SYSTEMATICS AND EVOLUTION OF THE NORTH AMERICAN MERLINS

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THE Merlin or Pigeon Hawk (*Falco columbarius*) is a polytypic species of panboreal distribution. In North America it breeds in the taiga, Pacific coastal forest, and prairie-parkland biomes and migrates southward. Four North American subspecies are recognized by Peters (1931) and the A.O.U. Check-list (1957). *F. c. columbarius* Linnaeus and *F. c. bendirei* Swann occur in the eastern and western portions of the taiga, respectively; *F. c. suckleyi* Ridgway occurs in the humid Pacific coastal forest; and *F. c. richardsonii* Ridgway occurs in the prairie-parklands.

Some controversy exists over the validity of these forms, particularly *F. c. bendirei* and *F. c. suckleyi* (Bent, 1938; Hellmayr and Conover, 1949). Swarth (1935) questioned the validity of *F. c. bendirei* on the grounds that it is not phenotypically distinguishable from *F. c. columbarius*. He also questioned *F. c. suckleyi* because its geographic distribution was poorly defined and seemed to overlap that of *F. c. bendirei*. More recently several authors have tried to circumvent the problems of *F. c. bendirei* and *suckleyi* by synonymizing the former with the latter (Dementiev and Gladkov, 1951) or with *F. c. columbarius* (Brown and Amadon, 1969; Stresemann, MS). The authors offer no justification for these synonymies.

Despite these disagreements, little systematic work has been done on the North American Merlins since Peters' (1927) review. In fact, the Merlin remains one of the least studied of the North American falcons in most aspects of its biology. The objectives of this study are to analyze the phenotypic variation in the North American Merlins, to interpret the evolutionary origins of the observed variations and geographic distributions, and from this information to reevaluate the present subspecific designations.

MATERIALS AND METHODS

The comparative aspects of this study are based upon examination of 1,585 museum study skins from five populations of Merlins as delineated in Figure 1. The taiga, coastal forest, and prairie-parkland populations are separated on the basis of Pitelka's (1941) biome classification although his terminology is not used. The divisions of the taiga are made at the Continental Divide, a natural geographic division, and at the western edge of the Hudson Bay, the presently accepted boundary between *F. c. columbarius* and *bendirei*.

Unless otherwise noted, only specimens taken between 15 May and 15 September, and within the recognized breeding range of the Merlin, were used for comparisons. This was done on the assumption that these birds were taken on or near their breeding grounds (see Reilly, 1954, for a discussion of this criterion).
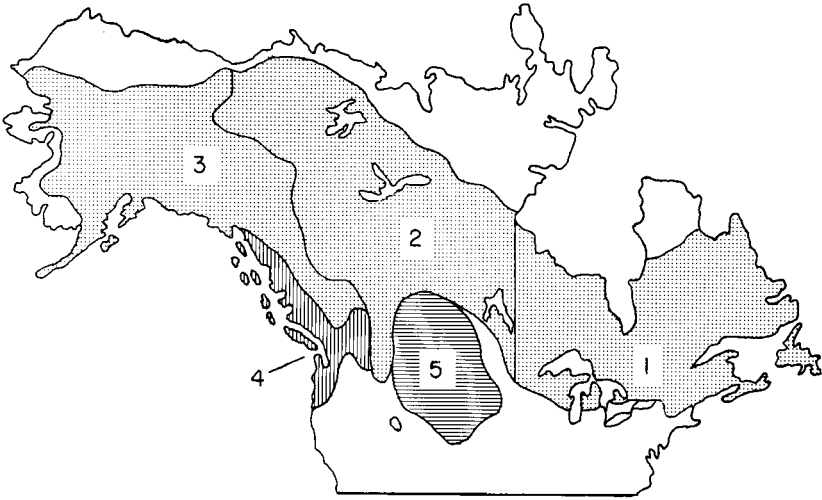
Figure 1. Breeding ranges of study populations and subspecies of North American Merlins. 1, eastern taiga (*F. c. columbarius*); 2, central taiga (*F. c. bendirei*); 3, western taiga (*F. c. bendirei*); 4, coastal forest (*F. c. suckleyi*); 5, prairie-parkland (*F. c. richardsonii*).

Characters which best demonstrated patterns of variation were used for making comparisons. The following techniques were used in analyzing specimens:

Size characters.—Standard linear measurements were taken in accordance with the methods described by Baldwin et al. (1931): (1) wing length: the chord of the unflattened wing; (2) tail length; (3) tarsus length; (4) toe length: length of middle toe less talon; (5) culmen length from cere; (6) wing loading index: wing loading was approximated by dividing the cube root of the body weight (g) by the chord of the wing (cm). This wing loading index showed a high correlation with the actual wing loading value computed as body weight in grams per total wing area in cm^2 (for 8 specimens, r $=$ 0.877). All measurements are in millimeters.

Plumage characters.—Specimens were scored on the following plumage characters: (1) crown streaking class: the relative width of the longitudinal black streaks on the crown (see Table 4 for descriptions of classes); (2) number of tail bands: the number of light bands in the tail bordered both proximally and distally by dark bands; (3) barring on the anterior web of the outermost primary: whether present or absent; (4) barring on the posterior web of the outermost primary: whether the next to most distal bar extended from the feather shaft to the posterior feather margin or not.

Colorimetric characters.—Certain colorimetric data were taken from randomly selected study skins collected between 31 August and 15 October. This temporal restriction was placed on specimens to reduce the adverse effects of fading and wear on the recently molted plumage. Colorimetric readings were taken from the center of the interscapular region of the dorsum. All readings were made on a Bausch and Lomb Spectronic 20 equipped with a Color Analyzer Attachment modified after the suggestions of Selander et al. (1964). For each specimen a curve of the spectral re-

flectance over the wavelength range of 400 to 700 mμ was constructed. From this curve the trichromatic coefficients (x_s, y_s, z_s) were determined using the 10-selected ordinate system (Hardy, 1936). The dominant wavelength, brightness, and excitation purity of the plumage color were computed from these coefficients.

Four randomly selected study skins were washed using the techniques described by Selander and Johnston (1967). None of the changes in colorimetric characters attributable to washing were significant; therefore, washing of outwardly clean skins was not judged necessary.

All calculations and statistical analyses were done with the computing facilities of Cornell University. Statistical methods follow Steele and Torrie (1960). In the text and tables a significant difference is taken to mean the 5 percent level of probability ($p < 0.05$) by the indicated statistical test.

RESULTS

SEX AND AGE VARIATION

As Merlins show both sexual and age dimorphism, these types of variation are considered before geographic variation is discussed.

Variation in size characters.—As typical in the order Falconiformes, sexual dimorphism in Merlins is reversed from that in many other birds; females are larger than males in most measurements. The degree of sexual dimorphism in size characters is similar in all populations.

Age variation in size occurs in Merlins as in many other birds. Frequently juvenile flight feathers are longer than those of the subsequent adult plumage, thus affording young birds lighter wing loading while they develop their powers of flight. Age variation in wing and tail lengths of Merlins is consistent with this pattern. No significant age variation exists for tarsus length, toe length, or culmen length.

Variation in plumage characters.—For a falcon, sexual dichromatism is marked in the Merlin, and this difference is most pronounced in the adult plumages. Friedmann (1950) describes the plumages of the North American Merlins in detail. In brief, the adult male's dorsum is blue-gray and the adult female's is brownish. The dorsum coloration of juvenile males and females is similar to that of the adult female; the adult female rump is more grayish. Table I presents colorimetric data on the dorsum coloration of adult Merlins. The sexual dichromatism in adult plumages is clearly shown by the differences in their dominant wavelengths.

No significant sexual or age variation occurs for any of the other plumage characters examined, and specimens were pooled as to sex and age when making interpopulation comparisons of these characters.

GEOGRAPHIC VARIATION

Variation in size characters.—Analysis of variance for size characters show no significant geographic variation for tarsus length, toe length, or culmen length, but wing and tail lengths do show significant patterns of

TABLE 1

INTERPOPULATION VARIATION IN DORSUM COLOR
OF NORTH AMERICAN MERLINS[1]

Population	No. of specimens	Brightness (%)	Dominant wavelength (mμ)	Purity (%)
Adult males				
Eastern taiga	5	17.0 ± 0.7	478.6 ± 2.9	4.0
Central taiga	4	17.9 ± 0.4	475.3 ± 4.1	3.5
Western taiga	6	17.4 ± 0.6	477.1 ± 5.3	4.1
Coastal forest	4	15.7 ± 0.3	476.0 ± 1.6	4.0
Prairie-parkland	7	21.0 ± 0.6	472.4 ± 4.9	5.1
Adult females				
Eastern taiga	7	24.1 ± 0.4	581.3 ± 4.3	1.5
Central taiga	6	24.9 ± 0.7	582.5 ± 3.6	1.2
Western taiga	6	25.8 ± 0.6	584.4 ± 2.9	1.5
Coastal forest	5	23.4 ± 0.3	575.7 ± 2.1	1.7
Prairie-parkland	6	29.8 ± 0.4	590.6 ± 3.2	5.0

[1] Values are the mean ± SE.

geographic variation. Linear product-moment correlation coefficients of the means of each population indicate that variations in wing and tail lengths are also highly concordant. Wing and tail length data are given in Figure 2. Data for juveniles are not shown as interpopulation relationships in juveniles are the same as in adults.

Geographic variation was found in wing loading values (see Table 2). The prairie-parkland population is significantly different from all other populations, having the lightest wing loading. The coastal forest population is also significantly different from all other populations, having the heaviest wing loading. None of the taiga populations is significantly different, and all are intermediate between the other two populations.

Variation in plumage characters.—Merlins show considerable geographic variation in plumage characters, and, consequently, plumage differences are the main criteria used to distinguish the North American subspecies.

The plumage coloration of North American populations generally varies according to Gloger's ecogeographical rule. For colorimetric data see Table 1. Little interpopulation variation occurs in the dominant wavelength or excitation purity of the plumage color for any sex or age class, suggesting that the pigmentation responsible for plumage color in Merlins tends to be conservative. Interpopulation variation in color brightness is significant; Merlins from the prairie-parkland population are the lightest in color, Merlins from the coastal forest the darkest, and Merlins from
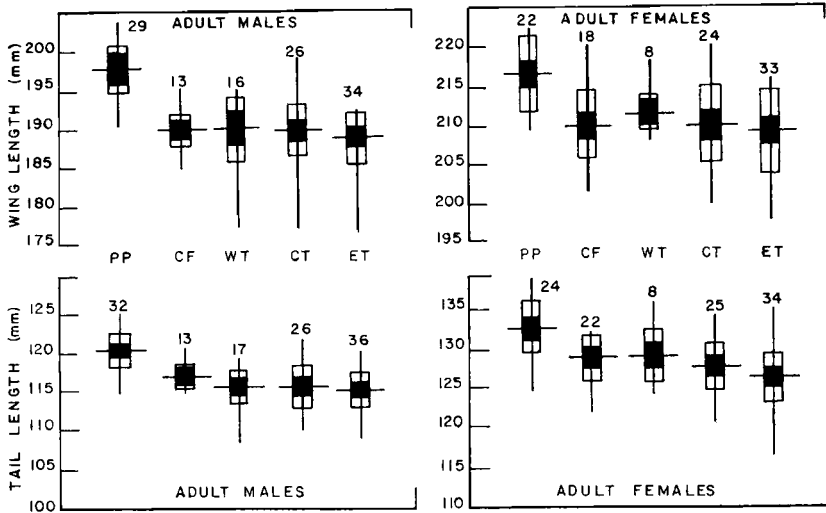
Figure 2. Interpopulation variation in wing and tail lengths of North American Merlins. Horizontal lines indicate means; vertical lines show observed range; open rectangles mark ± 1 SD and solid black mark ± 95 percent confidence intervals of means; adjoining numerals are sample sizes. Population abbreviations: PP, prairie-parkland; CF, coastal forest; WT, western taiga; CT, central taiga; ET, eastern taiga.

the taiga intermediate. Both the prairie-parkland and coastal forest populations are significantly different from all other populations, but within the taiga no significant variation occurs (significance determined by *t*-tests).

A considerable amount of geographic variation is present in the number of tail bands (Table 3, significance determined by χ^2 tests). The prairie-parkland population is significantly different from all other populations in that these Merlins have five tail bands. The coastal forest population is also significantly different from all other populations, and this differ-

TABLE 2

INTERPOPULATION VARIATION IN WING LOADING OF
NORTH AMERICAN MERLINS[1]

	Wing loading indexes for indicated population[2]				
	PP	ET	CT	WT	CF
Adult males	0.19	0.23	0.23	0.25	0.28
Adult females	0.20	0.23	0.24	0.25	0.30

[1] Each value is the mean index (cube root of body weight in g ÷ chord of wing in cm) for 10 specimens; any two means not subtended by the same line are significantly different by Duncan's multiple range test.
[2] Populations abbreviated as in Figure 2.

TABLE 3

INTERPOPULATION VARIATION IN THE NUMBER
OF TAIL BANDS OF NORTH AMERICAN MERLINS

Population	No. of specimens[1]	Percent with indicated number of tail bands			
		3	4	5	6
Eastern taiga	137	3	92	5	0
Central taiga	99	2	91	7	0
Western taiga	106	3	85	12	0
Coastal forest	104	20	80	0	0
Prairie-parkland	116	0	10	88	2

[1] Specimens pooled with respect to sex and age.

ence is attributable to the higher frequency of birds with only three tail bands. Although no significant differences were found within the taiga populations, the number of tail bands decreases clinally from west to east.

The pattern of geographic variation in crown streaking closely parallels that of the number of tail bands (Table 4), and significant interpopulation differences exist (significance determined by χ^2 tests). The prairie-parkland population is significantly different from all other populations, having very thin black streaks on the crown and a resulting predominance of background color. The coastal forest population is also significantly different from all other populations, having broad black streaks that, in some individuals, all but obscure the background coloration. While no significant differences exist within the taiga populations, the relative width of the black streaking increases clinally eastward.

The patterns of primary barring show significant geographic variation

TABLE 4

INTERPOPULATION VARIATION IN CROWN STREAKING
OF NORTH AMERICAN MERLINS

Population	No. of specimens[1]	Percent in indicated crown streaking class[2]				
		1	2	3	4	5
Eastern taiga	137	0	15	46	33	6
Central taiga	99	0	7	43	34	16
Western taiga	106	0	2	38	31	29
Coastal forest	103	50	41	9	0	0
Prairie-parkland	116	0	0	0	11	89

[1] Specimens pooled with respect to sex and age.
[2] Crown streaking classes: 1, black much greater than background; 2, black greater than background; 3, black equals background; 4, black less than background; 5, black much less than background.

TABLE 5

INTERPOPULATION VARIATION IN PRIMARY BARRING
PATTERNS OF NORTH AMERICAN MERLINS

Population	No. of specimens[1]	Percent with anterior web barred	Percent with posterior web incompletely barred
Eastern taiga	137	13	2
Central taiga	99	14	1
Western taiga	106	41	5
Coastal forest	104	0	94
Prairie-parkland	116	96	0

[1] Specimens pooled with respect to sex and age.

and are almost population specific in two instances (see Table 5). The prairie-parkland population is essentially characterized by the presence of barring on the anterior web of the primaries and is significantly different from all other populations. No individuals in the costal forest population show this character, and it occurs in the taiga population at a very low frequency. The frequency of anterior primary barring in taiga Merlins does increase westward.

Incomplete barring on the posterior web of the primary is characteristic of the coastal forest Merlins. Incomplete barring occurs at a high frequency in this population and is absent or present at a very low frequency in all other populations (see Table 5).

Variation in migration patterns.—Salomonsen (1955) suggests that the migration patterns and winter ranges of birds may be of evolutionary significance. North American Merlin populations have rather complex migratory habits that may reflect their evolutionary histories.

The prairie-parkland population undergoes a relatively short migration into the southern Great Plains and is resident in parts of its breeding range. The coastal forest population is semiresident in the climatically stable coastal region, and only a small portion of the population migrates south of the breeding range. The taiga populations, on the other hand, are highly migratory. The western and central taiga Merlins migrate past the coastal forest and prairie-parkland populations in leapfrog fashion to winter in Central and South America. The eastern taiga Merlins are also highly migratory with many individuals crossing the Gulf of Mexico to winter in the Caribbean Archipelago and South America.

DISCUSSION

Geographic variation.—Interpopulation variation in size of Merlins cannot be readily explained by traditional ecogeographical rules. Behle (1942) and Pitelka (1951) noted that larks and jays that inhabit open

habitats such as prairies or deserts tend to have longer wings and tails than forms inhabiting denser vegetation. Presumably the longer wing and tail are adaptive because these birds are required routinely to fly greater distances than are birds in a more closed habitat. The prairie-parkland Merlins certainly conform to this generality. Correlated with having a longer wing and tail, these Merlins also have light wing loading that would be a definite selective advantage for frequent long flights. The coastal forest Merlins, in contrast, inhabit the densest habitat of all five populations. Perhaps reflecting this difference, these Merlins have the heaviest wing loading.

In view of the interpopulation differences in temperatures encountered both in the summer and winter ranges, it is surprising that no significant differences exist in tarsus or toe lengths as predicted by Allen's rule.

The brightness of Merlin plumage color varies as predicted by Gloger's rule. The climatic conditions within the range of the prairie-parkland population are the most arid of all five populations, and Merlins from this population show the lightest coloration. The climatic conditions in the range of the coastal forest Merlins are the most humid, and these Merlins show the darkest plumage coloration.

The variation in certain plumage patterns also follows Gloger's rule. The crown streaking classes are essentially measures of the intensity of dark pigmentation on the crown. On the basis of crown streaking, the lightest colored Merlins are from the prairie-parkland population while the darkest are from the coastal forests.

The barring on the posterior web of the primaries is probably another measure of the intensity of dark pigmentation. The high frequency of incomplete barring in the coastal forest population indicates that the dark pigmentation in the primary is so intense that the light colored bars are actually reduced to spots.

The interpopulation variation in barring on the anterior web of the primaries cannot be explained adequately on the basis of ecogeographical correlations. The presence of this character is probably an ancestral characteristic (*sensu* Mayr, 1969) and is treated in the discussion of Merlin evolution.

Interpopulation differences in the number of tail bands appear to be a combination of ancestral characteristics and strong environmental correlations. The large number of tail bands in the prairie-parkland population is presumed to be an ancestral condition to be discussed under evolutionary history. In the coastal forest population the reduction in the number of tail bands is largely attributable to color saturation in the same way as primary barring. The dark pigmentation is so intense that it obliterates the narrower proximal bands in the tail. The intermediate condition of

the taiga populations is best explained by the proposed evolutionary history of these populations.

Historical interpretation of Merlin evolution.—Mayr (1946) and Udvardy (1958) discuss the origins of the North American avifauna and agree that almost all North American birds had either Palearctic or Neotropical origins. The strong affinities the North American Merlins seem to have with those of the Palearctic region indicate a Palearctic origin for the Merlin. Darlington (1957) suggests that dispersion in the genus *Falco* was rapid and complex and believes that some groups of the genus reached the Nearctic fairly recently. While the fossil record of Merlins is poor, North American fossils indicate that Merlins had reached the Nearctic at least by the late Pleistocene (Brodkorb, 1964).

The habitat affinities of Palearctic Merlins are essentially identical to those in the Nearctic region. As in North America, the largest portion of the Palearctic Merlins' range is taiga, but open steppe and dense coastal forests are also included. Examination of 91 specimens representing all the Palearctic forms showed that several plumage characteristics were common to all. These specimens showed a large number of tail bands (ranging from 5 to 8), barring on the anterior webs of the primaries, and relatively light coloration. If the North American merlins are compared phenotypically with these Palearctic forms, an unexpected relationship is suggested. Assuming that selection pressures are similar in both the Palearctic and Nearctic taiga, it is surprising that Palearctic taiga Merlins are so different from the North America taiga Merlins yet so similar to the prairie-parkland Merlins.

This evidence suggests that there was gene flow between the Palearctic Merlins and the prairie-parkland population more recently than with the other North American populations. One way to account for this is to suppose a double invasion of Merlins from the Palearctic, with the first stock becoming the taiga and coastal forest populations and the more recent stock becoming the prairie-parkland population. The glacial events of the late Pleistocene could have allowed such a situation to occur. A hypothetical series of steps in the evolution of North American Merlins based upon glacial events are shown in Figure 3.

During periods of glacial advance, a Bering land bridge connected Asia with an unglaciated refugium in Alaska (Colinvaux, 1964). Asian Merlins could easily have reached North America via this route (see Figure 3A). With the amelioration of the climate during subsequent periods of glacial retreats, these Merlins had the opportunity to spread across the extensive taiga zone of North America (see Figure 3B).

During the latter periods of glacial advance, these Merlins would have been forced into coniferous refugia south of the ice along with the other
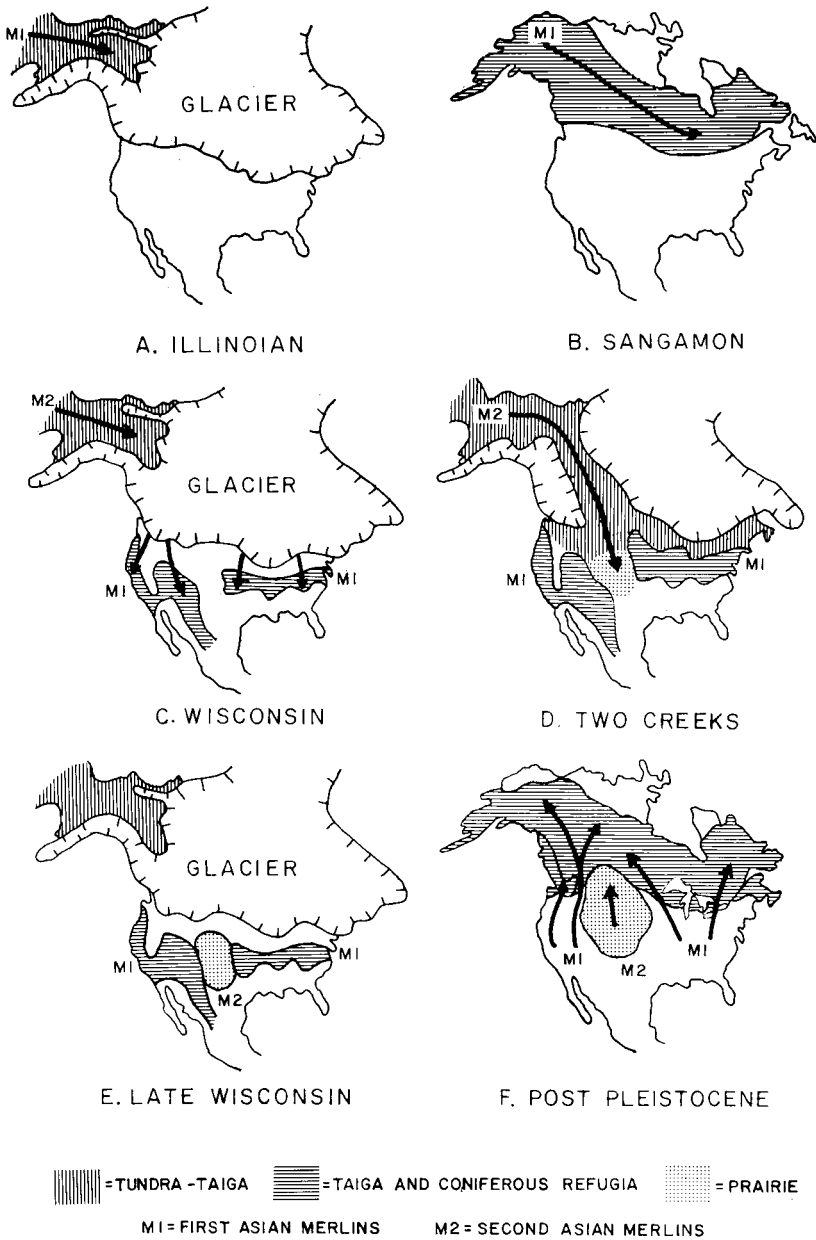
Figure 3. A model sequence of events in race formation of the North American Merlins during the indicated period of the Pleistocene. Boundaries of continents, glaciers, and biomes are only approximate.

boreal fauna (Hultén, 1937). At the same time, a Bering land bridge again connected Asia and the Alaskan refugium, and a second Asian Merlin stock was able to reach North America (see Figure 3C). During the Wisconsin glaciation, both northeastern Asia and the Alaskan refugium were sparsely vegetated (Colinvaux, 1964), and presumably any Asian Merlins that successfully reached North America via the Bering land bridge were adapted for this open habitat.

Several times during the late stages of the Wisconsin glaciation sizeable ice-free corridors opened between the Cordilleran and Laurentian ice caps, thereby connecting the Alaskan refugium with unglaciated regions south of the ice (Flint, 1957). The Merlins in the Alaskan refugium may have moved southward along these corridors as is suspected to have occurred with other animals (Haynes, 1966) (see Figures 3D and E). Being adapted for an open habitat, these Merlins would have found an unexploited niche available to them in the central prairie-parklands as no other small bird-eating hawk had successfully invaded this habitat in North America.

With the final retreat of the Wisconsin glaciers, the taiga expanded northward to dominate the boreal regions of North America and with it moved the taiga and coastal forest Merlin populations. The prairie-parklands became more extensive in xeric post-Pleistocene times (Wells, 1970), and the Merlins in this population expanded their range accordingly (see Figure 3F).

While any such model based upon indirect evidence is subject to indeterminable error, the proposed model appears tenable for several reasons. It explains the presence of ancestral plumage patterns in the prairie-parkland population by virtue of its more recent connection with the Palearctic gene pool. It explains the color saturation seen in other North American populations as these Merlins were subjected to long periods of mesic conditions in glacial refugia. The extreme color saturation of the coastal forest population is probably the result of a long *in situ* evolution in the humid coastal forests. The high incidence of ancestral characters in the western taiga population can also be explained, for after the glacial retreat there would have been gene flow between the northward moving taiga Merlins and the Merlins remaining in the Alaskan refugium.

Taxonomic considerations.—From the foregoing discussion, several taxonomic conclusions can be made. Certainly phenotypically and probably phylogenetically, the prairie-parkland population is distinctly separate from the other North American populations. The name *F. c. richardsonii* Ridgway has been and should continue to be used for this population.

The coastal forest population is also rather distinct phenotypically,

and the proposed evolution of this population in the Pacific coast region also suggests a distinct phylogenetic history. Phenotypically, Merlins breeding in the coastal forest biome are markedly different from those of the adjoining taiga, and an exclusive range for this phenotype is indicated. I would conclude that the coastal forest population is taxonomically distinct, and the name *F. c. suckleyi* Ridgway should be applied to Merlins from this population.

Taxonomic decisions become more difficult to make within the taiga populations. Phenotypically no basis exists for separating the taiga populations geographically in the manner the present subspecific designations indicate. The clinal nature of geographic variation in these populations makes it clear that any attempts at dividing the taiga populations will be arbitrary and not reflect accurately either phenotypic or phylogenetic differences as discussed in this paper. I therefore suggest that the present nomenclature applied to the taiga populations be revised as follows: *F. c. bendirei* Swann should be considered a synonym of *F. c. columbarius* Linnaeus, and the name *F. c. columbarius* Linnaeus should be applied to all North American taiga populations of the Merlin as they have been delineated in this study.

SUMMARY

The North American subspecies of the Merlin have been subjected to little systematic work, and the validity of two forms has been questioned. Sex, age, and geographic variations as well as the presumed phylogeny of each form were studied to evaluate the validity of the subspecies.

Sex and age variation in size characters are similar in all populations. Sexual dichromatism is marked in adults and slight in immatures. The immatures of both sexes resemble the adult female. Little sex or age variation exists in plumage patterns.

Geographic variation exists for wing length and tail length, and these two characters are highly concordant. No geographic variation occurs in the other size characters examined. Size characters do not vary as predicted by classical ecogeographical rules. Wing and tail length seem to be best correlated with the density of the vegetation in the Merlin's range; Merlins from open country have the longest wings and tail. Plumage color varies according to Gloger's rule. Variations in plumage patterns are correlated with environmental conditions and also with the phylogeny of the population. Interpopulation differences in migratory patterns and winter ranges are complicated.

A conjectural evolutionary history of the North American Merlins is constructed, and a double invasion of Merlins from Asia during the Pleistocene is proposed. The first Asian Merlin stock became the taiga and coastal Merlins, and the second Asian Merlin stock became the prairie-parkland Merlins.

Taxonomic suggestions made on the basis of the above evidence are as follows: *F. c. richardsonii* and *F. c. suckleyi* should remain as presently described. *F. c. bendirei* should be considered a synonym of *F. c. columbarius*, which should be used for all of the taiga-inhabiting North American Merlins.

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