HARLAN'S HAWK (*BUTEO JAMAICENSIS HARLANI*): A VALID SUBSPECIES

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ABSTRACT.—During surveys of 19 different rivers in central and southwestern Alaska, north of the Alaska Peninsula, all Red-tailed Hawks (*Buteo jamaicensis*) seen were either *B. j. harlani* or *harlani* intergrades, demonstrating that *harlani* does have a breeding range exclusive of other Red-tailed Hawk subspecies and is, therefore, a legitimate subspecies. The range of *harlani* intergrades was widespread and overlapped the *harlani* breeding range entirely. The findings presented suggest that the breeding range for *harlani* and its intergrade forms, exclusive of other Red-tailed Hawk subspecies, is: west to Norton Sound, east to the Alaska Range west slope, north to the tree line, and south to the Alaska Peninsula. *Harlani* may have diverged morphologically from other Red-tailed Hawks by isolation in a Pleistocene epoch glacial refugium, as has been suggested for other northern bird groups. The possibility of paripatric speciation, however, must also be considered. The characteristics of red in the tail (even small amounts) and white body plumage are discussed as likely intergrade traits. *Received 22 March 1982, accepted 23 September 1982.*

OF the seven North American Red-tailed Hawk subspecies recognized by the American Ornithologists' Union (1957, 1973), *harlani* is the most strongly differentiated and, together with *alascensis* and perhaps *umbrinus*, the least well known. Extensive variation of plumage within subspecies, combined with considerable subspecific breeding-range overlap and interbreeding, complicates the application of the rules of taxonomy.

Confusion concerning the Harlan's Hawk form can be traced back as far as 1829, when no less a person than John James Audubon described as *Falco harlani* (after R. Harlan a physician and naturalist) a hawk he had shot in Louisiana and called the Black Warrior (Audubon 1830: Plate LXXXVI; 1840). Despite doubts about the eventual adult plumage of the apparently immature type specimens painted by Audubon (Taverner 1927), one type specimen in the British Museum showed the characteristic Harlan's Hawk mottled tail pattern (Hellmayr and Conover 1949). It gradually became evident that the Harlan's Hawk was a member of the genus *Buteo* and was related to the Red-tailed Hawk, but whether it should be considered a separate species or a subspecies of the Red-tailed Hawk has remained in some doubt. Another opinion was that Harlan's Hawk was simply a local color phase of the Red-tailed Hawk, which did not require a scientific name of its own. At Ridgway's (1890) suggestion, the Harlan's Hawk was regarded as a subspecies of the Red-tailed Hawk (A.O.U. 1895). Some, however, still considered Harlan's Hawk a distinct species (Peters 1931). Harlan's Hawk was again considered a species in 1957 (A.O.U. 1957) but then reassigned subspecific status in 1973 (A.O.U. 1973).

Because *harlani* interbreeds freely with neighboring subspecies, it is clearly unacceptable as a species under the biological species concept (Mayr 1969). Subspecies by definition must possess a geographic breeding range exclusive of conspecific subspecies, however, and no such range was previously found for *harlani* (Taverner 1936, Gabrielson and Lincoln 1959, Godfrey, 1966). Taverner (1927: 8) analyzed records in the Yukon Territory and northern British Columbia and concluded that "If *harlani* is not racially pure here it seems hopeless to look for racial purity in it anywhere."

This paper presents new information from the field showing that *harlani* does have a discrete breeding range exclusive of other Red-tailed Hawk subspecies, along with discussion of causes for divergence and intergrade traits.

STUDY AREA AND METHODS

Subspecific identifications were made in the field during June, July, and August 1979, 1980, and 1981

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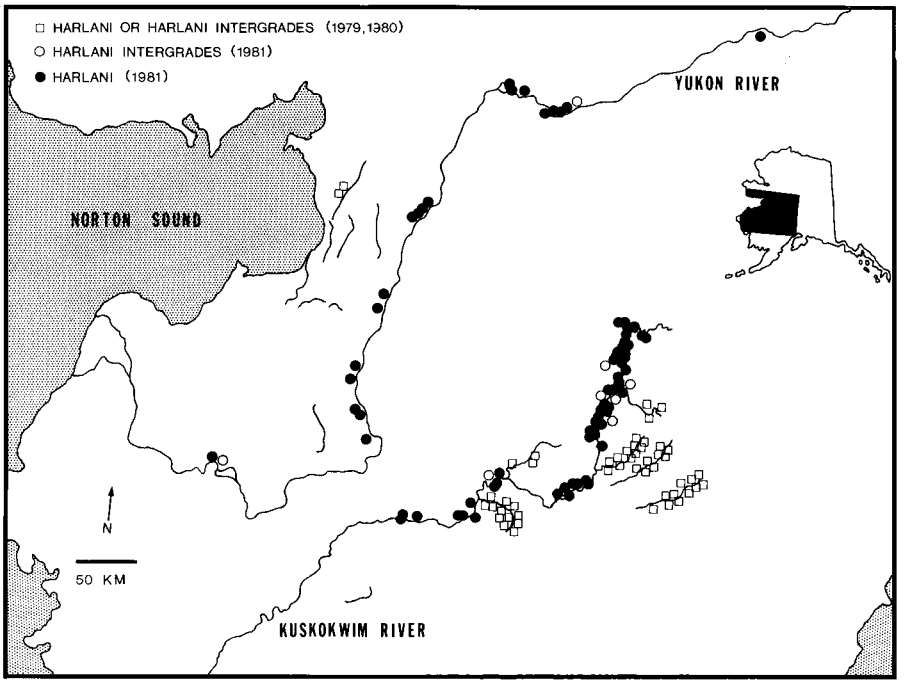

Fig. 1. Study area and distribution of Red-tailed Hawk sightings in southwestern Alaska during 1979–1981. All Red-tailed Hawks seen were either *Buteo jamaicensis harlani* or *B. j. harlani* intergrades. Distinction between these two groups was made during 1981 only. Surveys were conducted on all rivers shown.

in central and southwestern Alaska north of the Alaska Peninsula (Fig. 1). Nineteen rivers were travelled in the Kuskokwim, Yukon, and Unalakleet river drainages. Rivers in the Kuskokwim drainage included the Kuskokwim, Takotna, Tuluksak, Stony, Selatna, Tatlawiksuk, Cheeneetnuk, Gagaryah, East Fork George, and Oskawalik. Those west of or within the Yukon River drainage included the Yukon, North, South, Chiroskey, Old Woman, Golsovia, Otter Creek, Canyon Creek, and Stuyahok. All rivers were in the range of boreal forest and between 60° and 65° latitude and 154° and 162° longitude. Principal vegetation types were spruce-hardwood forest, consisting of white and black spruce (*Picea glauca, P. mariana*), paper birch (*Betula papyrifera*), and balsam poplar (*Populus balsamifera*), shrub thickets, and moist tundra (Viereck and Little 1972). Fuller descriptions of the survey rivers are found in Mindell (1983).

During 1979 and 1980, adult Red-tailed Hawks, which I could see well through 7 × 50 binoculars or a 20× spotting scope, were classified as either being or not being of the group *harlani* and *harlani* intergrades. No attempt was made to distinguish intergrades from "pure" *harlani*. In 1981, Red-tailed Hawks were classified as either *harlani*, *harlani* intergrades, or hawks with red-colored tails (Fig. 2). I used dorsal views of the tail in classifying Red-tailed Hawks whenever possible.

Red-tailed Hawks having tails with various combinations of white and dark-brown mottling, freckling, and streaking and with less than approximately 10% red color were counted as *harlani*. *Harlani* is characteristically dark and lacks the predominating red color in the tail that other Red-tailed Hawk subspecies have. *Harlani* frequently has a light or mottled bib; it is not consistently found, however. Light spotting on the breast, back, and wing linings is also a good field mark, when present. Hawks with tails having more than 10% red color but still having white and/or brown mottling and streaking were considered *harlani* intergrades. Hawks with tails having less than 10% red color but with extensive barring (n = 2) were also classed as intergrades. Intergrades showed wide variation in the amounts of red, mottling, and barring in the tail and in the amount of light breast color. Hawks with tails of more than 85% red color and lacking any of the distinctive *harlani* mottling were classed as hawks with red-colored tails.

Three Red-tailed Hawk subspecies, with tails predominantly red in color, have apparent zones of contact with *harlani*. *Calurus* frequently has a light colored breast, although often washed with rufous. Melanistic *calurus* individuals can be distinguished from *harlani* by their red-colored tails or lack of mottling and lack of light color in the tails. *Kriderii* could be mistaken for a light-phase *harlani* intergrade, as both may have tails with white and varying amounts

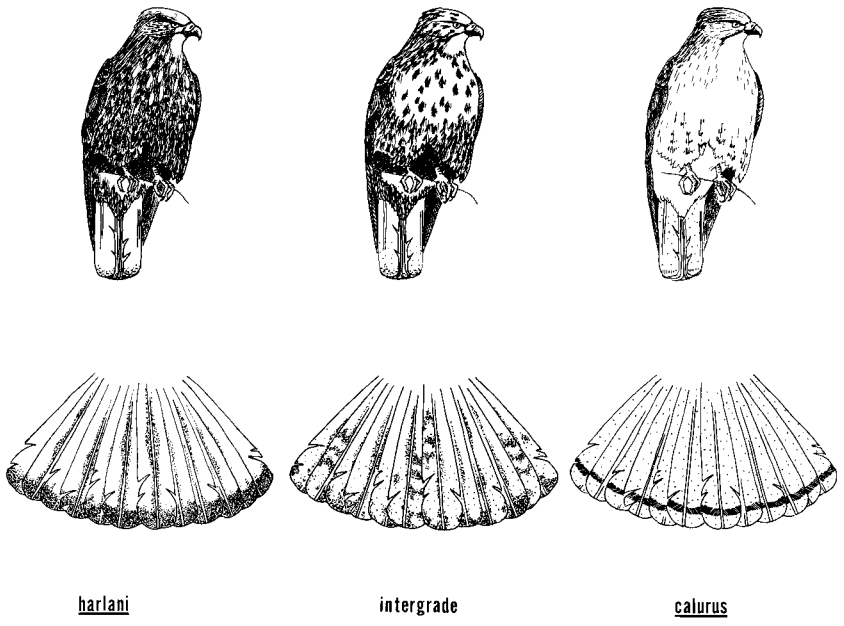

Fig. 2. Three forms of Red-tailed Hawk (*Buteo jamaicensis*) found in Alaska. The drawings are typical representations; characteristics varied widely within each of the forms, however. Widely spaced stipplings in the tails of the *calurus* (entire) and intergrade (distal half) forms denote red color.

of rufous color; however, *kriderii* are apt to be even paler than light *harlani* intergrades. *Alascensis*, although slightly smaller and darker, is virtually indistinguishable from *calurus* in the field (see Friedmann 1950 for subspecies descriptions). Red-tailed hawks in juvenile plumage were not classified to subspecies.

Results and Discussion

Subspecies and intergrade identification.—A total of 187 sightings of adult Red-tailed Hawks was made at a range close enough to allow subspecific identification in 1979–1981. All were either *harlani* or *harlani* intergrades (Fig. 1). One hawk had a tail about 70% red and 30% white with mottling, and two had tails about 60% red and 40% white with mottling. The rest had tails that were 25% or less red. The majority showed no discernable amounts of red. The Alaskan breeding range found to be exclusive to Red-tailed Hawks of the *harlani* subspecies ran from Farewell at the east slope of the Alaska range, north to Tanana and the Yukon River, west to Norton Sound, and south to St. Marys and Aniak.

I differentiated between individuals of apparently pure *harlani* and partial *harlani* (intergrades) ancestry on the basis of tail plumage in 1981, when a total of 82 Red-tailed Hawks was seen at close range on the Yukon, Kuskokwim, and Stony rivers. Of these, 73 (89%) were pure *harlani* and 9 (11%) were *harlani* intergrades. Ratios of *harlani* to intergrades were 89% to 11%, considering the Kuskokwim River alone (n = 52), and 90% to 10% on the Yukon River alone (n = 19). Field observations are an imperfect substitute for examination of preserved specimens. Specimens collected during migration or winter, however, are inappropriate for a determination of breeding range, and collected Alaskan breeding birds are few. The field identifications probably provide a conservative estimate of the frequency of occurrence of intergrades, because they were based only on tail characteristics, and some hawks with subtle intergrade characters may have been misclassified as *harlani*.

Taxonomic status and breeding range.—Because *harlani* freely interbreeds with other Red-tailed Hawk subspecies in zones of contact (Taverner 1927, Lowe 1978), it cannot be a good species. Treatment of *harlani* as a semispecies (*sensu* Amadon 1966) would assume partial reproductive isolation in contact zones with other subspecies. The evidence available does not suggest this; more data on subspecific ratios

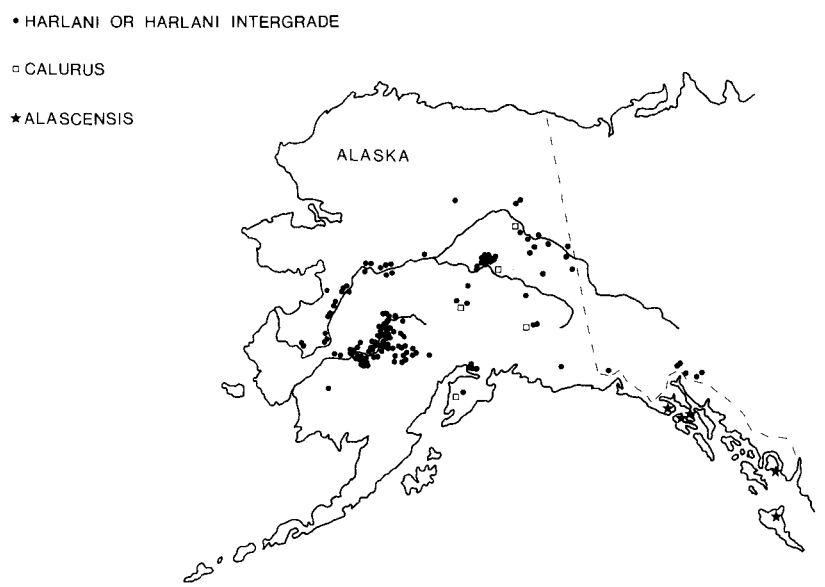

Fig. 3. Distribution of Red-tailed Hawk subspecies in Alaska and adjacent Canada. Locations for *calurus* and *alascensis* are based on specimens only. Records not from the present study are from: Grinnell (1909), Swarth (1911), Cumming (1931), Gabrielson and Lincoln (1959), Williamson et al. (1965), Kessel and Springer (1966), White and Haugh (1969), Lowe (1978), Ritchie and Curatolo (1980), and from D. Weir, C. M. White, S. Ambrose, and M. Amaral (pers. comm.).

within pairs in contact zones, however, are needed. This leaves two possibilities: *harlani* is either a distinct subspecies of the Red-tailed Hawk or a color phase of another subspecies, either *calurus* or *kriderii* (Mayr 1942: 150).

Two factors made the possibility of *harlani* being a color morph of *kriderii* initially attractive. *Harlani* and *kriderii* share the morphological character of often having large amounts of white in the tail, a trait unique among Red-tailed Hawks. *Harlani* and *kriderii* overlap in the location of core wintering areas on the Great Plains of the south-central United States. During migration, *harlani* passes over the breeding range of *kriderii* in southern west-central Canada and adjacent portions of the United States, and overlaps the general migratory route of *kriderii* as well. *Calurus* has a strongly marked melanistic phase and can resemble *harlani*; *calurus*, however, retains the red tail color.

Despite similarities, however, *harlani* does not qualify as a polymorph variant of either *kriderii* or *calurus*. Polymorphism is an intrapopulation phenomenon, and the genes involved in polymorphism have, in general, conspicuous discontinuous effects (Mayr 1970: 90). Thus, if *kriderii* and *harlani* were different morphs of the same subspecies, one would expect to see both varieties in mixed occurrence through most of their range. Overlap in breeding range has been recorded (Taverner 1936, Gabrielson and Lincoln 1959), although to only a minor degree. The Alaskan *harlani* breeding population and the *kriderii* population of the north-central U.S. and southern prairie-provinces of Canada remain distinct, with little mixing (see Friedmann 1950 for general *kriderii* range). The same can be said of *calurus* and *harlani*, although their zone of breeding range contact is broader than that for *harlani* and *kriderii*. As distinct populations with different geographic core areas, *harlani*, *kriderii*, and *calurus* are good subspecies. The similarities between *harlani* and *kriderii* suggest a close historical affinity.

The fact that all individuals seen in central and southwestern Alaska were either *harlani* or *harlani* intergrades clearly indicates the existence of a breeding range for *harlani* in which other Red-tailed Hawk subspecies do not occur (Fig. 3). Subspecies by definition must possess an exclusive geographic breeding range, and, thus, the field observations from Alaska provide the information that has previously been

lacking to support subspecific status for *harlani* (cf. Mayr and Short 1970: 38, 89).

The presence of intergrades within the breeding range of a subspecies does not invalidate the exclusiveness of the range. Interbreeding can be expected to occur where two subspecies come into contact, and intergrade forms will often penetrate farther into the opposing parental ranges than will pure forms (Mayr 1942, 1963). The zone of intergradation for *harlani* entirely overlaps its breeding range within the study area (Fig. 1) and, I suspect, in the remainder of its range as well. Intergrades in the study area occured at a southwestern extreme of Pilot Village, east to the McGrath vicinity, and north to Galena. Intergrades outside the study area are recorded from Fairbanks (Lowe 1978), Atlin, British Columbia, and two southwestern Yukon Territory locations (Taverner 1927). *Harlani* remains a meaningful subspecies, regardless of the wide intergradation zone, due to its recognizability in migration and on wintering grounds and the usefulness of this trait in studying geographic variation in the species. Even individuals of partial *harlani* ancestry can often be recognized as such.

Harlani makes the longest migration of any Red-tailed Hawk subspecies and passes over (leapfrogs) some populations of other subspecies. This further illustrates *harlani*'s uniqueness and weakens any consideration of it as a color morph of another subspecies. Differences in length, duration, and chronology of migration for different subspecies influence differences in physiological timing of breeding cycles. Vaurie (1961a) and White (1968) point out the importance of migratory habits in showing a taxon's nomenclatural distinctiveness.

The exclusive breeding range of *harlani* is not strictly limited to the present study area, although it appears to include the core. Reports of Red-tailed Hawks identified to subspecies in Alaska and adjacent Canada are few, and sometimes unreliable. Twitchell's reports of *calurus* from the Innoko, Nushagak, lower Kuskokwim, and Iditarod rivers (Gabrielson and Lincoln 1959) around 1917 are not included in Fig. 3. These locations are in or near the present study area and conflict with recent observations. The reports make no mention of *harlani* intergrades, and it seems possible that Red-tailed Hawks with red-colored tails seen by him had some less visible *harlani* tail characteristics.

Five specimens identified by Gabrielson and Lincoln (1959) indicate that *harlani*'s zone of contact in central and eastern Alaska is with *calurus*, which is generally the predominant subspecies throughout most of western North America (Friedmann 1950, Brown and Amadon 1968). *Alascensis*, a smaller and richly pigmented subspecies of southeast Alaska and coastal British Columbia (Grinnell 1909, Cumming 1931), probably contacts both *harlani* and *calurus* inland. *Borealis*, with the core of its range in eastern North America, has poorly known western range limits and no demonstrated contact zone with breeding *harlani*. Todd's (1950) *B. j. abieticola* may replace *borealis* in the spruce-fir belt of Canada, although it is infrequently recognized. *Kriderii*, generally of the central North American plains, may contact *harlani*, although the evidence is small, based on possible intergrades discussed by Taverner (1927) and a juvenile specimen from Eagle, Alaska identified by Robert Ridgway (Bailey 1916).

The summer and breeding records of *calurus* closest to the eastern limit of the present study area are from the Chatenika River and Minto Lakes west of Fairbanks, the Kasilof River and Tustumena Lake on Kenai Peninsula (Gabrielson and Lincoln 1959), and in the vicinity of Ferry along the Fairbanks Highway (Kessel and Springer 1966). Some of these sightings may have been of *harlani* intergrades. Specimens identified as *calurus* by Gabrielson and Lincoln (1959) came from Salcha Slough (50 km southeast of Fairbanks), Chitina River (a Copper River tributary in south central Alaska), Denali National Park, and Circle. Additional *calurus* reports are from the Chandalar River, Robertson River, Circle, Gulkana, and Chitina River (Gabrielson and Lincoln 1959).

In the only detailed previous study of Red-tailed Hawks in Alaska, Lowe (1978) reports that, of 285 Red-tailed Hawk sightings within a 300-mi^2 study area in the Fairbanks vicinity, 83.9% were pure *harlani*. Although Lowe classified the remainder as either *calurus*, *borealis*, or unknown, he reveals the mixed character of most of them in stating (1978: 32), "Most of the hawks classified as *borealis* or *calurus* were not typical of these forms . . . many had tails only washed with red . . . and portions being mottled, barred or white." Lowe gives a photo-

graph of an adult labeled as *calurus* that clearly has intergrade characters.

In the Yukon Territory, *harlani* are apparently predominant in the southwestern portion of the province (Yukon River drainage), *harlani* intergrades and hawks with red tails are mixed on the west slope of the Ogilvie Mountains, and hawks with red tails are common northeast of the Ogilvie Mountains in the Peel and Porcupine river drainages (David Mossop pers. comm.). More fieldwork and specimens are needed throughout northwestern Canada and Alaska to fill in details of Red-tailed Hawk geographic variation.

Reports of *harlani* occur throughout central and eastern Alaska south of the Brooks Range. The northernmost record is from the Porcupine River near the Alaska-Yukon border (Ritchie and Curatolo 1980). Additional records are from the Yukon River between Circle and the Fortymile River confluence (White and Haugh 1969), the Fairbanks vicinity (Kessel and Springer 1966, Lowe 1978), Ferry and Denali National Park (Kessel and Springer 1966), Tok and Northway (D. Weir pers. comm.), the Charley River (S. Ambrose, M. Amaral, and C. M. White pers. comm.), and Kechumstuk and McCarthy (Gabrielson and Lincoln 1959). Williamson et al. (1965) report seeing only *harlani* during the breeding season at unspecific locations in the area "west of the Copper River Valley, including the Cook Inlet region." They also record nests of *harlani* near Anchorage and at Hidden Lake on the Kenai Peninsula and two specimens collected at mile 20 on the Tok Cutoff Road.

The findings suggest that the breeding range for *harlani* and its intermediate forms, exclusive of other Red-tailed Hawk subspecies, can be outlined as follows: west to Norton Sound and the western limit of the taiga approaching the Yukon-Kuskokwim Delta; east to the Alaska Range west slope; north at least to the Koyukuk River mouth and probably up to tree line south of the Brooks Range; and south to the Iliamna Lake region. Even if a few other Red-tailed Hawks are located in this area, domination of *harlani* in subspecific ratios would not be changed. Breeding sites for *harlani* found during the present study represent a westward extension in the Red-tailed Hawk's reported range (A.O.U. 1957, Brown and Amadon 1968).

Causes for divergence.—The two basic patterns of speciation resulting in geographic variants within a widespread species are allopatric and paripatric (also alloparipatric) (Endler 1977) or geographic and semigeographic (Mayr 1942, 1963). Allopatric speciation involves the isolation and subsequent divergence of a population caused by extrinsic, geographic barriers. Allopatric speciation due to glaciation and concomitant biotic refugia has been hypothesized by Hultén (1937) to explain phytogeographic patterns and the present ranges of Alaskan plants. Pleistocene glaciation as an isolating mechanism allowing speciation among northern birds has been discussed by Austin (1932), Rand (1948), Pitelka (1950), Drury (1953), Cade (1955), Fay and Cade (1959), and Selander (1965). Much supportive information on geology, oceanography, palynology, and paleontology around the Bering Land Bridge is presented by Hopkins (1967).

The morphologically distinctive *harlani* population may also have developed through isolation in a Pleistocene epoch glacial refugium. The Bering Sea-Yukon Refugium and its possible relationship with geographic variation in the Rough-legged Hawk (*Buteo lagopus*) has been discussed by Cade (1955). A similiar argument for the evolution of *harlani* in Alaska can be made. A northern population of *B. jamaicensis* might have become isolated by surrounding ice sheets in a land area encompassing southwestern Alaska, part of eastern Siberia and the interlying Bering Sea. Morphological divergence occurring during isolation developed more rapidly than did any intrinsic isolating mechanisms that might have prevented breeding with the parental stock. Thus, *harlani* was still able to breed with Red-tailed Hawks from unglaciated regions in southern North America when corridors opened during the retreat of the last glaciation. Evolution of *harlani*'s migration is another matter, as present migration patterns for all species have apparently evolved since the end of the last glaciation (Moreau 1972, see Dingle 1980).

Buteo jamaicensis and *B. buteo* are considered by some to be members of the same superspecies group (Voous 1960, Mayr and Short 1970), although relationships in this group remain obscure. *Harlani* isolation in the Bering Sea-Yukon Refugium suggests the possibility of contact (gene flow) during that period with the easternmost form of *B. buteo, japonicus*. *Buteo buteo* has not been recorded in the Soviet Union east of the Kolyma River system, including

Kamchatka Peninsula (Vaurie 1961b); the eastern limit of *japonicus*, however, may be incompletely known.

Glaciation and paleoclimatological refugia represent only one of the two broad patterns of speciation. Although Mayr (1963) has previously argued against the likelihood of paripatric speciation, Endler (1977) presents a strong case for its feasibility and further demonstrates that it is not possible to distinguish between the result of paripatric or allopatric speciation simply by interpreting a particular geographic pattern. Under the paripatric mode of speciation, *harlani* would have developed through the formation of clines, without any barriers to gene flow occurring in the contiguous Red-tailed Hawk range. Isolation would be more by distance from similar conspecifics than by geographical, ecological, or temporal factors (Huxley 1939, Timofeef-Ressovsky 1940, Mayr 1942, Murray 1972, Endler 1973).

The wide *harlani* intergrade range may imply incomplete divergence of morphological characters, assuming the variance arose through primary intergradation and paripatric differentiation, or, if one assumes the events of secondary intergradation and allopatric speciation, the wide intergrade range may suggest that the intergrades are not "unbalanced" enough to produce a well-defined intergrade zone (see discussion of hybrid zones in Mayr 1963, Endler 1977). In other words, the intergrade characters do not cause a selective disadvantage, thus allowing breeding success and spread of intergrade forms. Just as one would expect disadvantageous genetic combinations to be selected against, one could expect that characters not disadvantageous would penetrate farther into the parent populations. The character of red in the tail may fit the latter description. This could explain the frequent occurrence of small amounts of red in the tails of adults that are otherwise "pure" *harlani* in character. Friedmann (1950) describes *harlani*'s tail as having ". . . from scarcely any admixture of ochraceous to a definite cinnamoneous wash . . . ." It is questionable that pure *harlani* has any red color in the tail, and the not uncommon "cinnamoneous wash" may be an intergrade trait.

On the Yukon and Kuskokwim rivers during 1981, 3 (6.5%) of 46 *harlani* seen were light breasted, while 5 (41.6%) of 12 intergrades observed were light breasted. Light body plumage for hawks with *harlani* characteristics may also be the result of subspecific interbreeding, similar to red color in the tail. The greater percentage of light-breasted forms among intergrades than among *harlani* seen during the present study suggests this possibility. Independent segregation of such traits can also be expected and would account for the three hawks seen in 1981 with light breasts but no red in the tail. Considering the degree of color variation seen in other Red-tailed Hawk subspecies, however, the existence of light phase "pure" *harlani* seems possible. Observations on the parentage of light phase *harlani* are needed.

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The **American Ornithologists' Union** will hold its Annual Meeting in New York from **26 September to 1 October, 1983.** A formal call for papers will be mailed to members by mid-April with the deadline for submission of abstracts for papers and poster sessions of **15 June 1983.** For further information on the scientific program, contact **Dr. George Barrowclough, Department of Ornithology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024.**

Fellows and Elective Members are reminded that **nominations for Elective Members or Fellows** may be submitted to the Secretary on the prescribed form up until five months prior to the opening of the next dated meeting. The deadline for 1983 is **26 April.** Nominations for Vice President and three Elective Councillors may be made in writing to the Secretary at any time prior to the annual meeting.

The American Ornithologists' Union invites applications by **1 March 1983** for the following competitive research awards:

Josselyn Van Tyne Memorial Fund supports projects in any area of ornithology, with awards of a few hundred to a thousand dollars each. Successful applications usually focus on one or a few carefully defined, incisive questions, rather than on general biology or management.

Alexander Wetmore Memorial Fund supports projects involving systematics and/or the taxonomy of birds and, secondarily, studies of neotropical birds. Awards are of a few hundred to a thousand dollars. Successful applications are usually built around a well-focused, interesting question.

Herbert and Betty Carnes Awards are intended to promote excellence in the scientific study of birds by permitting individuals an opportunity to expand the design of field or laboratory work and to explore new methods of data analysis. Applications are judged on the basis of scientific merit, importance, and originality. One or two awards of $1,000–$2,000 are made.

Students, amateurs, and others with limited or no access to major granting agencies are encouraged to apply for the Van Tyne or Wetmore Awards, while the Carnes Award is open to all individuals. Application forms and further information on the **Van Tyne and Wetmore Awards** may be obtained from **Dr. Erica Dunn, 30 Davidson Road, Aurora, Ontario L4G 2B1 Canada;** applications for the **Carnes Award** should be addressed to **Dr. Ellen D. Ketterson, Department of Biology, University of Indiana, Bloomington, Indiana 47405 USA**.