂ | | | 1 | – | – | | |
| | ♀ | | | – | – | 1 | | |
| *texanus* (Texas) | ♂ | | | 8 | 2 | – | | |
| | ♀ | | | 2 | 4 | 5 | | |
| *elegans* (California) | ♂ | 2 | 3 | 2 | | | | |
| | ♀ | – | – | 6 | | | | |
| | ? | – | – | 1 | | | | |

* See footnotes of Table 1 for explanations of superscripts.

*Adult plumage.*—The adults of the various races of *B. lineatus* seem to possess essentially the same type of ventral body plumage markings (Figure 3); they are distinguished in this plumage chiefly on the basis of size and intensity of pigmentation of the underparts. Concerning the pattern of the tail, however, there is an obvious tendency for adults of *B. l. elegans* to possess fewer contrasting dark bands, on the average, than the other four races (Table 2), although most individuals of all races of the species show three bands. Table 2 further reveals that within a race the adult females seem to have more tail bands than the adult males.

### *Buteo platypterus*

*Juvenal plumage.*—As described by Friedmann (1950: 309) the breast of the juvenile Broad-winged Hawk in normal phase is "spotted with elongated tear-shaped marks of wood brown to Saccardo's umber." However, the marks do not typically become "smaller and rounder on the sides, flanks, upper abdomen, and thighs" as he states. More often the

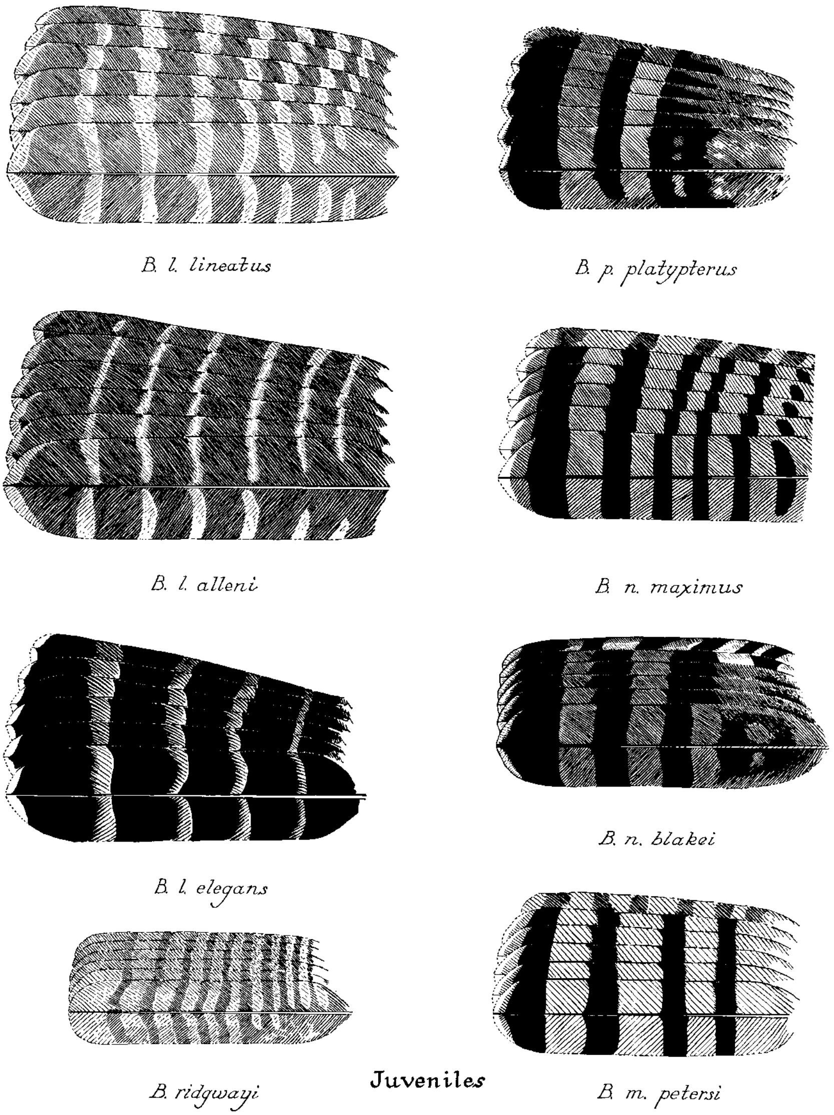

Figure 4. Dorsal view of left rectrices of juveniles of eight forms of *Buteo*.

tear-shaped marks characteristic of the breast feathers become flared laterally into the shapes of diamonds, triangles, hearts, or V's on the flanks and thighs (Figure 2). In dorsal aspect the rectrices also show considerable variability in pattern beyond that described by Friedmann. The "five or six narrow, indistinct bars of fuscous" above the broad subterminal band show conspicuous individual differences in width (Figure 4); in some specimens these bands may be nearly as broad as the subterminal band. A further diagnostic point is that the proximal bands are often much more irregular or wavy in pattern than the subterminal band. Concerning the dark or melanistic phase of the juvenal plumage, Friedmann writes that it is "similar to the normal phase, but with more rufous, especially on the breast." Two juvenile Broad-winged Hawks in melanistic plumage that we have examined do not seem to fit this generalization. Museum of Vertebrate Zoology (M.V.Z.) number 99825 has rufous feather margins, occurring ventrally from the throat to the under tail coverts, that surround exceptionally broad fuscous central shaft streaks which occupy almost the entire distal portions of these feathers. The other juvenile (M.V.Z. 99827) shows extreme saturation, a condition not mentioned by Friedmann, in which the entire body plumage is dark fuscous or sooty black with only a hint of rufous on the distalmost barbs of certain feathers of the breast, abdomen, and on a few wing coverts.

We agree with the suggestion of Friedmann (1950: 308–309) that the "immature" plumage as outlined is "rather indefinite," but the view that it "may really be nothing but the transition from the juvenal to the adult stage" is not supported. There is no evidence in any of the material we have examined of a distinctive plumage acquired by molt of the juvenile teleoptile feather generation, when the bird is approximately one year old, that is recognizably different from succeeding plumages. In other words, according to the evidence now available, the appearance of the bird after the postjuvenal molt is that of the "adult." We cannot, of course, rule out the possibility that there is a gradual change in the adult plumage, from generation to generation of feathers, leading toward more extensive barring of a more "advanced" sort on the breast. In fact our hypothesis of ontogenetic pattern change implies that this would occur (see discussion, p. 440).

*Adult plumage.*—Friedmann has adequately characterized the adult plumage of this species; thus it will not be reviewed here. Figures 3 and 5 illustrate the typical pattern shown by the ventral body feathers from selected areas and by the rectrices.

### *Buteo nitidus*

*Juvenal plumage.*—Friedmann (1950: 360–367) has presented useful descriptions of this plumage for the races *B. n. plagiatus*, *B. n. maximus*, *B. n. micrus*, and *B. n. blakei*. The first three races of this series differ little in juvenal plumage; their uniformity in this regard is as impressive as is the relatively wide variation seen among the juveniles of the various races of *B. lineatus*. The examination of approximately 50 juveniles of these three races of the Gray Hawk has confirmed the descriptions of

Friedmann; typical patterns of markings on ventral body feathers and on dorsal surfaces of the rectrices of *B. n. maximus* are shown in Figures 2 and 4. Note that the patterns are very similar to those seen in juveniles of *B. platypterus* except that the latter has spotted rather than barred or vermiculated leg feathers, as are found in *B. nitidus.*

TABLE 3

OCCURRENCE OF TAIL PATTERNS IN JUVENILES OF *BUTEO NITIDUS*

| *Subspecies* | *Sex* | *Number of dark bands*[1] | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | *3* | *3½* | *4* | *4½* | *5* | *5½* | *6* | *6½* | *7* | *7½* | *8* | *8½* | *9* |
| *plagiatus*[2] | ♂ | | | | | – | – | 4 | – | 3 | – | 5 | – | – |
| | ♀ | | | | | 1 | – | – | – | 4 | – | 1 | – | 4 |
| | ? | | | | | – | – | 1 | – | – | – | – | – | – |
| *maximus*[3] | ♂ | | | | | | | 3 | – | 2 | – | 1 | – | – |
| | ♀ | | | | | | | – | – | 4 | – | 2 | – | 2 |
| | ? | | | | | | | – | – | 1 | – | – | – | 1 |
| *micrus*[4] | ♂ | | | | | | | 3 | – | – | – | 1 | | |
| | ♀ | | | | | | | – | – | 3 | – | 3 | | |
| | ? | | | | | | | – | – | 1 | – | – | | |
| *blakei*[5] | ♂ | | 1 | – | – | | | | | | | | | |
| | ♀ | | – | – | 1 | | | | | | | | | |
| *nitidus*[6] | ♂ | 1 | 1 | 2 | – | 3 | | | | | | | | |
| | ♀ | – | 1 | 4 | – | 2 | | | | | | | | |
| | ? | – | – | 5 | 2 | 1 | | | | | | | | |

[1] Beyond upper tail coverts.
[2] Specimens examined from Colima, Jalisco, Guerrero, Oaxaca, Tamaulipas, and Veracruz.
[3] Specimens from Sonora, Sinaloa, Nayarit, and San Luis Potosí.
[4] Specimens from Guatemala, Nicaragua, and El Salvador.
[5] Specimens from Panama.
[6] Specimens from Trinidad, Colombia, Venezuela, British Guiana, Surinam, and Brazil.

*Buteo n. blakei* and *B. n. nitidus* (present study), and *B. n. pallidus* (Hellmayr and Conover, 1949: 163), possess a juvenal plumage that is rather distinct from that of the three northern races. Contrasting *B. n. blakei* with *B. n. plagiatus*, Friedmann writes (1950: 367) that the former has more rounded, less streaklike spots on the breast, abdomen, sides, and flanks. The rectrices of *B. n. blakei* are described as having "fewer but broader bands (four or five blackish bands as compared with seven fuscous-black ones in *plagiatus*)." In Table 3 we have categorized juveniles of this species that we have examined according to the number of dark bands visible on the dorsal surface of the tail beyond the upper tail coverts. Striking differences between the races are obvious. A further similarity between *B. n. blakei* and *B. n. nitidus* concerns the markings on the thighs. The northern races invariably have barred thigh feathers (Figure 2); in *B. n. blakei* and *B. n. nitidus,* in contrast, the thighs are often immaculate (14 of 22 juveniles of both races examined). The remaining 8 specimens had tiny vertically-oriented vermiculations, faint streaks, or small irregular spots on these feathers.

It is also of interest that the rather abrupt change of juvenal plumage type in this species coincides with the striking development of dorsal barring in the adult plumage of the three southern races (see beyond). This plumage change evidently occurs in Costa Rica where the range of *B. n. micrus* approaches, but does not touch, that of *B. n. blakei.* Friedmann (1950: 217, footnote) has already commented on the possibility that the southern three races, *B. n. nitidus, B. n. blakei,* and *B. n. pallidus* represent a species distinct from the northern races. The relations in Costa Rica of *B. n. micrus* and *B. n. blakei,* the two representatives of the northern and southern groups of races, respectively, should now be investigated to see if interbreeding occurs.

Friedmann (*loc. cit.*) mentions the definite existence of both juvenal and immature plumages in *B. n. nitidus,* with the chief difference between the two being the color of the pale interspaces of the rectrices, those feathers of the juvenal plumage having "dusky hair brown" interspaces and those of the immature plumage having whitish interspaces. He also mentions that the existence of an immature plumage is uncertain in *B. n. blakei.* We have seen no evidence, in the examination of 23 streaked "young" of *B. n. nitidus,* to support the contention that it has a distinctive immature plumage and thus feel that the specimen evidence indicates that a streaked juvenal plumage directly succeeding the natal down is worn for approximately one year until a complete molt produces the heavily barred "adult" plumage. The occurrence of whitish bands on the rectrices of some young individuals can be better interpreted as resulting from the fading of the pale brown bands on the interspaces of the rectrices of the juvenal generation.

The occurrence of fewer and relatively contrasting dark bands on the rectrices of juvenile *B. n. blakei* and *B. n. nitidus* suggests that the plumages of these races are ontogenetically more advanced in the pattern system than are the plumages of the northern races of this species. However, the ventral body markings of the southern races do not appear to fit into a comparably advanced stage, in that there is no tendency toward the development of diamond-shaped figures or barred patterns; the feather marks are instead broad streaks and roundish spots.

*Adult plumage.*—The adults of *Buteo nitidus* all fall at approximately the same "level" of plumage pattern (Figures 3 and 5). The various races are distinguished chiefly on the basis of size, coloration, and degree of development of white tail bands. As has already been noted, the southern three races, in contrast to the northern three races, have the "entire upperparts obscurely to fairly definitely barred" (Friedmann, 1950: 367). The tail of adult *B. nitidus* can also be considered to have reached an advanced ontogenetic level, comparable to that attained by adults of *B. platypterus*, because of the few bands that are the ultimate in degree of contrast (black and white).

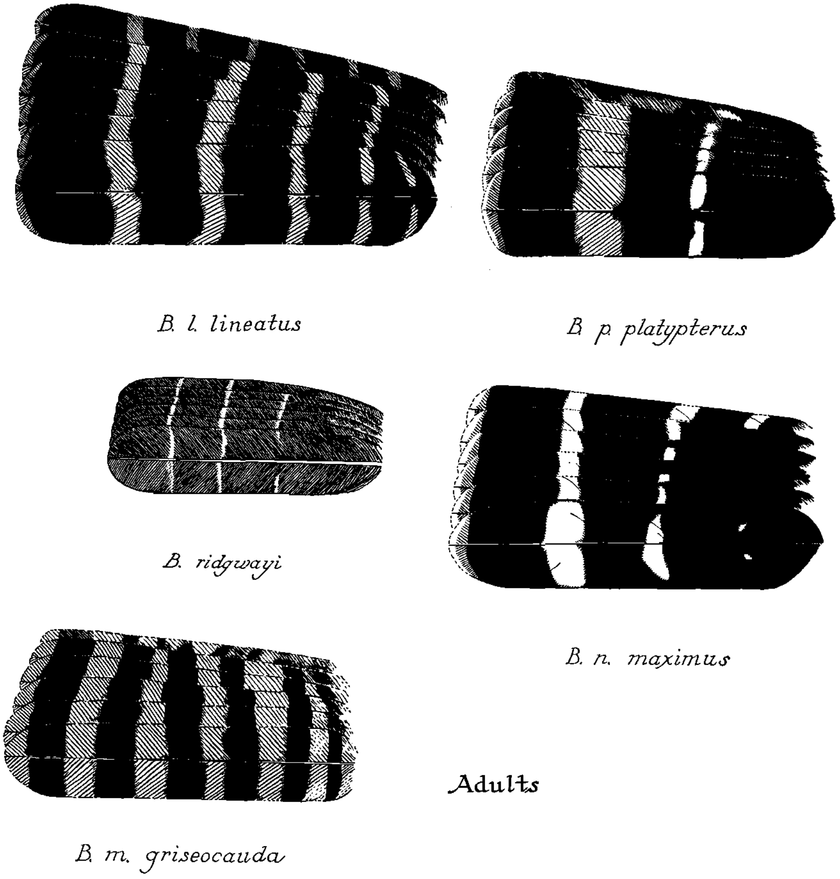

Figure 5. Dorsal view of left rectrices of adults of five species of *Buteo*.

## FREQUENCY OF MELANISM

Dark or melanistic phases have not been reported in any of the woodland buteos with the exception of *B. platypterus*, in which species black individuals are rare (Friedmann, 1950: 308). Many of the prairie–savannah buteos (*B. jamaicensis*, *B. swainsoni*, *B. lagopus*, *B. regalis*), in contrast, typically have a black phase. It is of further interest that most of the melanistic examples of *B. platypterus* that have been reported come from the western and northwestern parts of the range of that species (Peterson, 1961: 68; Burns, 1911: 155–157); Bailey (1917) named a race, *B. p. iowensis,* based on melanistic individuals from that area. There are several recent sight records and specimens of black Broad-winged Hawks from Alberta (Dr. Victor Lewin, *in litt.* March 30, 1962), at the northwestern periphery of the range of this species; all three melanistic specimens in the Museum of Vertebrate Zoology are from Edmonton. This fact correlates well with the finding that melanism in North American buteos in general reaches its greatest expression in the western and northwestern parts of the continent. In this region are found two essentially western species with black phases, *B. swainsoni* and *B. regalis,* in addition to *B. harlani,* a blackish form closely related to *B. jamaicensis* and perhaps conspecific with it. The preponderance of melanistic birds in *B. jamaicensis* occurs in the western American race *calurus*; dark-phased individuals are rare or absent in all other races of this species (Friedmann, 1950: 237–267; Bent, 1937: 156). In *B. lagopus,* Cade (1955: 336) has shown that the greatest frequency of black-phased birds occurs in the region of the Aleutian Islands and southwestern Alaska.

The occurrence of occasional melanistic *B. platypterus,* then, is not seriously out of keeping with the lack of such dark individuals in other species of woodland buteo that do not reach the general area in North America that seems to "favor" the development of melanism.

## TAXONOMIC BACKGROUND

There has been no attempt in recent literature to group the woodland species in any manner that might indicate close relationship. All have been either widely scattered through the genus *Buteo,* with rather different species often placed between them, or have been placed in other genera.

Peters (1931) indicated no subgeneric breakdown within his seriation of 26 species of *Buteo*; the evidence of relationship he provides between the species, other than the comment that *B. ridgwayi* is "undoubtedly not distantly related to *Buteo lineatus*" (*op. cit.*: 228), is that "*Magnirostris* appears to have its nearest affinities with *Buteo platypterus.*" In addition he placed the Gray Hawk in the genus *Asturina,* following both *Buteo* and *Parabuteo.*

Hellmayr and Conover (1949: 84–164) list *B. lineatus* and *B. ridgwayi* in sequence; they separate these two species from *B. platypterus* and *B. magnirostris* by two dissimilar forms, *B. swainsoni* and *B. lagopus.*

Furthermore, they list five other species between *B. magnirostris* and *B. nitidus*, with the latter placed at the end of the genus.

Friedmann presents a classification in which the subgenus *Buteo* Lacépède includes, among several other species, *B. lineatus*, *B. ridgwayi*, and *B. platypterus* (the latter species is separated from the former two species by *B. swainsoni*); the subgenus *Rupornis* Kaup includes *B. magnirostris*; and the subgenus *Asturina* Vieillot is monotypic, being represented by [*B.*] *nitidus*. Furthermore, Friedmann places the subgenus *Butaetes* Moeschler (includes *B. lagopus*) between the subgenera *Buteo* and *Rupornis* and places the monotypic subgenus *Buteola* Bonaparte (containing *B. brachyurus*) between *Rupornis* and *Asturina*.

On osteologic evidence, Sushkin (1899) grouped together *Astur* [*Accipiter*], *Buteo*, *Asturina*, and *Rupornis* in addition to a number of other genera. In comparing skeletons of *Asturina* and *Rupornis* with those of *Buteo*, he stated (1899: 518) that *Asturina* may be called a *Buteo* with a less broad furculum. This difference emerges even more clearly in *Rupornis*. This bird already possesses a goshawk-like stature; furthermore, its prefrontal, with its steeply sloping superior edge, and also the impression of the temporal muscle are decidedly goshawk-like (translation).

Stresemann and Stresemann (1960) agree with Sushkin and accord separate generic rank to both *magnirostris* and *nitidus* as a result of their findings on molt patterns in diurnal raptors. Following Heinroth's (1898) division of molt types, they distinguish three principal modes: (1) the molt begins with the fourth primary. This mode is restricted to members of the family Falconidae. (2) Descending molt, a mode which begins with the first (proximal) primary and continues in a regular fashion to the tenth. This mode is found in a number of subfamilies and within some of these may be replaced by mode (3), which represents a random renewal of the primaries by the use of several molt centers. They subdivide mode 3 into mode 3a, which includes a descending molt (i.e., mode 2) when the year-old bird assumes the adult plumage, and irregular molts in successive years, and mode 3b, in which the bird molts in an irregular fashion during each cyclic feather replacement. On the basis of these criteria, Stresemann and Stresemann agree with Sushkin on the status of *Rupornis* and *Asturina*, because *magnirostris* and *nitidus*, like all members of the genus *Accipiter*, molt according to mode 2 and not modes 3a or 3b as do the species of hawks they place in the genus *Buteo*.

Within the Accipitrinae, as defined by the Stresemanns, several modes and combinations of modes may occur, as illustrated by the following examples (see table on pages 396–398 in their paper): *Accipiter* (mode 2), *Buteo* (3a, 3b), *Parabuteo* (2, 3), *Lophaëtus* (2 to 3), and *Hieraaëtus*

(3). In view of the authors' statement that they were able to subdivide mode 3 into 3a and 3b, it is puzzling that the modes of 11 of the genera included in the subfamily have been designated simply as "3." Furthermore, it is not clear what is meant by "2 to 3," the mode(s) assigned to the genus *Lophaëtus.* Moreover, modes 2 and 3, offered by the Stresemanns as evidence for the separation of *Rupornis* and *Asturina* from *Buteo, both* occur in the genus *Parabuteo,* which is monotypic. Thus we have an example of a single species which shows a latitude of variation in mode of molt equivalent to that found between genera and even subfamilies. Furthermore, if the difference in mode of molt were assumed to be great enough to justify removal of *Asturina* and *Rupornis* from *Buteo,* by the same reasoning could we not also justify *lumping Asturina* and *Rupornis* because they are similar in mode of molt? It is appropriate here also to recall that Sushkin (1899) and Miller (*in* van Rossem, 1934; see also comments below) both stated that *Asturina* and *Rupornis* are very similar osteologically.

Van Rossem (1934: 429) believed that if *Rupornis* were recognized it would need to include not only *Buteo magnirostris,* but also *Buteo platypterus,* and possibly *Buteo lineatus.* He further commented that if these three species were combined in *Rupornis, Asturina* would also need to be included because it is "very close to *Buteo lineatus.*" Moreover, van Rossem states that according to Dr. Loye Miller there is so little osteologic difference between *B. nitidus* (there called *Buteo plagiatus*) and *B. magnirostris* that "were this evidence alone considered . . . they could scarcely be distinguished as species." He concluded that to combine *Rupornis, Asturina,* and *Buteo* is preferable to either (1) grouping *Buteo platypterus* with "*Buteo*" *magnirostris* into the genus *Rupornis,* or (2) the recognition of *Asturina* as a connecting link between *Rupornis* and *Buteo.* We agree with this conclusion and would go one step further and suggest that *within* the rather heterogeneous genus *Buteo,* the species *B. magnirostris, B. ridgwayi, B. lineatus, B. platypterus,* and *B. nitidus* should be placed in sequence to indicate their probable close relationship.

## CONVERGENCE BETWEEN WOODLAND BUTEOS AND CERTAIN ACCIPITERS

There are numerous points by which the woodland buteos have apparently diverged from the buteos that inhabit open country and converged toward some species of woodland accipiters. These are discussed immediately.

*Plumage pattern.*—The plumage pattern of woodland buteos markedly resembles that of several species of *Accipiter* that also live predominantly in woodland, although such a pattern is not found in the prairie–savannah buteos. Furthermore, hawks of other widely different genera that live in tropical woodlands and forests, such as *Spizaetus*, *Micrastur*, and *Harpagus*, also tend to be barred below. A barred ventral plumage pattern probably has selective advantage in woodland hawks, perhaps because of its concealing effect.

Two North American accipiters, the Cooper's Hawk (*Accipiter cooperii*) and the Sharp-shinned Hawk (*Accipiter striatus*), possess a plumage sequence nearly identical with that of woodland buteos and similarly including a progression from streaks to either diamonds or to more or less distinct bars. A third North American (and pan-boreal) accipiter, the Goshawk (*Accipiter gentilis*), molts directly from a ventrally-streaked juvenal plumage into a barred or vermiculated plumage. Taverner (1940) believed that the width of the bars was probably dependent on the age of the bird, with the fineness of the vermiculations increasing with successive feather generations. The central European race of this species, *A. g. gallinarum*, which inhabits both deciduous woodland and mixed deciduous and coniferous growth to a large extent, molts from a streaked juvenal plumage into an adult plumage with a pattern of bold arrowhead- or triangle-shaped marks. With consecutive molts, these marks become narrower and take the form of bars, rather than fine vermiculations as found in the American race. It is of interest that the European form, that is more broadly barred below, occurs frequently in deciduous woodland, whereas the American form, that is more vermiculated below, occurs predominantly in coniferous forest.

Another European accipiter, the Sparrow Hawk (*Accipiter nisus*), also a species living in deciduous and mixed woodland, possesses a broadly-barred ventral pattern even in the juvenal plumage; an Asiatic race of this species, *A. n. nisosimilis*, shows a composite of streaks and broad ventral bars when in the same plumage. Both of these races molt into an adult plumage that is more finely barred.

Whereas a streaked or barred plumage pattern is thus of common occurrence in woodland hawks of temperate zones, in subtropical and tropical species of woodland and forest this pattern may be replaced by either a strongly contrasting dark-and-light pattern or by an almost entirely dark plumage. Plumages of this type are observed in very different species, for example, in *Accipiter chionogaster*, *Spizastur melanoleucus*, *Buteo brachyurus*, and in some forms of *Micrastur semitorquatus*. It is therefore possible that certain subtropical or tropical species may belong with the woodland buteos of this paper, but that their true relationship is not readily apparent because selection has favored either dark-and-light plumages or dark plumages, but has suppressed the development of barred plumages in some tropical woodland hawks.

*Wing shape.*—When seen in the field, the woodland buteos seem to show distinctly more rounded wings than the open-country species, and their general appearance in flight is strongly reminiscent of that of the accipiters. However, whether the primaries of woodland buteos are actually shorter in relation to the length of the secondaries in comparison with prairie–savannah species, and hence resulting in a more round-winged appearance, remains to be tested.

*Tail length.*—The proportionately longer tails of woodland buteos in comparison with most open-country species (Figure 6) are an obvious feature of the former group and once more remind one of the accipiters. Comparatively longer tails are perhaps selected for in woodland habitat because they theoretically improve steering ability in a situation where maneuverability is essential in capturing prey. Tail length may be further correlated with the evasiveness of prey items; the bird-catching accipiters possess very long tails, whereas the tails of woodland buteos, which feed to a large degree on slower prey, are relatively shorter.

*Tarsal length.*—The tarsi of both woodland buteos and accipiters are also relatively longer than those of prairie–savannah buteos (Figure 6). A long-legged raptor is presumably at an advantage in capturing prey in thick foliage and interlacing branches; furthermore, certain woodland accipiters are known to be swift runners and may follow their prey on foot into heavy cover (Voous, 1960: 74). Although to our knowledge such a foraging habit has not been reported in the literature as a characteristic of the woodland buteos, their varied diets imply considerable foraging flexibility and suggest that they may occasionally also chase prey in a similar manner.

Also, possibly in take-offs from trees and bushes, woodland hawks need the increased catapult effect offered by longer tarsi because of the presumed difficulty in such vegetation of dropping from a perch in order to gain flight speed by loss of altitude.

*Body size.*—The fact that the woodland buteos are all of relatively medium or small body size is an additional point of similarity; the open-country species are larger in comparison. There may well be a selective advantage in medium or small size for hawks in a woodland environment.

*Foraging of woodland hawks.*—Presumably in response to the nature of the habitat, woodland hawks have evolved remarkably similar foraging methods (Table 4). The following techniques may be distinguished.

(a) The still hunt, as noted by Marshall (1957: 69), appears to be a very effective and widespread method. The hawk perches quietly in a dense tree or other inconspicuous place and awaits the appearance of prey, which is then attacked with a sudden dash or stoop.

(b) The direct search flight involves systematic investigation of areas where prey is likely to be found. With intermittent or steady wing-beats,

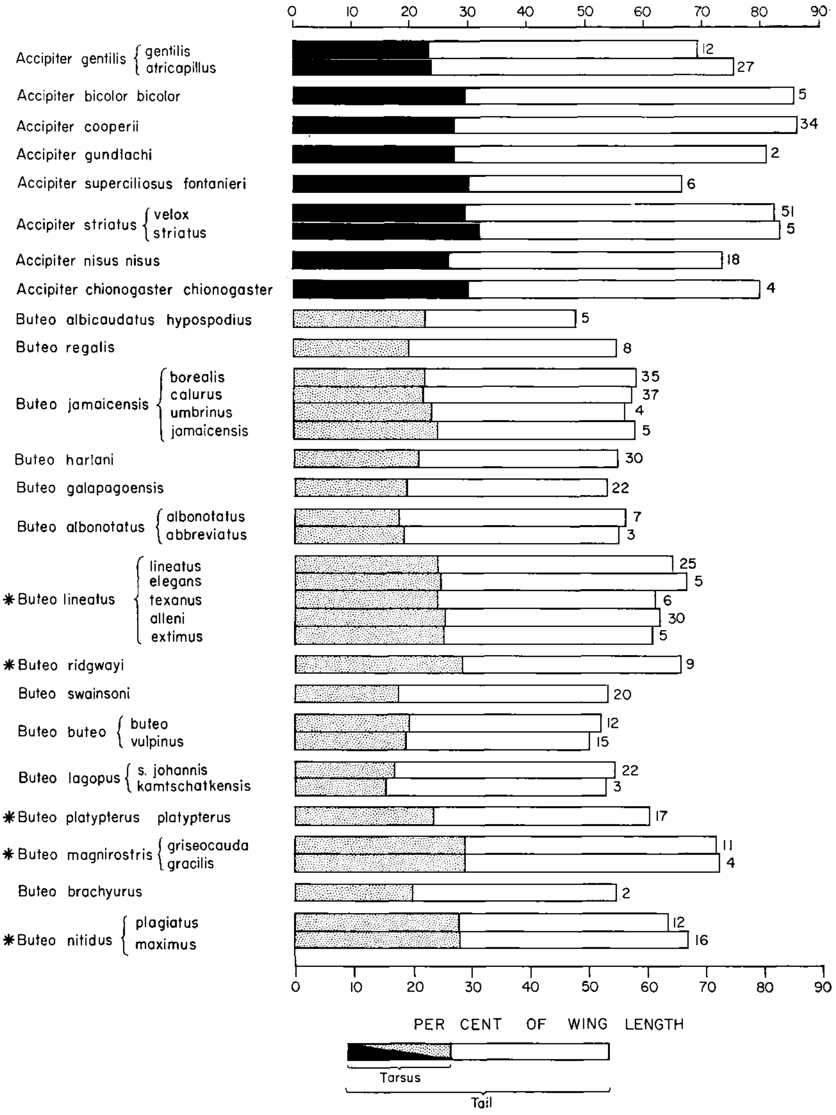

Figure 6. Relative lengths of tail and tarsi expressed as a percentage of wing length in 8 species of *Accipiter* and 15 species of *Buteo*. Measurements from which the percentages were calculated are predominantly from Friedmann (1950); those for species found only in the Old World are from Witherby *et al.* (1939). Note in particular the tendency of the woodland buteos (each species marked by an asterisk) to have relatively longer tarsi and tails than many of the other species of *Buteo* that live in more open country. Sample size given at right of bar representing each form.

TABLE 4

MAJOR FORAGING METHODS OF HAWKS[1]

| *Woodland–forest species* | *Still hunt* | *Direct search* | *Soar–stoop* | *Soar–sneak* |
|---|---|---|---|---|
| Goshawk (Brüll, 1937) | 2[2] | 1 | 4 | 3 |
| Cooper's Hawk (Marshall, 1957) | 1 | 2 | ? | 3 |
| Sharp-shinned Hawk (Peeters, MS) | 1(♂♂),<br>2(♀♀) | 2(♂♂),<br>1(♀♀) | 3(♀♀) | 2 |
| Red-shouldered Hawk (Bent, 1937; Grinnell and Storer, 1924) | 2 | 1 | ? | ? |
| Broad-winged Hawk (Burns, 1911) | 1 | 2 | 3 | ? |
| Roadside Hawk (Wetmore, 1943; Haverschmidt, 1962) | 1 | 2 | ? | ? |
| Gray Hawk (Haverschmidt, 1962) | 1 | 2 | ? | ? |
| *Prairie–savannah species*[3] | | | | |
| Red-tailed Hawk[4] (Grinnell and Storer, 1924) | 2 | ? | 1 | ? |
| Swainson's Hawk (Bent, 1937) | 2 | x[5] | 1 | ? |
| Zone-tailed Hawk (May, 1935) | ? | 1 | 2 | ? |
| White-tailed Hawk (Sprunt, 1955) | 1 | ? | 2 | ? |
| Rough-legged Hawk (Bent, 1937) | 3 | 1 | 2 | ? |
| Ferruginous Hawk (Bent, 1937) | 1 | 2 | 3 | ? |

[1] In some cases, observations made by the authors have been added to those supplied by the authorities cited above.

[2] Numbers indicate relative frequency with which a particular method is used by a species, i.e., 1 is most frequently used, etc.

[3] Open-country buteos often rest on conspicuous perches and probably thereby give the incorrect impression of engaging in extensive still hunting.

[4] Eastern and western races differ (see text, pages 438–439).

[5] Occasionally hunts insects on foot.

the hawk courses low either over or through woodland or open areas. High treetops, hedgerows, and shrubbery are frequently used as screens, especially by accipiters (see Brüll, 1937: 105), when approaching clearings and fields; these vegetation features enable the hawk to surprise the prey by a sudden dash.

(c) The soar (or hover) and stoop method, commonly used by open-country raptors, is infrequently observed in woodland hawks. It involves soaring or hovering at some height and plunging down at prey which may be flying or on the ground.

(d) Soaring combined with a subsequent attack by stealth, as mentioned by Marshall (*op. cit.*), seems to be used more commonly by woodland

TABLE 5

FOOD HABITS OF CERTAIN NEW WORLD HAWKS[1]

| | | *Per cent of stomachs in which item occurred* | | | |
|---|---|---|---|---|---|
| | *Number* | *Mammals* | *Birds* | *Reptiles and amphibians* | *Arthropods* |
| *Woodland–forest species* | | | | | |
| Goshawk | 881 | 26.0 | 56.0 | 0.2 | 1.2 |
| Cooper's Hawk | 422 | 15.0 | 55.0 | 1.4 | 3.6 |
| Sharp-shinned Hawk | 1,030 | 2.7 | 83.0 | — | 4.3 |
| Red-shouldered Hawk | 444 | 64.6 | 7.2 | 28.6 | 20.7 |
| Broad-winged Hawk | 254 | 37.4 | 6.7 | 33.4 | 54.7 |
| Roadside Hawk[2] | — | — | — | x | x |
| Gray Hawk[3] | — | x | x | x | x |
| Ridgway's Hawk[4] | 3 | x | x | x | – |
| *Prairie–savannah species* | | | | | |
| Red-tailed Hawk | 1,013 | 84.6 | 19.4 | 11.6 | 13.0 |
| Swainson's Hawk[5] | 44 | 22.7 | 4.5 | 13.6 | 70.4 |
| Zone-tailed Hawk | 10 | 10.0 | 40.0 | 50.0 | — |
| Rough-legged Hawk | 221 | 100.0 | 4.5 | 3.6 | 10.0 |
| Ferruginous Hawk[6] | 24 | 87.5 | 8.3 | 8.3 | 8.3 |

[1] Except as otherwise noted, these percentages were calculated from May (1935), who summarized food habit data of raptors from numerous sources in the literature. Data on stomach contents presented in this manner can be misleading because they do not show the number of items, or the weight of prey taken from each category, information which has greater ecologic significance than a mere tabulation of per cent occurrence of a given category of food in the total number of stomachs. For our purposes, however, this table at least provides a basis for the generalization that the accipiters, the woodland buteos, and the prairie–savannah buteos are fundamentally different in their food habits (see text, page 439). More detailed information on the food of many of these species can be found in Fisher (1893), who provides lists of the contents of individual stomachs.

[2] Diet consists chiefly of lizards according to Lowery and Dalquest (1951), Eisenmann (1957), and Haverschmidt (1962). The latter author reports that frogs, snakes, and large insects are also taken.

[3] Reported to eat a variety of foods; evidently shows no general preference (Bent, 1937; Ligon, 1961).

[4] Data from notations on three specimen labels: "rat," "ground dove," and "lizards."

[5] McAtee (1935) provides information on 111 additional stomachs of this species, of which 62 contained ground squirrels; 5, pocket gophers; 8, mice; 3, rabbits; 9, snakes; 5, lizards; 5, toads; 1, a turtle; 1, a frog; 24, grasshoppers; 18, crickets; 8, caterpillars; and 20, other insects.

[6] McAtee (1935) provides data for an additional 17 stomachs of this species, of which 8 contained rabbits; 4, squirrels; 4, mice; 2, birds; and 1, a cricket.

hawks. While soaring the hawk apparently locates concentrations of prey animals, such as flocks of birds. It then approaches the prey much in the same manner as in the direct search flight. This method is particularly effective in capturing swift and alert prey and is hence observed often in accipiters.

The method most commonly used by each species (see Table 4) may be a function of that species' prey preference. Thus the woodland buteos, which feed principally on relatively slow-moving prey (see Table 5), more frequently employ still hunting than the bird-catching accipiters. The point to stress is that the foraging methods of the woodland buteos are much more similar to those of the accipiters than to those of the prairie–savannah buteos. It is thus reasonable to assume that these methods have probably evolved in response to the nature of the habitat. This is supported by Marshall's statement (*op. cit.*) concerning the foraging of the Red-tailed Hawk. The eastern race (*B. j. borealis*), a bird of broken woodland and meadows, commonly employs the still hunt method, whereas the western race (*B. j. calurus*), which inhabits prairie–savannah country, typically uses the soar and stoop method.

*Food habits of woodland hawks.*—Divergence in food habits probably plays an important role in permitting local sympatry of woodland hawks. For example, where the Goshawk and the Sharp-shinned Hawk coexist, competition for food is apparently reduced to a minimum because of the great difference in the average size of prey taken. The fact that one of the two small accipiters will displace the other, but will tolerate a woodland buteo may also be based on the differences in prey preference. Food studies of breeding Cooper's Hawks and Red-shouldered Hawks, two species which commonly nest in local sympatry, elucidate this point (Meng, 1959: 170; Craighead and Craighead, 1956: 276).

The stomach analyses supplied by May (1935) illustrate that the diets of woodland buteos are much more varied than those of the accipiters (Table 5), a difference likely permitting these two groups to live in local sympatry because of lessened competition (see Lack, 1946: 123). The diets of prairie–savannah buteos are also varied, although each species nevertheless tends to have a strong prey preference. The occurrence of an apparently predominant prey item in the diet of a woodland buteo in no case reaches the high percentage of a staple item in the diet of an open-country buteo. Thus, although the woodland buteos may reduce or avoid competition with other raptors, particularly the accipiters, through diversity of prey items selected in a woodland habitat, they show basic resemblance in diet to their congeners inhabiting open country.

There seems to be no woodland buteo in Europe, a fact perhaps related both to the paucity of the herpetofauna in the Palaearctic (Mertens, 1960: 33) and to competition with accipiters (*A. gentilis* and *A. nisus*). *Buteo buteo* partially fills the "woodland buteo niche" in Europe by occupying the edges of broken woodland and meadows and by taking an extremely varied diet (Voous, 1960: 55). Raptors from other genera in Europe may act as partial ecologic equivalents to the North American woodland buteos. For example, the Lesser Spotted Eagle (*Aquila pomarina*) of the Palaearctic has a varied diet, obtained chiefly in woodland meadows, which includes a high percentage of frogs (Uttendörfer, 1939), and the Snake Eagle (*Circaëtus gallicus*) feeds almost exclusively on snakes by still hunting in woodland and forest situations (Engelmann, 1928: 232). These eagles are not common in Europe, hence their roles as predators in or near woodlands may be insignificant. In southern Europe, two accipiters (*A. badius* and *A. brevipes*) have unexpectedly varied diets (Voous, 1960: 74; Engelmann, 1928: 293), perhaps thereby compensating for the lack of a woodland *Buteo.*

*Adaptations for sympatry in woodland hawks.*—Two or more species of woodland hawks occasionally breed in local sympatry (see Bent, 1937: 186), although only species with marked differences in body size, plumage characteristics, and food habits seem to coexist. Within the three strongly heteromorphic North American accipiters, habitat overlap occurs most often between the Goshawk and the Sharp-shinned Hawk, the two species that show the greatest size and plumage divergence. However, where the habitat of the Sharp-shinned Hawk overlaps with that of the Cooper's Hawk, one species usually displaces the other locally, although it may tolerate co-occupancy by one of the woodland buteos (Bent, 1937).

The five species of woodland buteos have apparently developed adaptations for sympatry in North and Central America and in the West Indies comparable to those shown by the accipiters. Dissimilarities in body size and/or in color of adult plumage exist between the species pairs that are sympatric, *B. platypterus–B. lineatus* and *B. magnirostris–B. nitidus.* Differences in details of habitat preference also promote local allopatry between members of sympatric species pairs. Conversely, species of very similar size and plumage, the Ridgway's Hawk, Broad-winged Hawk, and Roadside Hawk, are completely allopatric. For example, in the West Indies, *B. ridgwayi* and *B. platypterus* (races *B. p. cubanensis, B. p. brunnescens, B. p. insulicola, B. p. rivierei,* and *B. p. antillarum*) do not overlap in distribution (Bond, 1961: 58–59) in spite of the fact that their northern counterparts, *B. lineatus* and *B. p. platypterus* (strongly divergent in size and in color), occur together in many areas in the eastern United States.

## DISCUSSION

*Plumage pattern.*—The theory of our ontogenetic plumage pattern system is based on the observation that the patterns of the ten plumages of the five species of woodland buteos can be arranged in a sequence in which the feather markings of a given plumage provide, however imperfectly, transitional stages between the markings of other plumages. By this means we can identify two "sequences of patterns," one of which involves a progression in pattern of the ventral body plumage from streaks or tear-drop marks through diamond or heart-shaped marks to bars, and the other involving a change in the tail pattern from a tail with numerous, narrow and slightly contrasting alternate bands to a tail with a few, wide and obviously contrasting alternate bands. We are not suggesting that any of the buteos under discussion passes through *each* of these progressive stages as it attains its definitive adult plumage, but merely that the two plumages of each species may be fitted easily into the system.

There are two main lines of evidence suggesting such a direction of ontogenetic change in plumage pattern: (1) the difference between the juvenal and the adult plumages of a given species always involves a change in the pattern system as described above, and (2) within the development of a *single* generation of feathers, the markings of the feathers appearing later represent more advanced levels in the pattern system than those appearing earlier.

An assumption that serves as a partial basis for the preceding comments on plumage is that ontogenetic change in feather markings in a species can provide clues concerning the probable evolution of the plumage pattern. Further implications are (1) that within a species the juvenal plumage is probably closer to the ancestral plumage than is that of the adult, (2) that the "original" adult plumage was similar if not identical to the ancestral juvenal plumage, and (3) that the evolution of a distinctive adult plumage very likely involved an elaboration or a manipulation of the developmental pattern that originally produced the pattern of the juvenal plumage.

The pigment giving rise to the pattern of a given feather is not deposited in a continuous fashion from one feather generation to the next because of the intervening molt. It is reasonable to assume that at least some of the same physiologic pathways by which the juvenal feather pigment is deposited are also followed when the pattern is being organized for an adult feather. Theoretically, when the adult pattern began gradually to diverge from that of the juvenile, the change in site of pigment deposition leading to a distinctive pattern was also gradual. Certain of the steps in the juvenal patterning process were perhaps modified or omitted, so that eventually the physiological mechanism producing the adult pattern probably involved the use of only part of the juvenal process. Selection would likely favor certain aspects of feather pattern development used in the production of the juvenal plumage, as the adult pattern-forming mechanism evolved.

It is postulated that during the evolution of the adult plumage of a particular species a transitional series of patterns existed that emanated at least in part from the juvenal pattern. If we accept this hypothesis it is conceivable that an important source of heritable variation in plumage pattern is available to a species by selection for certain developmental steps, and therefore on different stages in the pattern system.

Evidence that evolution may have stressed certain stages during the development of the plumage patterns of the woodland buteos is found in *Buteo lineatus*. From the previous descriptive remarks it is apparent that the juvenal ventral body plumage shown by a particular race of Red-shouldered Hawk can readily be fitted into the hypothetical pattern system outlined earlier. The various races have juvenal plumages which show differences that go beyond mere changes in the number, color, and distribution of the ventral body markings. The geographic variation in size and, particularly, in *shape* of markings, manifested by an emphasis on streaking in the east and on barring in the west, can be explained as resulting from the use of later ontogenetic stages of the pattern system by the western populations. The geographic concurrence of changes in tail banding with changes in ventral body feather pattern that occur from one race to another also support this concept. Although the adult ventral plumage markings of *B. lineatus* are more uniform from one race to another than are those of the juveniles, the tail banding suggests that the western populations of the adults have also used later ontogenetic stages than those in the south and east.

If patterns of intraspecific geographic variation in *Buteo lineatus* fall along ontogenetic lines, it is logical to suppose by extension that the patterns of all these woodland buteos are fundamentally similar, and that they could have been arrived at through manipulation of developmental pathways used during pattern development by a single phyletic line.

Differences in somatic developmental rates could very likely influence the level in the pattern system reached by a given plumage of a given species. Thus, the concept of proterogenesis (Rensch, 1960: 258–259) may be applicable here, in which the retardation or acceleration of somatic developmental rates typical of one plumage could result, for example, in the juvenal plumage of one species resembling the adult plumage of another.

*Taxonomic recommendations.*—The use of a common plumage pattern system by the woodland buteos does not in itself provide evidence of close relationship; there are a number of other unrelated species of raptors that have a streaked juvenal plumage followed by an adult plumage characterized by numerous ventral diamond-shaped marks or bars. However, the existence of many important additional similarities in both structure and behavior, *in the absence of significant structural dissimilarities*, argues in support of natural relationship rather than implying the convergence of two or more basically distinct phyletic lines. Considering the rather wide divergence in types that one sees generally in the present-day members of the genus, the woodland species are a surprisingly uniform group in such features as plumage pattern, body proportions and size, flight habits, foraging methods, food habits, and habitat selection. Although all or most of these similarities could be a result of occupation of woodland by distantly related members of this complex genus, equally probable is that a closely related group of congeners evolved as an adaptive unit in the woodland niche. There are other examples of species groups or subgenera that have apparently evolved as adaptive units for particular modes of life. For example, in the genus *Parus* we find the *Poecile* group of species distinct from the *Baeolophus* group in important features of locomotion and foraging niche (Dixon, 1961). Hamilton (1962) has shown that in the genus *Vireo*, most members of one major group of species (subgenus *Vireo*) prefer thicket foraging, and that all the members of another group of species (subgenus *Vireosylva*) have arboreal foraging tendencies.

We think that the evidence most strongly supports the view that *B. magnirostris*, *B. ridgwayi*, *B. lineatus*, *B. platypterus*, and *B. nitidus* are closely related, although it would be unwise to group them into a formal subgenus until the remainder of the species in the genus can be analyzed in a comparable fashion. Nevertheless, until the other members of *Buteo* are better known, we conclude that there is sufficient evidence for placing the woodland species together in the linear sequence offered above.

*Relationships within the woodland buteo group.* — The following remarks are offered as partial justification for our proposed sequence of species. In agreement with several earlier workers, it is our impression that *B. magnirostris* and *B. nitidus* stand somewhat apart from the other three species. *B. magnirostris* is rather accipitrine in proportions, and the juvenal and adult plumages do not fit as neatly into the pattern system as do the plumages of the other woodland species. *Buteo nitidus*, particularly as represented by the southern races, also possesses a rather distinctive juvenal plumage. In spite of these differences, however, both species seem much closer to the woodland buteos than to other members of the genus. By starting a revised sequence of species of *Buteo* with *B. magnirostris*, following a listing of the species of *Accipiter*, we recognize the accipitrine proportions of this form and provide an appropriate "link" between *Accipiter* and *Buteo*, two genera of close relationship (see Sibley, 1960: 241). A point of speculation is that the accipitrine proportions of the Roadside Hawk may be related to the success of this species in Neotropical lowlands where sympatric species of *Accipiter* of similar size are rare or absent. The degree to which this buteo may participate in an unfilled "accipiter niche" remains to be determined.

From our examination of study skins we agree with Peters (1931) that *B. ridgwayi* is most closely related to *B. lineatus*; these two species have essentially the same patterning of juvenal and adult plumages in addition to similar wing–tarsus and wing–tail ratios. Both possess rufous "shoulders," although this point is of dubious significance. Similarities in color and size that we regard as superficial apparently led certain past workers to link *B. ridgwayi* with *B. magnirostris* into the genus *Rupornis*. The rather different wing–tail ratios and juvenal plumages shown by these latter species, however, do not support the idea of very close relationship.

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## SUMMARY

This paper presents evidence that five species of New World hawks, widely scattered in the genus *Buteo* or placed in other genera in current classifications, are actually closely related. These species are the Roadside Hawk, Ridgway's Hawk, Red-shouldered Hawk, Broad-winged Hawk, and Gray Hawk. All occupy woodland or woodland-edge habitats and belong to what is here described as a "common ontogenetic plumage pattern system." Plumage patterning is reviewed in detail for each species; certain errors in the literature concerning the plumages of several forms are corrected. Additional similarities between these species that distinguish them from open-country or "prairie–savannah" buteos are the lack or rarity of a melanistic phase, comparatively long tail and tarsus, medium or small body size, common use of still hunt and direct search methods rather than the soar–stoop method of foraging, and extremely varied diet with no obvious staple food item.

Convergence with certain accipiters is shown by the woodland buteos in habitat preference, plumage sequence and patterning, body size and proportions, and in foraging habits. Competition between the woodland buteos and the accipiters is probably reduced as a result of differences in food preference. Adaptations for sympatry by woodland hawks involve divergence in body size, plumage characteristics, and food habits.

Because there are no important structural dissimilarities between the woodland buteos that provide meaningful evidence of convergence, we think the numerous morphologic and behavioral similarities are a result of close relationship within the genus and that the five species evolved in parallel fashion, probably from a common ancestor that was adapted to the woodland niche.

Pending a review of the entire genus *Buteo*, it is proposed that the sequence of species as presented above should be adopted without the delineation of a formal subgenus.

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