Plumage variation and winter range of Harlan's Hawk (Buteo jamaicensis harlani)

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PASTOR C. L. BREHM (1787-1864) described hundreds of species from his native haunts near Thuringen, Germany, at a time when our current concept of species as populations unified by reproductive compatability was in its infancy. Brehm's descriptions include 14 different species of House Sparrows alone, and reflect the then common view of species as "types," rigidly defined by appearance, and mostly lacking variation. We now recognize that within species variation is more the rule than the exception, and is in some instances a result of natural selection At least 315 subspecies of North American breeding birds, including Harlan's Hawk (Buteo jamaicensis harlani), were described initially as full species (Mayr and Short 1970). Different species may show different amounts of variation both locally and throughout their ranges. This requires us to learn not only the principal species characteristics, but also the nature and geographic distribution of its variation. Although the work of early naturalists such as Brehm, and in our own country Alexander Wilson and John James Audubon, as seen in hindsight, gave rise to a classification top-heavy with species, their focus on variation remains a modern concern, providing insight into relationships of populations both within and between species.

The Red-tailed Hawk (*Buteo jamaicensis*) is one of several North American *Buteo* species that show sufficient geographic variation to warrant naming of subspecies (polytypy), as well as discontinuous variation within local populations (polymorphism). The subspecies *B. j. harlani* breeds in portions of Alaska and western Canada where relatively few observers have an opportunity to become familiar with its plumage variations.

During the winter, when Harlan's Hawks are visible to more people, they are mixed with other Red-tailed Hawks, and the advantage of knowing a bird's geographic origin for identification purposes is lost. Those that do not show "typical" characters of harlani, such as extreme melanism and an unbarred tail, may not be recognized as being harlani. Despite published descriptions of light-phase harlani (Ridgway 1880, Taverner 1927, Friedmann 1950) doubt persists as to its existence. This may stem from the frequently dark characteristics of harlani and the often vague nature of subspecific distinctions. The race harlani, however, has tail characteristics that can frequently be recognized in the field. Recent field work in Alaska supports harlani's subspecific status and describes the widespread occurrence of highly variable forms having harlani ancestry (Mindell 1983).

In this article I present photographs of Red-tailed Hawks with and without *harlani* ancestry, showing some of the range in plumage color and pattern that occurs. Updated information on the winter range of this race, and an analysis of changing frequency of occurrence in the western United States, are also given.

MORPHOLOGY

Two SIBLING Red-tailed Hawks of harlani ancestry from the Kuskokwim River in southwestern Alaska (Figs. 1-3) were taken into captivity as nestlings in 1982. One is light in plumage, while the other is moderately dark with a somewhat rufous bib. One of the parents, seen and photographed, was a "typical" dark Harlan's, with a tail mostly white with a dark terminal band, some dark mottling, and no red (similar to Fig. 4). At 17 months of age the same siblings show their second-year plumage (Figs. 5-8). Both have darkened. The darker one has developed the characteristic white spotting on the belly, flanks and underwing linings, while the other has a darkened band on the belly, with the upper breast and crown still light. In this first "adult" plumage the siblings have similar tails (Figs. 5 and 7), showing a mix of barring and mottling with rufous, white and light brown background colors. Brown to black mottling and streaking in the tail are the most distinctive plumage trait of Harlan's Hawk.

A third captive Red-tailed Hawk of harlani ancestry from the Kuskokwim River (Figs. 9-11), shows the adult barred-tail morph. This bird was taken as a nestling in 1981, three km distant from the nest of the siblings mentioned above This bird's tail was nearly identical in its second- and third-year plumages. Both parents of this bird were moderate-todark harlani with tails having some barring and lacking any prominent red color A bird with the same appearance from south-central Alaska was identified as B j. calurus, a subspecies widespread in western North America, by Taverner (1927, Plate III, Fig. 2), although there is no evidence directly linking this morph to calurus parents. Field observations described above, have been made, however, linking this morph to parents of harlani ancestry. This morph could possibly be the result of interbreeding between harlani and calurus. Tail barring in harlani, varying from faint to pronounced, 1s fairly common in southwestern Alaska An injured bird of harlani ancestry found during March 1982 in Provo, Utah (Figs 12 and 13; for description see White et al 1983), further illustrates the great vari-



Fig. 1. Sibling Buteo jamaicensis harlani from the Kuskokwim River, southwestern Alaska, at age 1.5 months. The birds are identified from left to right as A and B. Note the differences between siblings in head and tail characters. Photo/D. P. Mindell.



Fig. 2. Sibling A at age 9 months, in "immature" plumage. Photo/D. P. Mindell.



Fig. 4. Adult harlani trapped in Tucson, Arizona, in April. Photo/W. S. Clark.



Fig. 5. Sibling A at age 17 months, in first "adult" plumage. Note overall darkening from Fig. 2. Photo/D. P. Mindell.



Fig. 3. Sibling B at age 9 months, in "immature" plumage. This is an example of a light-phase bird of harlani ancestry. Photo/D. P. Mindell.



Fig. 6. Sibling A at age 17 months, in first "adult" plumage. Note overall darkening from Fig. 2. Photo/D. P. Mindell.



Fig. 7. Sibling B at age 17 months, in first "adult" plumage. Note darkening in tail compared to Fig. 3. Photo/D. P. Mindell.



Fig. 10. Bird C at age 2 years and 4 months, in second "adult" plumage, showing the adult barred-tail morph. The first "adult" plumage was nearly identical. Note the darkening in eye color compared to Fig. 9. Photo/D. P. Mindell.



Fig. 8. Sibling B at age 17 months, in first "adult" plumage. Note slight darkening in breast and belly compared to Fig. 3. Photo/D. P. Mindell.



Fig. 9. Buteo jamaicensis harlani C taken as a nestling from the Kuskokwim River, southwestern Alaska, shown here at age 7.5 months, in "immature" plummage. Photo/D. P. Mindell.



Fig. 11. Bird C at age 2 years and 4 months, in second "adult" plumage, showing the adult barred-tail morph. The first "adult" plumage was nearly identical. Note the darkening in eye color compared to Fig. 9. Photo/D. P. Mindell.



Fig. 12. Male harlani (possibly an intergrade) found dead in Provo, Utah, in January (BYU 7622). This is another example of a light-phase bird with harlani ancestry. Photo/D. P. Mindell.

ation that can occur, and provides a second example of a light-phase Red-tailed Hawk with strong *harlani* tail characteristics. Figure 14 shows another example of an apparent *harlani* intergrade; having more red in the tail than "pure" *harlani*, yet showing characteristic *harlani* dark streaking and mottling in the tail.

Immature Harlan's Hawks share the general tail characteristics of gray-brown color, and about seven blackish bars, with immatures of other subspecies of the Red-tailed Hawk. In many instances it may not be possible to identify immatures to subspecies accurately. In observations of 22 nestlings and fledglings of harlani ancestry more than 25 days old in southwestern Alaska, I saw much variation in the plumage of both body and tail (especially in width of tail bars). A comparison of the immatures in Figures 1-3 and Figure 9 indicates their range. Nestlings from southwestern Alaska often had distinctive white highlights in the rectrices, especially on the inner portion of the vanes. In the captive birds, however, these faded quickly after about four months.

A pale subspecies, B. j. kriderii, has been described from the central North American plains (see Friedmann 1950; Figs. 15 and 16). The races harlani and kriderii are the only subspecies of Redtailed Hawk with white in the tail. Lightphase harlani and kriderii can appear quite similar (compare Figs. 7 and 8 with Figs. 15 and 16). However, neither kriderii nor calurus is known to show streaking and mottling in the tail. Krider's may be less abundant than other races of the Red-tailed Hawk even within its described range. Distribution and abundance of this pale morph are still poorly known, and await further study, especially on the breeding grounds.

WINTER RANGE

THE WINTER RANGE OF Harlan's Hawk L has traditionally been described as lying within the south-central United States, including Arkansas, northern and central Louisiana, southern Missouri, eastern and central Texas, Oklahoma, and Kansas (Wood 1932, Friedmann 1950). These areas contain the most obvious winter concentrations of harlani; they do not, however, represent all of the latter's winter range. Harlan's has been reported from every state west of the Mississippi River except Nevada, and at least once from the eastern and southern extremes of Massachusetts, South Carolina, and north-central Mexico. Lowe (1978) found that *harlani* comprised 8.6% of the wintering Red-tailed Hawks in an area in central Oklahoma. The density of wintering *harlani* is less outside of the south-central United States core area, but individuals and even populations are consistently found in certain areas in the western United States.

Among other sources on harlani winter range, I used Christmas Bird Count (hereafter, C.B.C.) results, reported annually in American Birds. Fortunately, harlani is still listed on current C.B.C. reporting forms, despite the fact that it is no longer considered a separate species. Not all compilers or participants are aware of or bother to recognize harlani as a separate entity, but at least some do. Based on C.B.C. data from 11 western states (Washington, Oregon, California, Idaho, Nevada, Arizona, Montana, Colorado, Utah, Wyoming, New Mexico), areas reporting one or more harlani in three or more years during 1978-1982 are: Denver, Ft. Collins, Boulder, and Pueblo, Colorado; Spokane and Walla Walla, Washington; and Panoche Valley, California. Denver has reported as many as twelve during one C.B.C. Harlani reports in two years during 1978-1982 were made in Weldona-Ft. Morgan, Colorado; Bosque del Apache, New Mexico; Nampa, Idaho; Phoenix, Arizona; and Padilla Bay, Washington. Except for Nevada, Harlan's Hawks were reported at least once during this period from all of the 11 western states. The lack of harlani reports from Nevada is likely due to the low number of observers there.

In compiling the above information. I noticed that many of the C.B.C. stations from the western states seemed to report harlani more often during 1978-1982 than during previous years. This led me to test the hypothesis that the incidence of reports of harlani in the western states had remained the same during the past 30 years. Since it is possible that any change in the harlani reporting rate in the western states is simply an artifact of the increasing number of C.B.C.s being run and of more knowledgeable observers, I tried to minimize these potential biases. As a control area I selected four southcentral states (Arkansas, Oklahoma, Kansas, and Louisiana). The number of C.B.C.s in the western states and the control area increased by similar proportions between 1951 and 1982 (21% and 25% respectively), and, presumably, change in proficiency of observers also were similar. Using C.B.C. data from three five-year blocks (1951-1955, 1965-1969, 1978-1982), I calculated the following percentage for each of the two areas: number of stations that were run for at least two years during the five-year block prior to the first harlani report, divided by the total number of stations that have ever reported harlani (10/44 for the south-central states, and 22/46 for the western states). This provides a comparative measure of the change in harlanı reporting rate over time, using only stations that have reported harlani at least once and that have been active for 15 or more years. This percentage can also be thought of as measuring the incidence of traditional C.B.C.s reporting harlant for the first time in recent years. I used the Test for Equality of Two Percentages (Sokal and Rohlf 1969:607) and found the two percentages to be significantly different (test statistic = 2.53; p < 05), with the western states showing a greater increase in harlani reporting rate over time. Caution must be used, however, in interpreting this result.

DISCUSSION

Plumage

THE PHOTOGRAPHS presented here indicate the broad range of plumage variation in harlani. Even greater variety can be seen in the field or in a large series of museum skins. Adult Red-tailed Hawks with harlani ancestry can occur in many color phases, grading from light to dark, as well as a morph with a barred tail. Despite these variations, adult harlani can often be recognized in migration and during winter by their unique tail characteristic of mottling and streaking, usually on a light background. The form with a barred tail can also be identified as harlani outside of the breeding range if it is seen at close enough range to determine that it is not an immature.

The source of the geographically widespread morphological variation in harlani is unclear. Intergrades, the result of interbreeding between subspecies, generally show a mixture of parental characters that can spread into parental populations to varying degrees. During the breeding season B. j. calurus generally replaces harlani to the east and south. "Typical" examples of harlani (Fig. 4) and calurus (Fig. 17) illustrate some of the variety of parental characters. Intergrades account for at least some of the variation, especially in zones of contact between subspecies' ranges. However, some may be due to polymorphism within harlani That is "pure" harlani may occur in light, dark, or intermediate color phases, with or without varying amounts of rufous



Fig. 13. Male harlani (possibly an intergrade) found dead in Provo, Utah, in January (BYU 7622). This is another example of a light-phase bird with harlani ancestry. Photo/D. P. Mindell.



Fig. 14. An apparent harlani intergrade trapped at Hawk Ridge Nature Reserve, Duluth, Minnesota, in October. Photo/D. L. Evans.



Fig. 15. Apparent Buteo jamaicensis kriderii trapped at Hawk Ridge Nature Reserve, Duluth, Minnesota, in October. Photo/D. L. Evans and R. N. Rosenfield

Fig. 16. Apparent Buteo jamaicensis kriderii trapped in Hawk Ridge Nature Reserve, Duluth, Minnesota, in October. Photo/R. N. Rosenfield.



and/or barring in the tail. Tail barring also occurs to a varying extent in *calurus*. The difference in plumage pattern and color between the Alaskan siblings (Figs. 1-3 and 5-8) demonstrates polymorphism within a family that is at least partially, and perhaps entirely, *harlani*.

In a detailed study of the Northern Oriole (*Icterus galbula*) Rising (1970:327) found variation within *I. g. bullocki*, with some characters that could be explained by introgression (genetic mixing). He stated: "Variation of this sort might be taken to support the introgression model promulgated by Sibley and Short (1964); however, these differences as easily may be taken as reflecting local adaptive variation (area effects) that is in no way related to introgression. Or, they may be of no (adaptive) significance whatsoever." This statement could also be applied to variation within the range of *harlani*.

Attempting to determine whether the variation is due to intergradation or to "pure" *harlani* variants must await analysis of many different characteristics, possibly both morphological and biochemical, from a large, geographically representative series of Red-tailed Hawks. It is likely that variation is caused by both polymorphism within *harlani* and interbreeding with other subspecies, although the two causes should differ in importance depending on locality.

Winter range

NALYSIS OF C.B.C. data must be A considered cautiously. As a subspecies, harlani is not given equal attention by all compilers and counters. Many C.B.C. participants are unaware of harlani as a separate entity, and there are likely many compilers who opt not to record harlani on their reporting forms even if it is observed. This could mask the actual distribution and change in reporting rate of harlani over time. The bias, however, exists in both the western and south-central areas, and should have a low net affect. During 1957-1973, when harlani was listed as a full species by the American Ornithologists' Union, inclination to report harlani on C.B.C.s was probably higher than at present. This would have served to create an effect (decrease in reporting rate after 1973) opposite to the increase in rate found in the western states. Another potential bias, the missing of many harlani reported simply as Red-tailed Hawks or even possibly as Rough-legged Hawks (Buteo la-



Fig. 17. Buteo jamaicensis calurus trapped in Tucson, Arizona. Photo/W. S. Clark.

gopus), would be a result of the great morphological variation. Some birds with *harlani* ancestry could be difficult to identify, even in the hand. In birds of mixed ancestry, visible *harlani* characteristics may not show up in each generation. The biasing factor of variation, however, likely effected past and recent C.B.C. results similarly.

The number of parties and observers per C.B.C. station has increased over time in both areas, possibly resulting in more reports of rare or uncommon occurrences. If this is the case then, it could be argued that *harlani* is not more common in the western United States now than in the recent past, but merely observed more often. But harlani is reported from only a percentage of the south-central states' C.B.C.s (20% of total in 1982), and, again, the effect of increased observers could be expected to result in more C.B.C.s reporting harlani for the first time in the control areas as well as the western states. Unequal representation of different habitats is another bias when comparing regional C.B.C. data. For this reason I considered in the analysis only C.B.C.s in which harlani was reported at least once, hoping to diminish this bias. Because I have used presence vs. absence rather than numeric abundance, I have not attempted to "standardize" the C.B.C. data using total partyhours or other measures of count effort.

The control area was used to test the effect of the potential biases discussed above. The biases should operate similarly in both areas, and on the basis of the significant difference found between the areas, a real difference is indicated. The large geographic area considered and the large sample size used, 3097 C.B.C.s during 15 years spanning a 30-year period, also serve to minimize local or shortterm effects, and provide a better indication of real patterns (Bock and Root 1981). Wintering harlani have apparently increased in occurrence in the western United States, to at least a small degree, over the past 30 years. The increase is

substantiated locally by documented "first occurrence in 1968 and occurrence since then with increasing regularity and increasing numbers . . ." in areas of Washington frequently visited by observers both before and during the increase (Lavers 1975:55).

Change in the winter range of harlani does pertain to morphological variation. Intergradation is a genetic phenomenon, and can affect genetically controlled behavior such as migration (see Biebach 1983), as well as morphology. Although zones of intergradation are known to remain fairly stable in some instances (Mayr 1970, Rising 1970, 1983), if intergradation were common and increasing in frequency in a migratory population such as harlani, characteristics of migratory behavior, such as length of migration and location of winter range, might also be influenced by both parental populations. Harlani apparently intergrades most often with calurus, a partially migratory Red-tailed Hawk subspecies of western North America during both breeding and winter seasons. Increasing genetic mixing between harlani and calurus could lead to greater incidence of wintering harlani in the western United States. If genetic mixing is an important factor, harlani breeding south of their normal range might also be seen. This is not to suggest that the winter range analysis discussed here demonstrates increasing introgression in harlani, but is merely to point out a situation that ornithologists might find interest in watching.

To some people, birds with *harlani* ancestry will be a frustrating group; difficult to describe with quick, present-orabsent type characters, and disrupting preconceived notions of the absolute distinctness of species and populations. Others will find in *harlani* an exciting chance to watch birds in an intermediate evolutionary stage.

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