

THE CONDOR

VOLUME 57

NOVEMBER-DECEMBER, 1955

NUMBER 6

VARIATION OF THE COMMON ROUGH-LEGGED HAWK IN NORTH AMERICA

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INTRODUCTION

The Common Rough-legged Hawk (*Buteo lagopus* Pontoppidan) is a polytypic species of panboreal distribution. During the breeding season it is restricted to the circumpolar tundra biome and to the tundra-forest ecotone, except on Kamchatka where, according to Dementiev *et al.* (1951:307), it also breeds in the true boreal forest.

Three or four subspecies are currently recognized. *Buteo lagopus lagopus* breeds from Scandinavia east nearly to the Yenisei River in the Soviet arctic. The Siberian form, which has usually been called *pallidus* Menzbier, breeds from the Yenisei eastward to the Anadyr Peninsula and to the shores of Bering Strait. A third described race in the Old World, *kamtschatkensis* Dementiev, is said to breed on the peninsula of Kamchatka, on Bering Island, on the western shore of the Sea of Okhotsk, and on the Kurile Islands (Dementiev *et al.*, 1951:314). Finally, there is *sanctijohannis* Gmelin [for orthography, see Article 15, Intern. Rules Zool. Nomen.], the breeding form of the American Arctic and Subarctic.

These subspecies have been poorly characterized in the literature because they are not defined by sharp differences. The American form is supposed to differ from *B. l. lagopus* by its smaller average size, by its polymorphism, and by the more variegated colors of the dorsal plumage. *B. l. lagopus* is said to be characterized by a more uniformly brown dorsal coloration, by a light-colored head relative to the back, and by the absence of a melanistic phase. The Siberian form is the most distinctive subspecies of the group. It differs from both *lagopus* and from *sanctijohannis* by its extremely pale coloration and, supposedly, by its larger average size. Finally, according to Dementiev (1931:54-55), who described *kamtschatkensis*, and Dementiev *et al.* (1951:315), who attempt to substantiate it, the Kamchatkan form differs from the Siberian form by its darker and more variegated colors (similar in this respect to *sanctijohannis*) and by its still larger average size.

Some Russian authors, notably Stegmann (1937:216), consider *kamtschatkensis* only a variant of the Siberian form. He has shown that specimens from Kamchatka fall within the range of variability of the Siberian population and further that three of them that he examined are indistinguishable in color from the pale form. Also he pointed out that Dementiev's type specimen is a juvenile and that juveniles are poorly separable even in large series. In further support of Stegmann's contention, I can mention three specimens examined in the present study, a nesting pair from the lower Lena River and an adult male from Cape Bolshaja, which fit the description of *kamtschatkensis* but which were taken deep within the breeding range of the Siberian subspecies as given by Dementiev *et al.* (1951:312-313).

A number of writers have noted differences between the Rough-legged Hawks of northwestern Alaska and those from the region of Hudson Bay, Labrador, and New-

foundland. Nelson (1887:142) pointed out that many Alaskan specimens are quite light, particularly on the head, and on this basis he referred northwestern Alaskan birds to the typical race *lagopus*. He was incorrect, however, in stating that the "melanistic phase" does not occur in this region, as were Macoun and Macoun (1909:61). Friedmann (1934:246) later referred one of Nelson's specimens from St. Michael's, Alaska, to the Siberian form *pallidus* and discussed several intergrades from that area, suggesting that in the region of intergradation between *pallidus* and *sanctijohannis* the difference in size remains more constant than that of coloration. In 1938 (pp. 290-291), he discussed the birds of northwestern Alaska again, this time referring them to the form *kamtschatkensis*, which he considered to be distinct from *pallidus*. Bailey (1942:305-306) reported an additional number of specimens from northwestern Alaska as *pallidus* and gave one definite breeding record from the Seward Peninsula; later (1948:182) he mentioned one other breeding record based on a collected specimen. He was inclined to doubt, rightly as I hope to prove, that Asiatic and American birds could be distinguished on the basis of size, and he also stated with clear insight that "while many of the rough-legs of northwestern and Arctic Alaska are no doubt colored like Siberian birds, the converse would probably be true—that many from the Asiatic side would be called *s. johannis* if compared with birds of our own continent" (*loc. cit.*).

In the twentieth supplement to the A.O.U. Check-list (Wetmore *et al.*, 1945), *Buteo lagopus pallidus* (Menzbier) was recognized as an additional subspecies for North America; in the twenty-third supplement (Wetmore *et al.*, 1948), the name was changed to *Buteo lagopus kamtschatkensis* Dementiev, "because of the prior *Buteo pallidus* Lesson, Traite d'Orn., livr. 2, May, 1830, p. 82, for another species." Friedmann (1950:336) has apparently recently followed this decision because he has placed *pallidus* in the synonymy of *kamtschatkensis* and the breeding range given is that of the Siberian form, including Kamchatka and northwestern Alaska.

It is apparent that there are conflicts in the names currently applied to subspecies of *Buteo lagopus*. Dementiev *et al.* (1951:312) have also recognized the priority of *Buteo pallidus* Lesson, and while retaining *kamtschatkensis* as a distinct subspecies, they have renamed *Buteo lagopus pallidus* (Menzbier) as *Buteo lagopus menzbieri*. Whether *menzbieri* or *kamtschatkensis* succeeds *pallidus* as the name for the pale-colored Siberian form appears to rest on whether or not *kamtschatkensis* is a valid subspecies.

Field work.—During the summer of 1952, I was one of the several persons assigned to study the birds of the Colville River, northern Alaska, under contract between the Office of Naval Research and the University of Alaska—Contract Nonr-768(00), Project NR 307 019, Dr. Brina Kessel, principal investigator. One of the purposes of this investigation was to gather critical material for taxonomic work. Field observations and collecting were carried out from June 4 to August 19, 1952. During that time 48 nesting pairs of Rough-legged Hawks were studied, a series of 8 adults and 3 juveniles was collected, and a number of fledglings was banded, one of which was recovered the following November in southern Alberta. Particular attention was paid to plumages and molt in the living birds, which could be observed in detail at their nests.

While in the field, I became aware of the great variability of size and plumage in this population. It was particularly striking to find extremely melanistic individuals mated with very pale ones, and thus I began to question the correctness of considering the northwestern Alaskan hawks a New World contingent of the Asiatic subspecies. The subsequent work with museum material was, therefore, an outgrowth of impressions received on the breeding grounds in Alaska.

Acknowledgements.—This study was carried out under the direction of Thomas R.

Howell of the Department of Zoology of the University of California, Los Angeles, to whom I am much indebted for help and advice throughout the course of the work. I would like to thank the following people for the loan of material under their care: Herbert Friedmann, United States National Museum (USNM); John T. Zimmer, American Museum of Natural History (AMNH); W. Earl Godfrey, Canadian National Museum (CNM); L. L. Snyder, Royal Ontario Museum of Zoology and Paleontology (ROMZ); Brina Kessel, University of Alaska (U of A); A. L. Rand, Chicago Natural History Museum (CNHM); H. K. Gloyd, Chicago Academy of Sciences (Chic. Acad. Sci.); J. C. Greenway, Jr., Museum of Comparative Zoology (MCZ); Robert W. Storer, University of Michigan Museum of Zoology (UMMZ); Alfred M. Bailey, Denver Museum of Natural History (DMNH); K. C. Parkes and W. E. Clyde Todd, Carnegie Museum (CM). Alden H. Miller very kindly provided me with study facilities at the Museum of Vertebrate Zoology (MVZ), and Robert T. Orr gave me access to the series of *Buteo lagopus* from Manchuria collected by A. S. Loukashkin and now deposited in the California Academy of Sciences (CAS). E. A. Simms of the British Museum (Natural History) was good enough to send me plumage descriptions of some specimens under his care. I am further indebted to L. L. Snyder for a discussion of sexual dimorphism in *Buteo lagopus*. Special acknowledgement is due my wife, Renetta Mae Cade, for invaluable assistance in the preparation of figures and tables.

MATERIAL AND METHODS

This study is based on an examination of 179 specimens, of which 73 were adult males, 65 adult females, and 41 juveniles. In so far as possible only material taken during the breeding season (May-August) has been used, the assumption being that such specimens were taken on, or reasonably near, their actual breeding grounds. Reilly (1954:162) has recently offered some justifiable objections to such an assumption, but for studies of variation requiring many specimens there seems to be no other recourse. The exception to this limitation is the sample from Asia, which consists of 10 summer- and 40 winter-taken individuals.

The geographic distribution of the specimens examined from North America is shown in figure 1. This distribution almost completely covers the known nearctic breeding range. Specimens were assigned to the following geographic groups for comparative study: (1) Asia; (2) Aleutian Islands and southwestern Alaska; (3) northwestern and northern Alaska; (4) western Canada; and (5) eastern Canada. The latter two groups were arbitrarily separated at 80 degrees west longitude. These groups can be considered more or less natural geographic units. The Bering Sea and the Arctic Ocean provide a hiatus in the breeding range between Asia and Alaska. In western Alaska just north of the base of the Alaska Peninsula there is the broad Yukon-Kuskokwim delta country, which because of its low, flat terrain is little suited to the nesting requirements of the Rough-legged Hawk and which, therefore, in terms of relative numbers acts as another hiatus between the abundant breeding populations of southwestern and northwestern Alaska. A similar situation is believed to exist in the region of the Mackenzie River delta, which separates the northern Alaskan hawks from those breeding east of the Mackenzie. In the eastern Canadian arctic the range is again disrupted by Hudson Bay, the east-west continuity of the population being maintained by only a few, scattered pairs nesting on islands.

Three measurements were taken: chord of the wing, diagonal of the tarsus, and chord of the entire culmen. The instructions of Baldwin, Oberholser, and Worley (1931:13, 76, 107) were followed. Measurements were read to the nearest millimeter only.

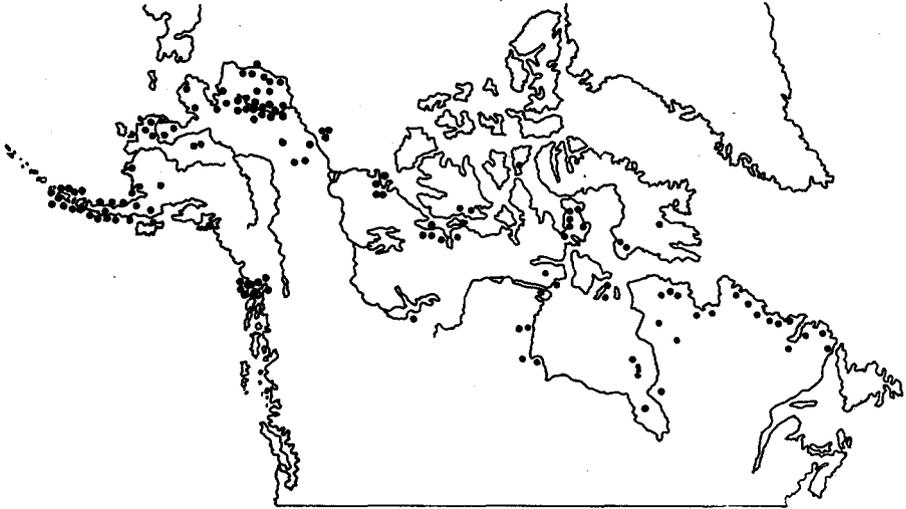


Fig. 1. Geographic distribution of specimens of *Buteo lagopus* from North America. Records include both adults and juveniles taken in the breeding season. Note peripheral nature of distribution.

The plumage traits employed in this study are those already used in descriptions of this species (see Friedmann, 1950; Witherby *et al.*, 1939). In addition, some other characters that proved to be important after an initial series had been examined were used. About a dozen plumage characters have been studied; these are described in table 4.

The original sex determination of all specimens has been accepted, although in a number of cases one may be practically certain that the specimen was incorrectly sexed. This increases the inaccuracy of the frequency distribution of the characters and tends to overemphasize the degree of overlap in traits between the sexes, but it has been done to avoid the criticism of biasing the data in favor of a particular result. On the other hand, in several instances where specimens that were recorded as adults were obviously birds of the year, a situation particularly easy to detect in males, I have felt justified in changing their status in the presentation of the data. Unsexed specimens, constituting less than 5 per cent of the total sample, were placed according to their appearance.

Formulae for all statistical calculations were taken from Simpson and Roe (1939), except as indicated in the footnote of table 3. Chi-square values were calculated directly from the raw data.

MOLT AND AGE CHARACTERS

Rough-legged Hawks undergo a single annual molt, which takes place mainly during the breeding season. Hence, specimens from the breeding range have only partly acquired fresh plumage, and this is the major disadvantage in studying a sample of breeding birds of this species. There is no postpuvinal molt, birds of the year retaining the feathers they acquire in the nest until the following spring, when they begin molting into a plumage that is essentially adult in character.

Bent (1937:273) has suggested that there is a second-year plumage somewhat intermediate between the juvenal and adult plumages, but I think his statements regarding the distinctions of these three are confusing and they are at variance with my own findings. After having examined a large series, however, I am left with the impression that there may be some progressive changes of the plumage with age. The older males in particular appear to become less pigmented, with fewer and smaller breast markings and

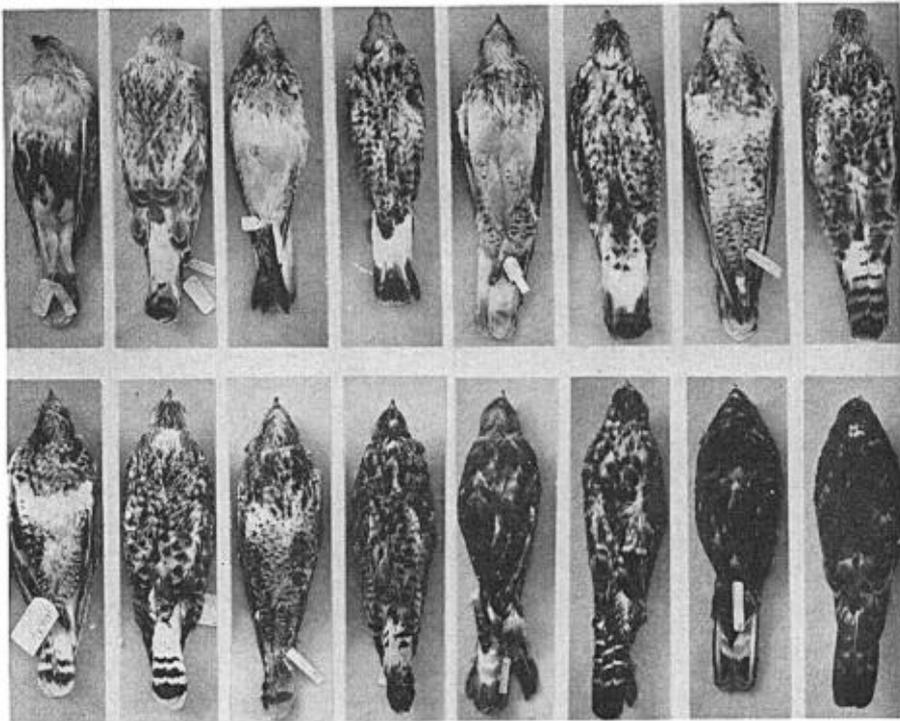


Fig. 2. Ventral and dorsal aspects of adult male Rough-legged Hawks. Upper row, from left to right: MCZ 92669, Altai Mountains; DMNH 22866, Wainwright, Alaska; U of A 614, Colville River, Alaska; AMNH 442641, Melville Peninsula, Canada. Lower row: CNHM 102133, Manchuria; CNM 16152, Labrador; USNM 299396, Izembek Bay, Alaska; DMNH 25277, Meade River, Alaska.

gradual reduction of the belly wash, until in some individuals (fig. 2) the ventral surface is almost immaculate. But certainly the major change in plumage occurs with the first molt.

According to Bent (*loc. cit.*), the annual molt occurs between April and November. From my sample it appears that most of the adults complete the greater part of their molt, especially that of the flight feathers, in June, July, August, and September. There is also an indication that the first annual molt begins earlier in the year than do subsequent ones; but few birds of the year survive to the time of molt, and hence there are few immature specimens for comparison.

In so far as possible detailed records were kept on the molting of Rough-legged Hawks observed along the Colville River in 1952. With practice it was possible to determine with considerable accuracy the condition of the remiges and rectrices of birds as they soared about their nests. Notes were also taken on the molt of freshly collected specimens. The primaries of this species are normally molted from the fourth outward, the innermost three molting in sequence with the secondaries; and the rectrices are molted from the central pair outward. It is therefore possible to determine the stage of molt of a particular individual by noting which feathers are missing. Table 1 summarizes data secured on the Colville River. Birds observed after July 26, the last date indi-

Table 1

Summary of Observations on the Molt of *Buteo lagopus* along the Colville River, Alaska, in 1955

Date	Males	Females
June 17	1 with right 7th primary just coming in and many new dorsal feathers.	2 with right and left 7th primaries and one central rectrix molted.
June 18	1 with right and left 7th primaries just coming in.	1 with right 4th and 5th coming in and left 4th coming in, left 5th complete.
June 20	2 with no visible molt.	1 with left 7th molted. 1 with right and left 7th primaries molted.
June 22	2 with right 7th primary molted. 1 with right and left 7th primaries molted.	3 with right 6th and 7th and left 7th primaries molted. 1 with right and left 7th primaries molted. 1 with right and left 6th primaries and one central rectrix molted. 1 with right and left 3rd or 4th primaries molted; 5-7th ones growing in.
June 25	1 with left 6th half in and right 7th half in; right central rectrix just coming in.	1 with 3rd or 4th primaries molted.
June 27	3 with no visible molt. 2 with right and left 7th primaries coming in. 1 with left 7th primary molted. 1 with right and left 3rd and 4th primaries molted (sex doubtful). 1 with 6th and 7th primaries coming in.	2 with right and left 2nd or 3rd primaries molted. 1 with left 7th molted. 2 with right and left 7th primaries molted. 1 with right and left 6th primaries molted; 7th ones coming in. 1 with 6th and 7th primaries and one central rectrix coming in.
July 5	1 with right and left 2nd or 3rd primaries molted.	1 with molted secondaries.
July 6	1 with right and left 3rd or 4th primaries molted.	1 with right 5th primary half in.
July 7	1 with right and left 2nd or 3rd primaries molted.	1 with secondaries molted on both wings.
July 8	1 with right and left 2nd or 3rd primaries molted. 1 with right and left 3rd or 4th primaries molted.	1 with all fresh primaries. 1 with a few molted secondaries.
July 10	1 with right and left 5th primaries just coming in.	1 with right and left 3rd primaries just coming in; one molted secondary on left and both central rectrices coming in. 1 with all new remiges and central rectrices molted.
July 26	1 with no visible molt.	1 with no visible molt.

cated in the table, were so far progressed in the molt of flight feathers that determinations were no longer possible.

In addition to showing that the main molting activity occurred in June and July in that population that year, the data also indicate that the females molt ahead of the males. This was even more evident when the male and female of a given pair were compared. A similar sexual difference in timing was observed for Peregrine Falcons (*Falco peregrinus*) breeding in the same region, and Beebe (1953:11) has recently recorded the same thing for this species on the islands off the coast of British Columbia. This may therefore be a widespread phenomenon among falconiform species, and it could be cor-

related with the usual social arrangement among mated hawks in which the male does most of the hunting, and hence most of the flying, during the incubating and nestling period, while the female remains close to the nest. After the young have fledged she then assumes a more active role as food provider.

There is no sexual dimorphism of the first-year plumage, and individual and geographic variation is much less than among adults (see table 5). Friedmann (1950:327) gives a concise and accurate description of the immature plumage. I will therefore restrict my statements to a consideration of the several traits studied in detail by me as they occur in the first-year bird.

The tail pattern is nearly always type D (table 4), occasionally type C, especially in the Asiatic sample, and occasionally type E in the American sample only; it is never type A or B. The belly pattern is most frequently type E, occasionally type D, especially in the Asiatic sample, and occasionally type F in the American sample only; it is never type A, B, or C.

The marginal coverts of the juvenal wing are most frequently type I; occasionally, especially in the Asiatic sample, they are type III; less frequently they are type II; also infrequently, in the American sample only, they are type IV.

Juvenal heads are more frequently type A than B, and the primaries are frequently type I, II, or III. These traits occur more frequently in juveniles of both continents than in their respective adult populations.

The shaft marks of individual feathers on juvenal breasts are usually wide and medium brown in color; but between the Asiatic and American samples there is almost a complete differentiation in the color of the feather margins. One hundred per cent of the Asiatic sample has whitish or creamy margins, and over 90 per cent of the American sample has buffy or reddish ones. The same difference holds for the feathers of the back.

The adult plumage of *Buteo lagopus* is extremely variable, being exceeded in this respect by only one other North American congener, *Buteo jamaicensis*. Friedmann's (1950:325-327) description, while accurate in its terms, suffers from being a composite of a series rather than a delineation of the range of adult variability. Again I shall discuss only those characters that I have subjected to quantitative study.

The adult tail pattern ranges through all types (see table 4e), although it is most frequently type A, B, or C, and much less frequently type D than in the case of the juvenal tail. The adult belly pattern also ranges through all types (table 4f), but it is less frequently type E than is the juvenal belly.

The marginal coverts of the adult wing are usually type I or II; occasionally in the Asiatic sample only they are type III, and occasionally in the American sample only they are type IV. The adult head is less frequently type A than is the juvenal head, and the adult primaries are less frequently type I or II than are those of the juvenal.

Adult hawks range through all the ventral and dorsal types of tables 4c and d.

INDIVIDUAL VARIABILITY

The variability of any sexually segregated sample of *Buteo lagopus* is great. For the mensural characters this is best seen by examining the statistics of table 2. An idea of the variability in plumage can be gained by looking at figures 2 and 3. Specimens DMNH 25277 and DMNH 22866 of figure 2 represent the observed extremes of male plumage. The females appear to be less variable in plumage than are the males.

The basic patterns of plumage remain relatively constant from individual to individual. Most of the gross differences in plumage can be attributed to the variable

Table 2

Measurements of *Buteo lagopus*

Dimension	Population	Sex	Number of specimens	Range	Mean with standard error	Standard deviation	
Wing	Asia	M	23	396-448	418±3.38	16.22	
		F	21	401-456	435±3.02	14.03	
	Aleutians, SW Alaska	M	12	396-445	418±3.22	11.16	
		F	13	430-461	445±2.52	9.11	
	NW Alaska	M	14	394-444	424±4.36	15.29	
		F	13	403-454	435±3.76	13.6	
	W Canada	M	12	395-426	411±2.96	10.25	
		F	8	413-459	436±4.87	13.77	
	E Canada	M	12	392-412	406±1.71	5.92	
		F	14	416-450	436±2.59	9.59	
	American juveniles	M	9	340-470	422±8.46	25.38	
		F	4	360-440	405	
	Asiatic juveniles	M	7	410-446	427±5.67	15.03	
		F	2	438-452	445	
	Tarsus	Asia	M	23	58-72	66.0±0.70	3.36
			F	20	61-75	68.6±0.89	4.02
		Aleutians, SW Alaska	M	12	65-71	68.3±0.55	1.92
			F	12	68-78	74.9±0.80	2.78
		NW Alaska	M	14	64-73	69.8±0.60	2.26
			F	13	67-77	71.9±0.88	3.19
W Canada		M	12	62-72	67.9±0.78	2.96	
		F	7	65-75	67.4±1.32	3.51	
E Canada		M	12	65-71	68.0±0.47	1.63	
		F	14	69-75	71.3±0.48	1.83	
American juveniles		M	8	62-74	67.8±1.52	4.55	
		F	5	68-72	69.4±0.66	1.49	
Asiatic juveniles		M	7	66-71	69.9±0.80	2.10	
		F	2	71-77	74.0	
Culmen		Asia	M	23	31-40	33.7±0.40	1.94
			F	21	32-38	35.6±0.37	1.69
		Aleutians, SW Alaska	M	12	33-38	34.8±0.36	1.25
			F	12	35-39	36.8±0.39	1.37
		NW Alaska	M	13	33-38	35.1±0.43	1.55
			F	12	35-39	36.9±0.38	1.19
	W Canada	M	10	34-37	35.1±0.27	0.84	
		F	7	35-39	37.0±0.53	1.41	
	E Canada	M	11	32-38	35.0±0.49	1.65	
		F	14	34-39	36.8±0.39	1.46	
	American juveniles	M	9	32-38	34.1±0.59	1.79	
		F	5	33-38	35.0±0.85	1.89	
	Asiatic juveniles	M	5	34-37	35.5±0.89	2.01	
		F	2	37-38	37.5	

amounts of melanin pigments deposited in the feather tracts. Concealed patterns are evident in even the most melanistic individuals upon close examination.

The American form of *Buteo lagopus* is said to be dimorphic or polymorphic. Thus Friedmann (1950:325-327) gives separate descriptions for the "light phase" and for the "melanistic phase," and there are numerous other references in the literature to the two-phase condition of *sanctijohannis*. Figures 2 and 3 show a complete range of intermediate plumages between the lightest and darkest specimen. The "two phases" of the

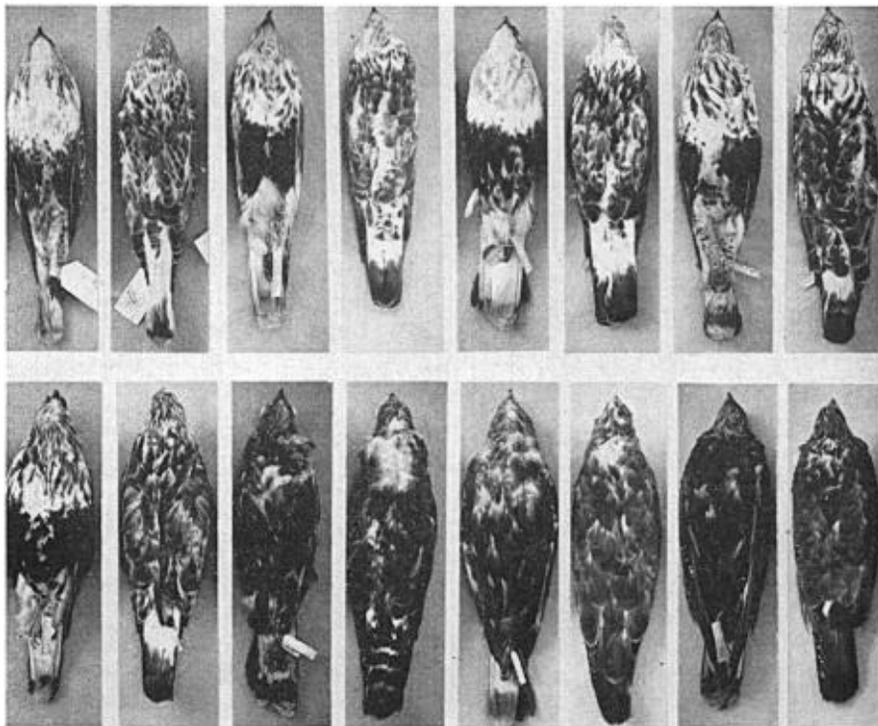


Fig. 3. Ventral and dorsal aspects of adult female Rough-legged Hawks. Upper row, from left to right: CNHM 101222, Manchuria; USNM 230742, Alaska Peninsula; DMNH 22867, Wainwright, Alaska; CNM 20984, Baffin Land, Canada. Lower row: DMNH 22868, Wainwright, Alaska; U of A 606, Colville River, Alaska; MCZ 234081, Amak Island, Aleutians; AMNH 269935, Port Moller, Alaska.

American Rough-legged Hawk are not discontinuous as is true of the Screech Owl (*Otus asio*) and some other species, and hence it is not polymorphic in the sense of Ford (1945), Huxley (1942:96), and others, especially Mayr (1942) and Mayr, Linsley and Usinger (1953:96). The condition can best be described as a wide range of continuous variation from a nearly uniform sooty plumage to a light brown one, the dark color being restricted ventrally to a few small marks on an otherwise white ground and dorsally by wide whitish edges on the individual feathers. Dark birds do not occur with the same frequency over the range of *sanctijohannis*, and in this respect they behave as a polymorph variant (see Mayr and Stresemann, 1950).

The variability within any population of *Buteo lagopus* is so great as to preclude accurate study of geographic variation without large series of skins. Even my samples, which are the largest yet compared, are inadequate for anything but approximations.

SEXUAL DIMORPHISM

Sexual dimorphism is clearly evident in many characters of *Buteo lagopus*, but as in every other aspect of variation, it is not marked by sharp discontinuities, that is, all males are not different from all females in any character studied, with one apparent exception to be mentioned later.

Size.—Following the rule among falconiforms, Rough-legged Hawks are sexually dimorphic in size, the female averaging larger than the male. There is, however, a great deal of overlap between the sexes in all mensural traits studied (table 2) except that of body weight. Table 3 compares the sexual dimorphism of these characters among the

Table 3

Comparison of Sexual Dimorphism in Mensural Characters among Sample Populations of *Buteo lagopus*

Population	Wing		Tarsus		Culmen	
	C.D.	P.J.N.	C.D.	P.J.N.	C.D.	P.J.N.
Asia	0.561	<75	0.189	<75	0.527	<75
Aleutian Islands and SW Alaska	1.33	<91	1.40	<92	0.769	>75
Northwest Alaska	0.384	<75	0.388	<75	0.666	<75
West Canada	1.04	85	0.08	<75	0.826	<80
East Canada	1.93	>96	1.06	>85	0.581	<75

C.D. stands for coefficient of difference; P.J.N. stands for per cent joint nonoverlap. See Mayr, Linsley, and Usinger, 1953:146, for explanation and interpretation of this statistic.

several geographic samples of this study. In 9 cases out of the 15 comparisons of table 3, the samples indicate only 75 per cent or less joint nonoverlap in size between the sexes. Some of the differences are not even statistically significant. There is, nevertheless, some apparent geographic variation in sexual dimorphism in size that will be dealt with later.

Because the data on body weight are meager, they are summarized here. The average weight in grams of 4 arctic Alaskan males collected on the Colville River in 1952 is 915 (883–943), and the average of 4 females from the same region is 1216 (1033–1400). Two specimens collected by O. J. Murie on the Old Crow River, Yukon Territory, have the following converted metric weights: female, 1176 gm.; male, 840 gm. Dementiev *et al.* (1951:312) give the average of 5 males of typical *lagopus* as 846 (800–930), and the average of 5 females as 1151.4 (990–1280). They also give (p. 315) the weight of one male *kamtschatkensis* as 900 gm., and of 2 females as 1050 and 1209 gm. Thus, in a total of 11 male weights and 12 female weights there is no *observed* overlap between the sexes, the largest male (943 gm.) and the smallest female (990 gm.), however, being separated by only 47 gm.

In view of the pronounced overlap in linear characters between the sexes, it is surprising not to find a corresponding amount of overlap in their weights. This circumstance suggests that none of the linear characters used in this study are accurate indices of over-all size in *Buteo lagopus*.

Plumage.—An entirely unsuspected finding of this study is the fact that the sexes of *Buteo lagopus* are partly dimorphic in plumage. I have found no mention of this in the literature, all authorities stating emphatically that the sexes are alike in this respect. Plate 65 (upper left fig.) of the "British Handbook" (Witherby *et al.*, 1939:33), painted by the late G. E. Lodge, correctly depicts some of the differences between the adult male and female, as well as differences between them and the juvenile, but no mention is made in the text of differences between the sexes.

Among the adult plumage traits previously mentioned, the following are in varying degrees sexually dimorphic: (1) tail pattern, (2) belly pattern, (3) marginal coverts

Table 4

Arbitrary Classifications of Plumage Characters

Character	Designation	Description
(a) Head types (crown and occiput)	A	Head distinctly lighter than rest of dorsal aspect; shaft streaks of feathers narrow.
	B	Head not distinctly lighter than rest of dorsal aspect; shaft streaks of feathers wide.
(b) Outer primaries (see fig. 5)	I	Outer 4 to 7 primaries with extensive (30-50 mm.) light area on outer webs distal to their coverts.
	II	Outer 3-5 primaries with moderate (10-20 mm.) light area on outer webs distal to the ends of their coverts.
	III	Outer 1-3 primaries with faint light area on outer webs.
	IV	All primaries lacking any light area on outer webs distal to the ends of their coverts.
(c) Breast	A	Light brown marks on feathers.
	B	Medium brown marks on feathers.
	C	Dark brown marks on feathers.
	D	Uniformly dark feathers.
	I	Shaft marks wide.
	II	Shaft marks narrow.
	a	Feather edgings whitish.
	b	Feather edgings reddish.
(d) Dorsum	ab	Feather edgings reddish and whitish.
	A	Light brown marks on feathers.
	B	Medium brown marks on feathers.
	C	Dark brown marks on feathers.
	D	Uniformly dark feathers.
	I	Shaft marks reduced; margins wide and intruding toward shaft.
	II	Shaft marks wide; margins narrow.
	a	Feather edgings whitish.
(e) Tail	b	Feather edgings reddish.
	ab	Feather edgings reddish and whitish.
	A	A dark subterminal band and 3 or more complete or incomplete ones proximal to it. Example, AMNH 442641 of fig. 2.
	B	A dark subterminal band and 1 or 2 complete or incomplete ones proximal to it. Example, CNHM 102133 of fig. 2.
	C	A distal "field" of brown with a faint darker subterminal band within it. Example, DMNH 23644 of fig. 6.
	D	A uniform distal field of brown; no subterminal band visible. Example, Chic. Acad. Sci. 4211 of fig. 6.
	E	Tail uniformly dark distal to the coverts (melanistic). Example, DMNH 25277 of fig. 2.
	(f) Belly	A
B		Moderate barring. Example, AMNH 442641 of fig. 2.
C		Heavy barring. Example, CNM 16152 of fig. 2.
D		Lateral blotching. Example, CNM 20984 of fig. 3.
E		Continuous band. Example, DMNH 22867 of fig. 3.
F		Uniformly dark venter. Example, MCZ 234081 of fig. 3.
(g) Marginal coverts	I	Feathers with longitudinal shaft marks.
	II	Feathers with subterminal wedge-shaped marks.
	III	Feathers uniformly light (creamy) colored.
	IV	Feathers uniformly dark (reddish to sooty) colored.

of wing, (4) relative lightness of head to back, and (5) pattern of the dorsal feathers. The dimorphism is most pronounced in the first two categories.

One finds that in the tail classes A through D of table 4e (class E is excluded because of its low and nearly equal frequency in the two sexes), most males are in classes A and B, and most females are in C and D. There is overlap into nearly all classes by some specimens of both sexes (see table 5), but when the frequencies of the sexes are grouped into two categories, A-B and C-D, and tested by the chi-square method, the difference between all adult males and all adult females is significant beyond the 1 per cent level of confidence (table 6a). Figure 4 shows the "typical" male and female types of tail compared with the usual juvenal (non-dimorphic) type.

Similarly, in the belly classes of table 4f (F, the melanistic class, is excluded) most males are in classes A through C and most females in C through E. The C class is the

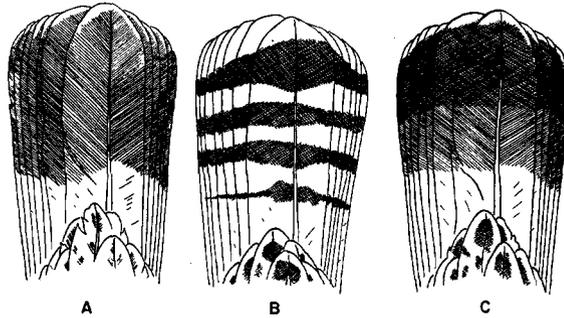


Fig. 4. Tail patterns of *Buteo lagopus*. A, juvenal (little variation); B, adult male (much variation); C, adult female (much variation).

principal area of overlap between the sexes, but this is at least partly a result of the arbitrariness of the classification and of the difficulty of deciding where to place borderline specimens between type B and C and between type C and D (see table 5). A significant difference beyond the 1 per cent level is again demonstrated (table 6h).

Among the classes of the marginal coverts of the wing, a large number of males occurs in class I and a large number of the females in class II. They are about equally distributed in classes III and IV. Testing male and female frequencies in the first two classes also yields a significant difference beyond the 1 per cent level (table 6aa and hh).

The ratio of type A to type B heads is greater in males than in females, and this difference proves to be highly significant (table 6s).

Finally, there are some subtle differences between males and females in the patterns and colors of the dorsum, but table 6gg reveals no statistical difference between the sexes for one dorsal character, and the classification of the others did not lend itself to statistical treatment. In general, it can be said that the male dorsum appears more variegated than the female, with much more white, brown, red, and often slate, showing in the individual feathers. The females appear more uniformly brown, with little white or reddish showing except on the margins, and seldom any slate. The individual feathers of males are frequently barred or blotched transversely in three or more rows with dark marks interspersed with reds, browns, and grays, whereas female feathers are seldom marked in this manner but usually show wide longitudinal shaft marks of brown, occasionally with indications of marginal blotching of the same color.

It is gratifying to have independent corroboration of these findings. L. L. Snyder, working with a much smaller series of Canadian specimens, but fortunately drawn from

an extremely homogeneous population, has found some of these same differences between the sexes.

A specimen that is masculine or feminine in one trait is usually masculine or feminine in the other sexually dimorphic traits also, but this is not always true. A few specimens combine typically male and female characters. Tail and belly patterns concord most completely and are the most reliable indicators of sex.

In a total of 137 adult specimens, only about 11 per cent are sexually heterogenous in tail and belly patterns. A closer discrimination of plumage types would probably have reduced this figure more. The differences between tail types B and C and between belly types C and D are quite arbitrarily defined.

About 9 per cent of the adult specimens have tail and belly types of the sex opposite to their recorded sex. I was at first tempted to explain this solely as the result of misidentification of sex on the part of earlier collectors. Since such a small percentage of the specimens is involved, this is not an unreasonable assumption. One of my own specimens, however, shows a sex reversal in plumage, so while incorrect sexing probably accounts for part of the 9 per cent, some biological factor must also be concerned.

GEOGRAPHIC VARIATION

Wing length.—The mean wing length of adult males ranges from 424 mm. in northwestern Alaska to 406 mm. in eastern Canada (table 2), and statistics derived from these two non-adjacent samples show about 80 per cent joint nonoverlap. Between any two adjacent samples, however, no joint nonoverlap approaches 75 per cent. There is an indication of a cline from short wings in eastern Canada to longer wings in northwestern Alaska and Asia, but the differences in the means of the several populations are scarcely significant statistically. There is certainly no difference among the northwestern Alaskan, Aleutian-southwestern Alaskan, and Asiatic populations.

The mean wing length of adult females ranges from 435 mm. in Asia and northwestern Alaska to 445 mm. in the Aleutians and southwestern Alaska. In this case the extreme populations are adjacent, but they show less than 75 per cent joint nonoverlap. The Aleutian-southwestern Alaskan females do, however, show a large divergence from the other samples, which are remarkably similar, differing by only one mm. in their means.

Diagonal of tarsus.—The mean tarsal length of adult males ranges from 66 mm. in Asia to 69.8 mm. in northwestern Alaska, and these two adjacent populations show nearly 75 per cent joint nonoverlap. Other adjacent populations of this series are statistically indistinguishable from each other, and no cline is indicated.

The mean tarsal length of adult females ranges from 68.6 mm. in Asia to 74.9 mm. in the Aleutians and southwestern Alaska, and these populations are separated by more than 82 per cent joint nonoverlap. Also the eastern Canadian and western Canadian populations show a joint nonoverlap of more than 75 per cent, and the northwestern Alaskan and western Canadian ones almost 75 per cent; but the pattern of variation is irregular. Northwestern Alaskan and Aleutian-southwestern Alaskan populations are not statistically different in this trait.

Length of culmen.—The mean culmen length of adult males ranges from 33.7 mm. in Asia to 35.1 mm. in northwestern Alaska and western Canada, but none of the differences is statistically significant, and no particular trend is indicated.

The mean culmen length of adult females ranges from 35.6 mm. in Asia to 37 mm. in western Canada, but this difference is not significant. The Asiatic sample shows the greatest deviation from the others in both males and females.

Table 5

Frequency Distribution of Plumage Characters among Sample Populations of *Buteo lagopus*

Population	Head		Web of primaries				Breast						Dorsum						Tail					Belly						Marginal coverts													
	A	B	I	II	III	IV	I	II	A	B	C	D	a	b	ab	I	II	A	B	C	D	a	b	ab	A	B	C	D	E	A	B	C	D	E	F	I	II	III	IV				
Asia																																											
Males	8	15	9	4	4	6	17	6	9	13	1	0	23	0	0	16	7	10	9	4	0	17	0	6	2	16	4	1	0	4	9	2	5	3	0	5	8	8	0				
Females	15	5	8	7	3	3	10	11	14	7	0	0	20	0	1	19	2	14	6	1	0	15	0	6	1	4	8	8	0	0	4	2	7	8	0	9	4	7	0				
SW Alaska																																											
Males	1	12	0	0	1	12	10	0	0	4	6	3	6	3	1	3	8	0	5	6	2	0	2	10	2	5	3	1	1	0	1	4	2	3	2	2	10	0	1				
Females	9	4	0	0	2	11	10	1	1	5	5	2	5	5	0	1	10	0	4	7	2	0	7	4	0	0	3	10	0	0	0	1	1	11	0	6	5	0	2				
NW Alaska																																											
Males	2	12	0	1	2	12	12	2	2	10	2	1	14	0	0	7	7	2	10	2	1	0	0	14	2	8	1	3	1	4	4	3	2	1	1	2	10	0	1				
Females	5	8	0	0	3	10	9	3	3	7	2	1	11	1	0	2	10	0	10	2	1	0	2	10	1	1	5	6	0	0	0	0	5	7	1	5	7	0	0				
West Canada																																											
Males	1	11	0	0	0	12	12	0	0	8	4	0	11	0	1	6	6	0	6	6	0	1	0	11	7	5	0	0	0	3	5	4	0	0	0	0	0	11	0	1			
Females	2	6	0	0	1	7	6	1	0	7	0	1	7	0	0	2	5	0	7	0	1	0	1	6	2	1	5	0	0	0	2	0	3	2	1	1	6	0	1				
East Canada																																											
Males	0	12	0	0	0	12	11	0	0	3	8	1	9	0	2	1	10	0	2	9	1	0	0	11	8	3	1	0	0	1	4	6	0	0	0	1	0	11	0	1			
Females	8	5	0	0	0	14	12	0	0	5	7	2	9	0	3	2	10	0	5	7	2	0	1	11	0	0	11	2	1	0	0	3	8	1	2	5	8	0	1				
Asiatic juv.																																											
Males	7	0	5	0	2	0	5	2	1	6	0	0	7	0	0	3	4	3	4	0	0	4	0	3	0	0	2	4	0	0	0	0	4	3	0	6	0	1	0				
Females	2	0	2	0	0	0	2	0	0	2	0	0	2	0	0	2	0	0	2	0	0	2	0	0	0	0	0	2	0	0	0	0	0	2	0	1	0	1	0				
American juv.																																											
Males	6	5	1	1	3	5	8	4	1	6	4	2	1	11	0	7	6	0	7	5	2	0	12	0	0	0	2	12	0	0	0	2	11	1	7	1	2	1					
Females	6	2	2	2	2	2	12	3	0	11	4	1	1	15	0	11	4	0	10	5	1	0	14	1	0	0	13	3	0	0	0	2	13	1	7	1	7	1					

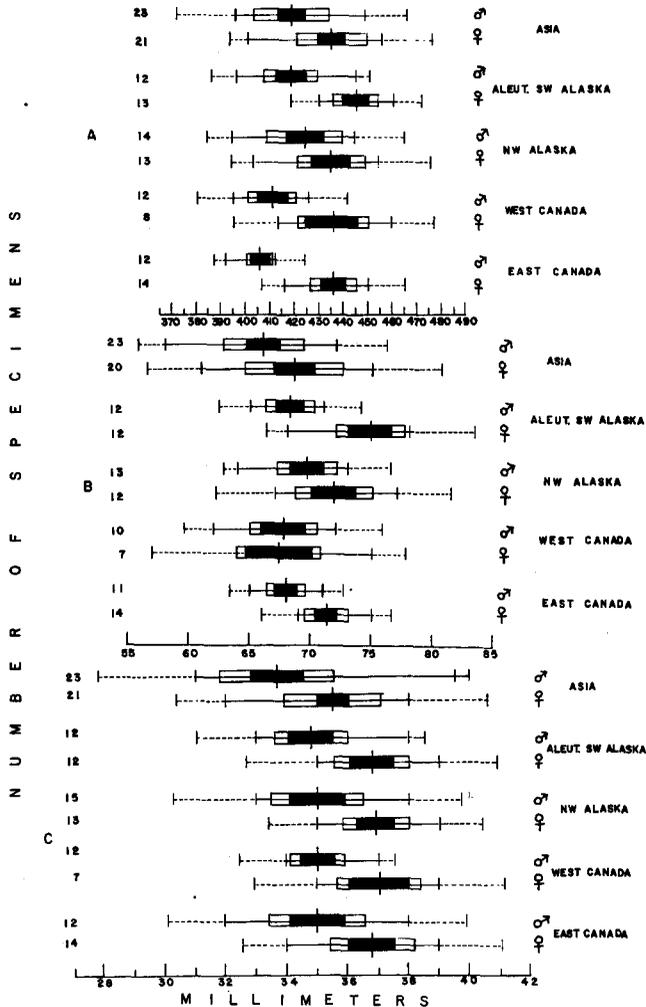


Fig. 5. Variation in measurements among sample populations of *Buteo lagopus* expressed as Dice squares. A, chord of wing; B, diagonal of tarsus; C, chord of entire culmen; see Hubbs and Perlmutter (1942) for discussion of use of Dice squares.

An important consideration emerges from a study of these measurements. Although any given population usually shows a wide range of variability, when geographic samples in a sexually segregated series are compared, the samples show remarkably little difference in their means. In other words, individual variability is great, but geographic variation is not. In every case standard errors of the means in the male series and in the female series overlap with one or more others. It appears impossible, therefore, to define geographic populations on the basis of measurements with the number of specimens now available by employing any accepted criterion of difference used to distinguish subspecies (Mayr, Linsley, and Usinger, 1953:143).

Although standard deviations are influenced by variables other than true biological ones, such as size of sample and non-random sampling, it is interesting to compare these

Table 6
Frequency Comparisons of Plumage Traits between Samples of *Buteo lagopus*

Comparisons	Break-down of classes		Chi-square values	P values	Comparisons	Break-down of classes		Chi-square values	P values
	A-B	C-D				D	All others		
TAIL									
(a) All adult males	58	10	57	<.01	(o) All adult Canadian females	11	11	3.7	>.05
All adult females	14	59			All adult Alaskan females	6	20		
(b)* Asiatic juveniles	2	6	5.4	<.02	(p) All adult Alaskan females	6	20	1	>.1
American juveniles	2	25			All adult Asiatic females	7	14		
	C	D			E All others				
(c)* All adult females	33	26	16	<.01	(q)* All adult Canadian females	3	19	12	<.01
All juveniles	4	31			All adult Alaskan females	18	8		
(d)* All adult Canadian females	16	2	10	<.01	(r) All adult Alaskan females	18	8	4.5	<.05
All adult Alaskan females	8	16			All adult Asiatic females	8	13		
(e) All adult Alaskan females	8	16	1	>.1	HEAD				
All adult Asiatic females	9	8			(s) All adult males	12	62	22	<.01
	A	B			All adult females	39	28		
(f)* All adult Canadian males	15	8	5.44	<.02	(t)* Asiatic juveniles	9	0	1.9	>.1
All adult Alaskan males	4	13			American juveniles	12	7		
(g) All adult Alaskan males	4	13	1	>.1	(u) All adult females	39	28	2.3	<.1
All adult Asiatic males	3	20			All juveniles		
					(v)* All Canadian males	1	23	1.0	>.1
BELLY									
(h) All adult males	54	16	49	<.01	All Alaskan males	3	24		
All adult females	12	53			(w)* All Alaskan males	3	24	2.6	<.1
(i)* All adult Canadian males	23	0	5.6	<.02	All Asiatic males		
All adult Alaskan males	16	8			(x) All Canadian females	10	11	1.0	>.1
(j) All adult Alaskan males	16	8	1	>.1	All Alaskan females	14	12		
All adult Asiatic males	15	8			(y) All Alaskan females	14	12	2.1	<.1
(k)* All adult Canadian females	5	14	2.8	<.1	All Asiatic females	15	5		
All adult Alaskan females	1	24			(z) All Canadian females	10	11	3.2	>.05
(l)* All adult Alaskan females	1	24	3.64	>.05	All Asiatic females		
All adult Asiatic females	6	15			MARGINAL PRIMARY COVERTS				
	D	E			(aa) All adult males	9	62	13	<.01
(m) Asiatic juveniles	4	5	2.05	<.1	All adult females	26	41		
American juveniles	4	24			(bb) All juveniles	21	14	5.4	<.05
(n) All adult females	24	29	5.24	<.02	All adult females	30	37		
All juveniles	8	29			(cc) All juveniles	21	14	2	>.1
					All adult males	50	21		
					(dd)* All adult Canadian males	0	24	2	>.1
					All adult Alaskan males	4	22		
					(ee)* All adult Alaskan males	4	22	1	>.1
					All adult Asiatic males	5	16		

Comparisons		Break-down of classes	Chi-square values	P values	Comparisons	Break-down of classes	Chi-square values	P values			
(ff)	All Canadian females	6	16	2	>.1	(oo)* All adult American males	4	46	1	>.1	
	All Alaskan females	11	14	2	>.1	All adult Asiatic males	0	21			
(gg)	All adult Alaskan females	11	14	1	>.1	(pp)* All adult American females	4	43	1	>.1	
	All adult Asiatic females	9	11			All adult Asiatic females	0	20			
		II	All others			DORSAL EDGINGS					
(hh)	All adult males	50	21	9	<.01	(qq)	All adult males	33	38	1	>.1
	All adult females	30	37				All adult females	24	39		
(ii)*	All adult Canadian males	22	2	3	<.1	(rr)	All adult females	24	39	1	>.1
	All adult Alaskan males	20	6				All juveniles	22	14		
(jj)	All adult Alaskan males	20	6	7	<.01	(ss)*	All east Canadian adults	3	20	2.3	<.1
	All adult Asiatic males	8	13				All west Canadian adults	8	11		
(kk)	All Canadian females	14	8	2	>.1	(tt)	All Alaskan adults	11	37	26	<.01
	All Alaskan females	12	13	2			All Asiatic adults	35	9		
(ll)*	All adult Alaskan females	12	13	2	>.1		DORSAL COLORS				
	All adult Asiatic females	4	16			(uu)	All east Canadian adults	7	19	29	<.01
		III	All others				All west Canadian adults	13	7		
(mm)*	All adult American males	0	50	17	<.01	(vv)	All west Canadian adults	13	7	2	>.1
	All adult Asiatic males	8	13				All NW Alaskan adults	22	6		
(nn)	All adult American females	0	47	14	<.01	(ww)	All NW Alaskan adults	22	6	18	<.01
	All adult Asiatic females	7	13				All Aleutian-SW Alaskan adults	9	17		
						(xx)	All NW Alaskan adults	22	6	2	>.1
							All Asiatic adults	39	5		

* Yates' adjustment applied (see, for example, Simpson and Roe, 1939:296-300).

statistics in table 2. One is impressed particularly by the homogeneity of the eastern Canadian but also of the western Canadian (excluding the small female sample) and of the Aleutian-southwestern Alaskan populations as compared to the extremely variable Asiatic and northwestern Alaskan ones.

It should be pointed out that the Asiatic sample cannot strictly be compared with the other samples in this respect. It is not as seasonally homogeneous, being composed of both summer- and winter-taken specimens, and it was drawn from a much larger geographic area than were any of the four North American samples.

Still I feel that the relatively greater variability which is indicated for the populations of the Bering Sea region, excluding the Aleutians, is biologically real, especially since it is associated with a correspondingly great variability of the plumage characters in these populations.

Tail pattern.—In the adult male series, type A tails range from about 66 per cent in eastern Canada to less than 10 per cent in Asia. This trend is unbroken in the intermediate populations, with the sharpest change occurring between western Canada and northwestern Alaska. The type B tail ranges from 70 per cent in Asia to about 25 per cent in eastern Canada, showing a trend opposite to that of type A tails. Again the major disjunction occurs between western Canada and northwestern Alaska. The difference in frequency of types A and B between all Alaskan males and all Canadian males is statistically significant (table 6f), but it is not between Alaskan and Asiatic males (table 6g). It will be remembered that both these types of tail pattern are masculine characters. When they are grouped together, consistently high percentages result: 80 per cent in Asia; 72 per cent in northwestern Alaska; 60 per cent in the Aleutians and southwestern Alaska; 100 per cent in western Canada; 92 per cent in eastern Canada.

The low figure for the Aleutian-southwestern Alaskan males is partly the result of the greater number of melanistic individuals in that population, but the feminine types C and D still constitute 33 per cent, the highest figure for any male sample. The other figures are: 20 per cent in Asia, 28 per cent in northwestern Alaska, 0 per cent in western Canada, and 8 per cent in eastern Canada. Thus, tails of adult Canadian males differ in two respects from those of adult Alaskan males—they have a much higher percentage of extreme masculine types and a much lower percentage of feminine types (C and D). Alaskan males do not differ in these respects from Asiatic ones.

In the adult female series, the "juvinal" type D tail ranges from about 78 per cent in the Aleutians and southwestern Alaska to 0 per cent in western Canada, but no cline is indicated for this trait. The greatest difference in frequency occurs between western Canada and northwestern Alaska. The "typical female" type C tail ranges from 80 per cent in eastern Canada to about 23 per cent in the Aleutians and southwestern Alaska. The difference in frequency of these two types between all Canadian females and all Alaskan females is statistically significant (table 6d), but it is not between the Alaskan and Asiatic samples (table 6e).

It is relevant to mention here that the difference in frequency of types D and C between all adult females and all juveniles is also statistically significant at the 1 per cent level of confidence (table 6c), the juveniles having a higher frequency of type D. The difference between American and Asiatic juveniles is significant at the 2 per cent level of confidence (table 6b), Asiatic juveniles having a higher frequency of type C.

In adult females type A and B tails range from 37 per cent in western Canada to 0 per cent in the Aleutians and southwestern Alaska and in eastern Canada. They constitute 22 per cent of the Asiatic sample, and about 16 per cent of the northwestern Alaskan sample. The high percentage for western Canada is probably over-emphasized by the small sample and also by the arbitrariness of the classification, since there was a number of specimens in this sample that were intermediate between the masculine types and type C. None of the differences in frequency of these types is significant.

Belly pattern.—In the adult male series, the type A belly ranges from 0 per cent in the Aleutians and southwestern Alaska to about 28 per cent in northwestern Alaska. No cline is indicated. The type B belly ranges from about 41 per cent in western Canada to only 9 per cent in the Aleutians and southwestern Alaska; again there is no cline. The type C belly ranges from 50 per cent in eastern Canada to about 9 per cent in Asia, and in this case there is an unbroken east-west cline. The type D belly ranges from 0 per cent in both Canadian samples to about 22 per cent in Asia, and there is again an east-west trend. The type E belly ranges from 0 per cent in both Canadian samples to about 25 per cent in the Aleutians and southwestern Alaska and 22 per cent in Asia;

the same cline is indicated for this trait as for the type D belly. The type F belly ranges from 18 per cent in the Aleutians and southwestern Alaska to 0 per cent in Asia.

When types A through C are combined in one group, and types D and E in another, the difference in frequency between all Canadian males and all Alaskan males is statistically significant (table 6i), but the difference between Alaskan and Asiatic males (table 6j) is not. Thus, it can be said, first, that there are fewer extreme masculine bellies (types A and B) in the Aleutians and southwestern Alaska than in any of the other samples, but the difference between this sample and the northwestern Alaskan one is not statistically different. Second, there are fewer males with feminine bellies (types D and E) in the Canadian samples than in the Alaskan and Asiatic ones.

In the adult female series the type A belly does not occur. The type B belly ranges from 0 per cent in all but two samples to about 19 per cent in Asia and about 25 per cent in western Canada. The type C belly ranges from 0 per cent in northwestern Alaska and western Canada to about 21 per cent in eastern Canada. The type D belly ranges from about 8 per cent in the Aleutians and southwestern Alaska to 58 per cent in eastern Canada; and the type E belly ranges from about 8 per cent in eastern Canada to about 86 per cent in Asia. There is an inverse relationship between the last two types. The type F belly ranges from 0 per cent in Asia to about 18 per cent in the Aleutians and southwestern Alaska.

By grouping the types into two categories, A to C and D to E, a nearly statistically significant difference is again found between the frequencies of all Alaskan females and all Asiatic ones (table 6l), but not between all Canadian and all Alaskan females (table 6k). This indicates that Asiatic females have a greater tendency toward masculine bellies (types A, B, and C) than do females from the other regions. On the other hand, when the type E belly is compared with all other types together, one obtains a statistically significant difference (table 6g) between its frequency in Canadian and Alaskan females and between Alaskan and Asiatic females (table 6r). This results from a very high frequency of the type E belly in the Alaskan sample. The type D belly was similarly tested (tables 6o and 6p), but no significant differences were found between any of the adult female samples, although the difference between Alaskan and Canadian samples gives a chi-square value near that required for P to equal .05.

Marginal coverts of wing.—In the adult male series, type I covert ranges from about 23 per cent in Asia to 0 per cent in both Canadian populations. The Alaskan populations are intermediate with about 15 per cent each. Type II covert ranges from about 92 per cent in both Canadian samples to 39 per cent in the Asiatic, both Alaskan samples being again intermediate with about 78 per cent. Type I and II coverts are thus inversely related. Type III covert constitutes about 39 per cent of the Asiatic sample; it does not occur in any of the North American ones. Type IV covert constitutes about 8 per cent of the eastern Canadian, northwestern Alaskan, and Aleutian-southwestern Alaskan samples; it does not occur in the western Canadian or Asiatic ones.

The differences in frequency of type I between all Canadian and all Alaskan males and between all Alaskan males and all Asiatic males are not statistically significant (tables 5dd and 6ee), but there does seem to be a trend toward higher frequency of this type from east to west. The difference in frequency of type II between all Canadian and all Alaskan males likewise is not statistically significant (table 6ii), but the difference between all Alaskan males and all Asiatic ones is (table 6jj).

Thus, Asiatic males differ in three respects from North American males. They have a higher frequency of the feminine type I covert and a decidedly lower frequency of the masculine type II. In addition, they have a type III covert not found in the North

American samples (table 6mm). In turn, North American males have a type IV covert not found in the Asiatic sample (table 6oo).

In the adult female series, type I covert ranges from about 45 per cent in the Asiatic and Aleutian-southwestern Alaskan samples to about 12 per cent in western Canada. As in the male series, the general trend is from low frequency in the eastern samples to higher frequencies in the western ones, but the differences between Canadian females and Alaskan females, and between Alaskan and Asiatic females, are not statistically significant (tables 6ff and 6gg). Type II covert ranges from about 74 per cent in western Canada to about 20 per cent in Asia, and again an inverse relationship is evident between types I and II; statistically significant differences, however, are not found between the samples (tables 6kk and 6ll). Type III covert is not found in any of the American female samples, but it comprises about 38 per cent of the Asiatic one; this difference is statistically significant (table 6nn). Type IV covert is found only in the North American samples, but the difference between all North American females and all Asiatic ones is not statistically significant (table 6pp) because of its low frequency in the American samples and the disproportionately small Asiatic sample.

Asiatic females appear to differ from American ones in exactly the same respects that the males differ in this character.

Head.—In the adult male series, type A head ranges from about 37 per cent in Asia to 0 per cent in eastern Canada, indicating a cline toward greater frequency from east to west; but none of the American samples contains more than 15 per cent, the greatest disjunction being between the continental samples. Since only two types are involved for this character, the type B frequencies are in every case inverse to the type A frequencies. There are no statistically significant differences between Canadian, Alaskan, and Asiatic samples (tables 6v and 6w), but when all North American males are compared with all Asiatic ones, the difference is significant at the 1 per cent level of confidence.

In the adult female series, the type A head ranges from about 75 per cent in Asia to about 27 per cent in western Canada. The trend is unbroken to this point, but it is disrupted by the eastern Canadian females, which have about 61 per cent type A. No statistically significant differences are found between any of the samples (tables 6x, y and z).

Thus, there appears to be a trend toward higher frequency of type A heads in both males and females from east to west, but the samples are not large enough to give great confidence to this conclusion.

Outer web of primaries.—In the Asiatic sample about 74 per cent of the adult males and about 86 per cent of the adult females fall in classes I, II, and III. In the Aleutian-southwestern Alaskan sample none of the specimens falls in classes I and II, and only about 8 per cent of the males and 15 per cent of the females are in class III; all others are class IV. About 7 per cent of the northwestern Alaskan males are in class II, and about 14 per cent of the males and 23 per cent of the females are in class III; all others are class IV. In the Canadian samples only one specimen from western Canada is in class III; all others are class IV. The variation of this character expresses the clearest east-west cline to be found among the several traits studied. The greatest difference between adjacent samples occurs between Asia and Alaska, but it is important to know that the northwestern Alaskan sample contains the largest number of examples that are like the majority of Asiatic specimens—that is, with some degree of light coloring on the outer webs of the primaries distal to the ends of the coverts. Important also is the fact that no North American specimen approaches the extreme Asiatic expression of this character.

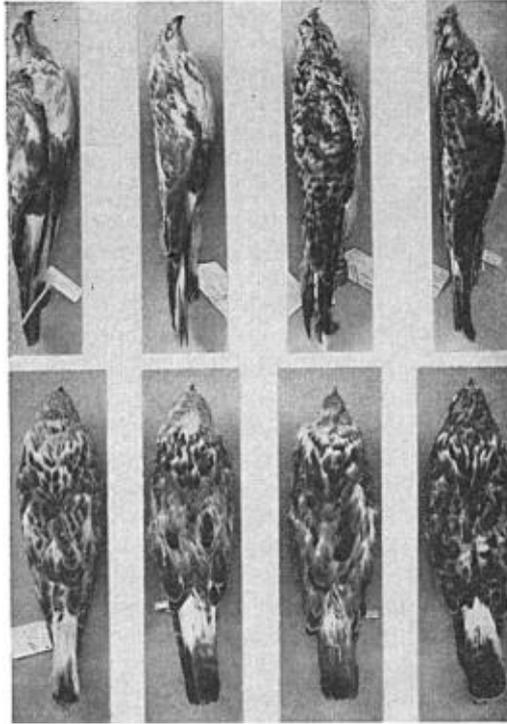


Fig. 6. Upper row, female specimens from left to right, showing, respectively, primary types I, II, III, and IV: USNM 370449, Manchuria; CNHM 101222, Manchuria; CNHM 101225, Manchuria; DMNH 22856, northwestern Alaska. Lower row, females: CNHM 101223, Manchuria; DMNH 19522, northwestern Alaska; Chic. Acad. Sci. 4211, northern Alaska; DMNH 23644, northwestern Alaska; note dark feathers on backs of two central specimens, contrasting sharply against an extremely worn and foxed plumage; these have been called *pallidus* by some authorities.

This character affords the best single criterion for separating adult Asiatic Rough-legged Hawks from American ones. On this basis alone about 80 per cent of all Asiatic adults are different from about 90 per cent of all American adults, and 80 per cent of all Asiatic adults are different from about 83 per cent of all Alaskan ones.

The trait of light areas on the outer primaries has a higher frequency among juveniles of both continents than among adults. It occurs on all Asiatic juveniles that have been examined (total of 9) and on 62 per cent of the American ones, but this difference cannot be considered significant because of the small Asiatic sample. There is a color difference that is perhaps more important. On all Asiatic juveniles the color of the light area is whitish or creamy, indistinguishable from the adult color. On nearly all North American specimens the area is buffy or reddish. Also, all the Asiatic juveniles have the extreme type I expression of this character; none of the American juveniles do.

Breast.—Frequencies of the several traits of the breast are presented in table 5. There is a trend toward higher frequency of the type II breast mark from east to west, and the greatest difference between adjacent samples occurs in the Bering Sea region, where over 50 per cent of the Asiatic females and 25 per cent of the males are type II, whereas only about 22 per cent of the northwestern Alaskan females and about 12 per cent of the males are type II. Again the northwestern Alaskan sample has the highest

frequency of this type among North American birds. Among the color classes there is also a tendency for light browns to increase in frequency in a westerly direction. The largest difference between adjacent samples is again in the Bering Sea region. There appear to be no pronounced differences among the samples in the edging classes *a*, *b*, and *ab*; there is a slightly, but not significantly higher frequency of the *a* type in the Asiatic sample, but the *b* and *ab* types are low in frequency in all the samples.

Back.—Frequencies of the various dorsal traits are also presented in table 5. In general these traits show the same trends as the ventral ones. Type II shows increase in frequency from east to west, and the lighter browns follow the same trend. The type *a* margin is much more frequent in the Asiatic sample, and the type *b* does not occur. The condition is reversed in the American samples. The difference in frequency of types I and II between all Alaskan adults and all Asiatic ones is statistically significant (table 6tt), but it is not between any of the other samples (tables 6gg, rr, and ss). When the dorsal color types are placed in two groups, A-B and C-D, and their frequencies compared among the samples, a statistically significant difference is found between all northwestern Alaskan adults and all Aleutian-southwestern Alaskan ones and between all eastern and western Canadian adults, but not between western Canadian and northwestern Alaskan adults or between northwestern Alaskan and Asiatic ones (tables 6uu, vv, ww, xx). In the latter comparison, however, there are important differences not brought out by this test: the D type does not occur at all in the Asiatic sample, and the A type does not occur in the northwestern Alaskan sample. When the frequency of the A type to all others is compared in the two samples, the difference is significant at the 1 per cent level of confidence.

SEXUAL DIMORPHISM

Size.—Turning again to table 3, it appears that there are some geographic differences in degree of sexual dimorphism. The Asiatic males and females show less than 75 per cent joint nonoverlap for all three measurements. The same is true of the northwestern Alaskan males and females, although their coefficients of difference average higher than in the Asiatic sample. In the Aleutian-southwestern Alaskan population the sexes show more than 75 per cent joint nonoverlap for each measurement, and indeed the two most reliable measurements, those of wing and tarsus, show more than 90 per cent joint nonoverlap. This population has the most consistent sexual divergence in size of any studied. The western Canadian sexes diverge to the extent of 85 and 80 per cent joint nonoverlap for two measurements but less than 75 per cent for the other. Also, the eastern Canadian sexes diverge to the extent of 96 per cent joint nonoverlap for the wing (the greatest for any measurement) and 85 per cent for the tarsus. The culmen shows less than 75 per cent. The small joint nonoverlap between the sexes in Asia and northwestern Alaska is at least in part the result of the greater variability of these populations, but the means of the males and females are actually closer in nearly every case.

Plumage.—For tail pattern there is a tendency among the samples for sexual dimorphism to break down in an east-to-west direction. This results from the fact that in the more westerly samples (Alaskan and Asiatic) both males and females have higher frequencies of characters that are in the overall population more characteristic of the opposite sex. Thus, in the Canadian samples more than 95 per cent of the adult males are separable from 100 per cent of the adult females; in the Alaskan samples slightly more than 62 per cent of the adult males are separable from slightly more than 92 per cent of the females; while in the Asiatic sample about 78 per cent of the males are separ-

able from about 74 per cent of the females. Expressing these relationships as percentages may overemphasize the actual difference between the populations, but the trend is the important thing.

A different relationship holds for belly pattern. Again the eastern Canadian sample shows the greatest sexual divergence and the greatest homogeneity of character in the two sexes; this condition breaks down in a westerly direction but not so completely as in the case of tail pattern. The male trend behaves exactly as it does for tail pattern, but the females show a slight but demonstrable reverse trend: that is, males have their highest frequency of masculine tails in the east and a progressively lower frequency westward, whereas females have their highest frequency of feminine tails in the west with progressively lower ones eastward. Thus, in eastern Canada about 95 per cent of the adult males are different from 63 per cent of the adult females; in Alaska about 59 per cent of the adult males are separable from more than 84 per cent of the females; and in Asia 65 per cent of the adult males are separable from more than 71 per cent of the adult females. The actual difference between the sexes is probably greater than these figures suggest because of the wide range of characters subsumed under the type C belly, which is the category of major overlap, and also because of a number of melanistic specimens in the American samples. Again it is the trend that is important.

Sexual dimorphism of the marginal wing coverts is somewhat obscured by the fact that the extremes in variability of this character, unmarked cream and unmarked dusky, do not appear to segregate sexually but do show a marked geographic difference. The type III covert, unmarked cream, constitutes 38 per cent of the adult Asiatic male sample and 35 per cent of the adult female sample; the type IV covert, unmarked dusky, constitutes 8 per cent of all North American adult males and slightly more than 8 per cent of all adult females. Both of these extremes occur on only one side of the Bering Sea.

In the Canadian samples more than 91 per cent of the adult males are separable from more than 27 per cent of the adult females on the basis of covert types I and II; in the Alaskan samples about 77 per cent of the adult males are separable from 44 per cent of the females; and in the Asiatic sample 38 per cent of the adult males are different from 45 per cent of the females. This variational trend is the same as that of belly pattern.

When percentages of difference between the sexes are calculated for head types, the same trend is again shown. In the Canadian samples 95 per cent of the males are different from 40 per cent of the females; in the Alaskan samples about 89 per cent of the adult males are separable from more than 53 per cent of the females; and in the Asiatic sample 65 per cent of the adult males are different from 75 per cent of the adult females.

The geographic trend in sexual divergence of tail pattern is more or less concordant with that of sexual dimorphism of size, although the latter is not as definitely clinal in nature as the former because of the disruption produced by the pronounced sexual dimorphism in size of the Aleutian-southwestern Alaskan population. In general, however, both males and females are more homogeneous for these characters in Canada, less so in Alaska (with the exception just above), and still less so in Asia. Assuming that these two characters are genetically independent, the phenotypic evidence indicates two parallel trends of gene frequency through the populations.

The close geographic concordance in the trend of sexual dimorphism of the belly pattern, marginal wing coverts, and head types is probably not to be construed as evidence of three parallel trends of gene frequency. Since the variability of these characters depends upon the degree of pigmentation generally in feathers, not upon specific local modifications, it seems most reasonable to suppose that they are determined by the

same genetic and physiological factors; hence, they probably indicate but a single trend of gene frequency.

MELANISM

Extreme melanism, that is, pigment saturation to the virtual obliteration of pattern, is not found in the Asiatic sample. It has already been pointed out, however, that melanism in *Buteo lagopus* is a matter of degree and that the dark phase grades continuously into the light phase. The type C dorsum, for instance, is patterned but it is also quite dark, and it could be considered melanistic on a relative basis. It has about a 12 per cent occurrence in the Asiatic sample; in this group only those individuals that have light areas on their primaries can be distinguished from Canadian specimens.

The uniformly dark examples at the extreme of the color continuum occur at different frequencies over the breeding range in North America. The situation is somewhat like that found in fulmar populations (Fisher, 1952), another species that shows the nondisjunctive kind of polymorphism. Thus, in the Aleutian-southwestern Alaskan sample the extreme melanistic individuals comprise about 19 per cent of the total, in northwestern Alaska about 7 per cent, in western Canada only 3 per cent, but in eastern Canada almost 12 per cent.

Beebe (1907:10) observed that the melanistic type has a center of abundance in Ungava and Labrador, and Grinnell (1909:213), finding dark birds from Glacier Bay, Alaska, identical to these dark eastern Canadian birds, suggested "that this 'dark phase' is really a geographic form occurring in regions of excessive humidity, and not identical with the 'light phase' . . ." Disregarding any taxonomic implication of Grinnell's statement, one does see a fairly good correspondence with Gloger's rule in this case.

ALLOCATION OF INDIVIDUAL SPECIMENS

Grinnell (1918:505-507) was one of the earliest antagonists of the idea of applying trinomials to individual specimens without regard to the geographic area from which they were taken. Now, nearly forty years later, the cogency of this position is not yet thoroughly appreciated by all ornithologists. For instance, the American Ornithologists' Union Check-list (1931) and its later supplements still contain a number of extralimital subspecies based on one or a few specimens. Unless such specimens can be demonstrated to fall entirely outside the range of variability of conspecific American forms, I fail to see any validity in their trinomial designation. Perhaps no one now disagrees with this statement in principle, but it is certainly violated in practice.

I have personally examined nine of the Alaskan specimens of *Buteo lagopus* that have been called *pallidus* or *kamtschatkensis* by one authority or another. Bailey (1948:181-182) lists five that I have not seen: DMNH 22868, 22869, 24590, 24589, and one in the Peet collection. In addition, there are two from Hooper Bay (Brandt, 1943) and one from St. Lawrence Island identified by Friedmann (Murie, 1936:367).

Specimen number 81215 USNM is the basis for the first published record of *pallidus* from Alaska (Friedmann, 1934:246). It is recorded as a male (Bailey, 1948:182, refers to this bird as a female), collected by E. W. Nelson at St. Michael's Alaska on September 16, 1879. Although not stated by Friedmann, the specimen is clearly in juvenal plumage. It has a light head, a very large continuous belly band, a distal field of brown on the tail becoming reddish proximally, and the third, fourth, fifth, and sixth primaries (from the outside) have a light reddish area on their outer webs distal to the ends of the coverts. In not one character of the plumage is it like an Asiatic juvenile; it is, in fact, indistinguishable in plumage from many juveniles from the Aleutian Islands and southwestern Alaska. It happens to be the largest specimen of any sex that I have meas-

ured from North America, with a wing of 470 mm. On this basis, it is almost certainly incorrectly sexed.

Bailey's first breeding record of *pallidus* is based on DMNH 22614, an individual taken with young at Golovin Bay, Seward Peninsula, on July 26, 1921. This specimen has been recorded both as a male (Bailey, 1942:305-306) and as a female (Bailey, 1948:182). I have not seen this specimen, but I have examined an unnumbered adult male from the Denver museum taken at the same locality on July 26, 1923. This specimen bears the name *pallidus* on its label. It looks very much like several males in the American Museum of Natural History taken on Bering Island; but it is also indistinguishable from several specimens taken in the Canadian Arctic. It has none of the exclusively Asiatic characters such as marginal covert type III or primary type I; in fact, its primaries are the extreme American type IV.

The second breeding record mentioned by Bailey (1948:182) is based on Chic. Acad. Sci. 4211, a female taken with eggs in the Romanoff (Romanzof?) Mountains of northern Alaska. Friedmann identified this bird as belonging to the Asiatic subspecies (*pallidus* or *kamtschatkensis*?). Again on the basis of plumage (see fig. 6), I would consider this bird to be a juvenile just beginning molt. The old feathers are much faded and worn and superficially resemble the light brown condition of most Asiatic birds, but the new feathers, clearly visible in the figure, are dark like most North American examples.

The same age and plumage conditions are evident in: DMNH 19522, a female from the Chipp River taken on May 24, 1938; DMNH 22867, a female taken at Wainwright on June 15, 1942; UMMZ 121719, a male taken at Brownlow Point on April 10, 1944; MVZ 32253, a male taken on the Kowak (Kobuk) River on May 10, 1899—the condition of the latter specimen having already been noted by A. H. Miller (quoted by Bailey, 1948:181).

DMNH 23645, an adult male taken at Point Barrow on June 9, 1943, has wide white margins on the feathers but is otherwise quite dark. It matches a few specimens from both Asia and Canada. DMNH 22866, an adult male from Wainwright taken on June 15, 1942, represents the extreme male example of depigmentation (see fig. 2). Birds approaching this extreme are more frequent in the Bering Sea regions of both continents, but several examples were also seen from the Canadian arctic.

Thus, it would appear that the grounds for considering any American specimen of *Buteo lagopus* as an example of the Asiatic subspecies are extremely weak, being based for the most part on an inadequate understanding of the nature of variation in this species. On the other hand, the presence of characters common to populations on both sides of the Bering Sea indicates that there is now, or has been, some genic exchange between the continents, but this does not mean that one can equate these populations taxonomically, or for that matter, genetically. The distribution of a character, or a group of genetically dependent characters, can be objectively determined, but the distribution of a subspecies is a matter of opinion and depends upon what combination and degree of expression of characters is used to characterize it.

DISCUSSION

Wilson and Brown (1953) have recently stressed examples to show the frailties of the subspecies concept. They particularly emphasize the lack of geographic concordance among infraspecific populations of characters presumed to be genetically independent, and they suggest that where populations are isolated or are undergoing secondary intergradation, the best, but still not entirely satisfactory, way to define a subspecies is in terms of peaks of character concordance.

In the case of *Buteo lagopus* it is, first of all, difficult to say which of the several characters that have been studied are genetically independent. One can presume by extrapolation from genetic studies of other species that the mensural characters are independent of plumage, but within these two groups it is not possible to know whether geographically concordant characters are genetically independent or not. I am inclined to doubt that there could be complete genetic independence of any character from another within these two groups. On the other hand, when characters are not geographically concordant, at least partial genetic independence seems assured, assuming that the characters are heritable.

Size of wing concords geographically with size of tarsus in both males and females; but the sexes are geographically discordant, that is, a population with females that possess relatively large wings and tarsi may have males that possess relatively small ones.

Among plumage characters, primaries of types I and II concord geographically with dorsal and breast colors of type A and with type III marginal wing coverts; type IV primaries concord well with dorsal and breast colors of types C and D and with marginal wing coverts of types II and IV, but the correspondence is never perfect.

A number of clines are indicated within the geographic area covered by this study. In general they parallel each other along an east-west line. Wing length of males shows a tendency toward increasing size in a westerly direction. The females show no mensural clines. There is, however, a tendency for the sexes to become less dimorphic in size from east to west, excluding the Aleutian-southwestern Alaskan population.

Nearly all the plumage characters are to some extent clinal. The light-headed individuals increase in frequency in a westerly direction; the same is true of light brown dorsal and ventral pigments. The light patch on the outer webs of primaries, the narrowly streaked breast, and the widely edged dorsal feather all follow this trend. Of even greater importance, however, is the fact that sexual dimorphism of plumage also follows this cline. The greatest sexual divergence of plumage occurs in eastern Canada and breaks down progressively toward Asia, again excluding the Aleutian-southwestern Alaskan sample in some cases.

There is one plumage character in which the extremes are restricted to one side of the Bering Sea or the other: the type III marginal wing covert is restricted to Asia, and the type IV covert to America. Primaries of types I, II, and III have a major disjunction in frequency between the Asiatic and Alaskan populations and do not exist at all in the Canadian ones.

Two American samples, the Aleutian-southwestern Alaskan and the eastern Canadian, are more homogeneous in phenotype than the other two, the western Canadian and northwestern Alaskan. The northwestern Alaskan sample in particular is extremely variable in both mensural and plumage characters. Some individuals of this population are nearly identical with the most frequent Asiatic type, a much larger number are identical with the usual Canadian examples, some are blending intermediates between these two, while others show a non-blending combination of characters. Nearly the full range in variability of each character is to be found in this population.

The Asiatic population, as examined by me, is also quite variable. This is probably the result in part of the large number of winter specimens that are included—a sample that undoubtedly contains a mixed aggregate of breeding populations. Dementiev *et al.* (1951:314) indicate that the pale-colored Asiatic form is rather homogeneous over most of its breeding range from the Anadyr to the Yenesei River, where it intergrades with typical *lagopus*. But the nature and areal extent of this intergradation, as well as that between the pale form and the so-called *kamtschatkensis*, is not stated. What appear to

be hybrids between the pale form and the darker American form occur in eastern Asia. Of the few breeding specimens examined, there are two such birds from the Lena River, the most westerly locality, and four from Bering Island. A number of winter specimens from Manchuria were also examined. All these breeding and wintering specimens fit Dementiev's description of *kamtschatkensis*, which appears therefore to be nothing more than one of the mixed types produced by crossings between the pale form of interior Asia and the American form. The Asiatic character most often expressed in such specimens is the light area on the outer webs of the primaries; the American characters most often expressed are dark color and variegation of the back, but the variability is great. Most of them appear distinctly more American-like than Asiatic, which suggests that the determiners of the pale characters are easily dominated by corresponding American ones.

On the basis of the samples examined by me, I believe that the entire population of the Bering Sea coasts and the immediately adjacent Arctic Ocean will prove to be practically indistinguishable from that of northwestern Alaska, both showing to some degree the full range of variability of the entire Asiatic and North American populations.

Such variability indicates that the Bering Sea region (excluding the Aleutian Islands) is a zone of allopatric hybridization or secondary intergradation (Mayr, Linsley, Usinger, 1953:101). The pale Siberian form and the darker, "polymorphic" American form, once separated by an extrinsic barrier, have since been able to disperse into the range of one another and there freely to interbreed. That completely random breeding occurs is indicated by the observations previously mentioned along the Colville River in 1952, where melanistic individuals were mated with very pale birds and all sorts of intermediates between these extremes occurred in the breeding population.

Although on the basis of the distribution of specific characters one can say that there is or has recently been gene flow between the continents, nevertheless on an inferential basis there are reasons for believing that the present rate of genic exchange is much less than that occurring between confluent populations on the continents. In other words, the Bering Sea now acts as a barrier to gene flow to some extent. The northwestern Alaskan population, although showing nearly the complete range of variability of the Asiatic and American forms, still has a preponderance of American types. The converse appears to hold true in Asia. Why is this so?

If one looks at a small scale map of the North American and Asiatic continents, he will see that in the region of their closest juxtaposition, namely, Bering Strait, they are opposed by a very limited coast line, which on both continents very quickly recedes away from the zone of near contact, both to the north and to the south. Thus, from a continental point of view, only a very small portion of the breeding ranges of Asiatic and American rough-legs are in near contact, and hence relatively few individuals are geographically situated for dispersal across the Bering Sea. This is one possible factor now operating to limit, but not necessarily to exclude, gene flow between the continents.

Another is the Bering Strait itself. The breeding grounds of *Buteo lagopus* are not continuous between Asia and America. They are separated by a narrow stretch of water, which again remains narrow in a very limited area only. I do not doubt that it is easily within the flying capability of *Buteo lagopus* to cross Bering Strait or even probably the widest expanse of the Bering Sea. On the other hand, Rudebeck (1950; cited by Thompson, 1953:173) has found that buteos in general show more reluctance to cross the sound between Sweden and Denmark than some other species of falconiforms during the fall passage, indicating the possibility that buzzards have an aversion to flight over water. Still, the species is well distributed in the Aleutian Islands as far out as

Umnak Island, the western limit of the distribution of voles (O. J. Murie, unpublished data), which are the principal prey of *Buteo lagopus*.

The weather of the Bering Sea could well be an additional factor discouraging passage. Frequent low fogs reduce visibility, and high winds of gale force, or stronger, make for difficult flying.

All these extrinsic factors probably sum up to reduce gene flow between the continents. Thus the perimetric populations of the Bering Sea should receive numerically greater genic contributions from the populations of their respective hinterlands than from each other.

On the other side of the picture, there are some intrinsic factors concerned with population structure that may tend to restrict gene flow over any large, continuous range of the species. Miller (1947:186-190) has presented an excellent discussion of some of these factors. It would be advantageous to be able to define panmictic populations of *Buteo lagopus* in genetic terms; this, of course, is impossible. But one can make some statements about the factors that probably influence panmixia in this species.

The breeding Rough-legged Hawk is a highly territorial individual, and pairs normally return to the same nesting area year after year; there is, therefore, little gene movement within the breeding population. Panmixia can be achieved only by the dispersal of non-territorial individuals, a situation that is widespread among avian species as pointed out by Miller (*op. cit.*:187). It becomes important to know two things about the dispersal of these unattached hawks: how far do they disperse, and how many of them reach the status of effective breeding individuals?

One can only guess at answers to these questions. The vagility of the species is great. It is not at all unlikely that a bird reared in Ungava, that migrated into the United States for the winter, could turn up the next spring in northern Alaska. It is within its physical capacity. On the other hand, nothing is known about the "homing" inclination of this species or to what extent geographic populations follow definite routes of migration. In all probability most immature birds return to the general region if not to the specific locality where they were reared.

But immature birds and other unmated individuals returning to the breeding grounds find a rigidly fixed population structure that nearly always occupies all the optimal breeding niches. A few of them gain entrance into this fixed social structure through the death of mated birds, but most of them must either remain unmated or occupy marginal breeding sites. In either case they contribute little to the reproductive success of the species. If Rough-legged Hawks are like most other falconiforms, these unmated individuals do not take up definite territories but tend instead to wander widely. Thus, even if homing is a factor tending to insure the return of the immature bird to its native region, once there it is more or less forced to move out. If these factors have been correctly interpreted, then the general movement of this dispersive segment of the summer population would be centrifugal, and one would expect to find the largest number of unmated birds and marginal pairs at the perimeter of the breeding range. There are no data for *Buteo lagopus* to support or to deny such a pattern of dispersion, and it would be difficult to show even if there were a large amount of comparative population data from different regions because the breeding distribution is itself essentially perimetric with respect to the North American continent. In the case of the Peregrine Falcon, a species with a much less linear breeding distribution in northern latitudes and one for which there are comparative population data (unpublished personal observations), there is indeed a higher incidence of marginal nestings and unattached individuals in the perimetric population compared to a more centrally located one. But despite the

questions concerning dispersion of unattached Rough-legged Hawks, one can say that the distance between the site of hatching and the site of breeding of any individual would seem to be determined largely by the essentially random occurrence of an available breeding niche into which the wandering individual could fit.

The number of birds available for dispersal is also a factor influencing the rate of gene flow. Neither the annual mortality of the population nor its annual reproductive success are known, but judging from the reports of Barth (1952) and Dementiev *et al.*, (1951), its reproduction in Scandinavia and arctic Russia fluctuates with the basic fluctuation in the numbers of microtine rodents. I would be surprised if more than 20 per cent of the fledged young reach breeding age on the average. It is quite likely to be lower. If a Rough-legged Hawk survives its first year, it has a life expectancy quite long for a bird—probably on the order of 10 years. When the annual decline is less than the annual increase over a number of years, there accrues in the population a segment of “reserve breeders”—highly mobile individuals capable of reproduction when the opportunity is afforded by the vacancy of a breeding niche. It is this segment of the population that is the effective mechanism of gene distribution. It probably renders the entire North American population potentially panmictic under the presently existing environmental conditions.

HISTORICAL INTERPRETATION

The present information about the populations of *Buteo lagopus* in the Bering Sea region suggests that there has recently been a slow amalgamation of what were formerly extrinsically separated populations. If this is true, then one should expect that formerly there existed a barrier to the dispersal of populations. The history of events in the Bering Sea region during the Pleistocene glaciations provides such a situation.

Current geological theory (see Flint, 1947, for review) supposes that during the Pleistocene much of the Bering Sea basin and the immediately contiguous basin on the Arctic Ocean alternated between dry land status, correlated with periods of maximal glaciation when sea levels were low, and inundation during interglacial periods when sea levels were high. The former concept of the Bering Strait “land-bridge” has thus gradually metamorphosed into the idea of the “Bering Sea-Yukon refugium,” an essentially unglaciated region of large extent roughly following the continental shelves, confluent with the lower river valleys, and well isolated from the rest of the coeval North American biota by several thousand miles of ice. It was not, however, isolated from the large unglaciated region of Siberia, which is inferred to have existed during the maximum of the Wisconsin (last) glaciation (see plate 3 of Flint, 1947). Other refugia of the northern biota are inferred on the basis of both geological and biogeographical evidence to have existed as isolated entities to the southwest and to the southeast of the great continental ice sheets.

The theory of biotic refugia within the glaciated regions was first clearly stated by Hulten (1937), primarily based on biogeographical data, and it was used by him and later by Raup (1946) to explain the phytogeographic patterns of present boreal floras. It has also provided a basis for cogent interpretations of certain trends in speciation among northern groups of birds (Rand, 1948; Pitelka, 1950) and mammals (Rand, 1954). Drury (1953) has shown a correspondence between the geographic affinities of plants in the St. Elias region of Yukon Territory and the geographic affinities of the birds there, based on Hulten's original scheme.

In all likelihood the Yukon-Bering Sea refugium provided suitable conditions for a breeding population of Rough-legged Hawks. Such a group of birds must have been completely cut off from the rest of the North American populations, which then resided

in refugia far to the south of their present breeding ranges. This Alaskan population, however, would have been continuous with the Asiatic one at this time, presumably sharing the characters now most typical of the pale Siberian form.

During the retreat of the last glaciation, one or more biotic corridors opened up gradually between the unglaciated southern regions of North America and the unglaciated region of Alaska and the Bering Sea. At the same time, the rising sea began to invade the basins that are now covered by the northern part of the Bering Sea and the contiguous Arctic Ocean. The first effect of this deglaciation allowed an avenue for dispersal of both Alaskan and North American Rough-legged Hawks. The latter, being a larger population, probably effected a faster and numerically greater dispersal than did the peripherically situated Alaskan hawks, which for a time may have maintained migratory affinities with the rest of the Asiatic population by crossing over the invading Bering Sea.

As the melting of the glaciers continued, the Bering Sea and the Arctic Ocean began more and more to separate the two continents, making it increasingly less likely for birds wintering in Asia to cross into Alaska. More and more voids were thus left in the ecologic niche occupied by *Buteo lagopus* in Alaska, and these were probably taken up by dispersing individuals from the North American population. But this displacement probably did not take place rapidly, and there was plenty of time for the two continental populations to mix their genes thoroughly in the zone of contact in Alaska. Some of this mixture was carried over to the Asiatic side of the Bering Sea before the continents were completely isolated by water, and as already indicated there has probably continued to be some admixture of Asiatic and North American genes right up to the present. The result is now a thoroughly hybridized population on both sides of Bering Strait, the "foreign" genes gradually being swamped out in the more interior segments of the continental populations.

The Aleutian Islands and southwestern Alaska were probably repopulated by Rough-legged Hawks following the retreat of the glaciers from a population that had been isolated in the refugium to the southwest of the ice sheets. These birds may have undergone change in the direction of greater saturation of pigment in the refugium, or they may not have done so until after establishment in the Aleutian Islands. In either case, on the basis of their characters, one can say that they do not appear to have been derived from the same recent stocks as either the northwestern Alaskan or the eastern Canadian populations.

The breeding populations of Canada were probably derived from birds residing in a refugium to the southeast of the ice sheets. These Rough-legged Hawks may have undergone a somewhat parallel change in the direction of pigment saturation, or again they may not have been modified until after their dispersal into Canada following the retreat of the glaciers. Alternatively, saturated pigmentation may have been common in all populations of *Buteo lagopus* prior to their isolation in refugia during the Pleistocene and then have been virtually lost in some populations during isolation.

While this suggested picture of the history of the Rough-legged Hawk populations in North America during late glacial and postglacial times is consistent with what is known about glaciation and the present patterns of geographic variation in the species, it must be considered a highly tentative model. Any attempt at a reconstruction of the history by indirect methods is subject to great and indeterminate error.

TAXONOMIC RECOMMENDATIONS

It should now be abundantly clear that attempts to describe subspecies of *Buteo lagopus* based on a few specimens, with no consideration of variation over the whole

range of the species, are misleading. Indeed, the patterns of variation manifested by the various characters of *Buteo lagopus* are ill-suited to the trinomial system because the so-called peaks of concordance are not conspicuous and because the variability of the characters at any given geographic locus is great. Clear-cut geographic differences simply do not exist except, perhaps, on a continental basis. I therefore suggest the following modifications of the existing taxonomic treatment of this species. The name, *sanctijohannis*, should be restricted to the breeding populations of Canada east of the Mackenzie River. Possibly the Aleutian-southwestern Alaskan population might be included to make a polytypic subspecies, but this I feel is not meaningful since the variation of this population suggests that it has undergone independent though somewhat parallel evolution at least since late Wisconsin time. Its distinctness is not, however, sufficient for subspecific recognition. The regions contiguous to the Bering Sea (excluding the Aleutians) and the adjacent Arctic Ocean should be considered a zone of hybridization, and birds from these areas should not be trinomially designated. The population of Kamchatka and adjacent regions falls in this same category, and thus *kamtschatkensis* in the sense of Dementiev should not be considered a valid subspecies. The name, *kamtschatkensis* Dementiev, therefore, becomes the first available synonym to replace *pallidus* Menzbier, as already recognized in the Twenty-third Supplement to the A.O.U. Checklist (*loc. cit.*), and the name, *menzbieri* Dementiev, newly proposed, should become a synonym of *kamtschatkensis*. Admittance of the Siberian subspecies to the North American list (Wetmore *et al.*, 1945) should be revoked since there is no unambiguous demonstration that examples unquestionably from Asia have occurred in Alaska.

SUMMARY AND CONCLUSIONS

The Common Rough-legged Hawk (*Buteo lagopus*) is a polytypic species, three or four subspecies currently being recognized. The present study was undertaken to determine the nature of the variation of this species in North America. A sample of Asiatic birds was also employed for comparative purposes.

Molt occurs from April until late fall, but is accomplished mainly during the breeding months of June, July, August, and early September. Males tend to molt later than females, and it is suggested that this is an adaptation to the primary role that the male assumes as food provider for the female and young during the first half of the breeding season.

Juveniles are best distinguished from adults by differences of pattern and color on the tail and belly. Adult males are more distinct from juveniles than are adult females. There is no clearly defined second-year plumage, but there may be some minor changes of plumage correlated with age.

The so-called polymorphism of the Common Rough-legged Hawk is nondisjunctive in nature, and the darkest extremes grade in unbroken series to the lightest extremes.

The individual variability of *Buteo lagopus* is so great as to preclude definitive study of variation without large series of skins.

Female Rough-legged Hawks are larger than males, but there is much overlap between the sexes for all measurements studied except that of gross body weight, for which no overlap is indicated. The adult plumage is also sexually dimorphic, a condition that has not heretofore been noted. Tail and belly patterns are the best indicators of sex, but head type, marginal wing coverts, and colors and patterns of the dorsum are also to some extent different.

There is remarkably slight geographic variation in mensural characters. No populations are clearly distinguishable on the basis of measurements used in this study. Geo-

graphic variation of plumage characters tends to show an east-west cline. Most characters parallel each other, but some are inversely related. The greatest disjunctions in the variation of characters usually occurs between Alaska and Asia.

Sexual dimorphism of size varies geographically, the most dimorphic population being in the Aleutians and southwestern Alaska, but the general trend seems to be toward lesser sexual dimorphism from eastern Canada west into Asia. Sexual dimorphism of plumage also varies geographically and shows an even greater tendency to break down in a westerly direction. The east Canadian population is the most sexually divergent in plumage.

Extreme melanistic examples appear to be more frequent in regions of high humidity, that is, in the Aleutians and southwestern Alaska and in Ungava and Labrador, but they occur at a low frequency throughout the breeding range in North America.

There is little geographic concordance of characters presumed to be genetically independent, and peaks of character concordance are not therefore definable.

Populations inhabiting regions adjacent to the Bering Sea show nearly the full range in variability of each character of both the North American and Asiatic populations, a condition that indicates a zone of hybridization. Even so, the continental configurations of Asia and North America, the interposition of the Bering Sea, and perhaps weather still appear to act in combination as an extrinsic barrier against free population dispersal. Structure of the breeding population may also limit dispersion in continuous continental populations, but the presence of a small, highly mobile reserve of potential breeders probably renders continental populations essentially panmictic.

During the Wisconsin glaciation, "Alaskan" Rough-legged Hawks inhabiting the Yukon-Bering Sea refugium were probably panmictic with Siberian ones. Amalgamation of this isolated population with more southern North American ones probably took place slowly as they came into contact through corridors which opened up with the retreat of the ice caps. It appears that the North American population by virtue of its greater numbers has contributed the largest amount of material to the gene pool in the Alaskan zone of hybridization.

The name *sanctijohannis* should be restricted to the breeding population of Canada east of the Mackenzie River. Specimens from regions contiguous to the Bering Sea and the adjacent Arctic Ocean should be considered intergrades and should not be trinominally designated. The form *kamtschatkensis* Dementiev, *sensu stricto*, is not distinguishable from the Siberian form and this name is therefore the first available to replace *pallidus* (Menzies) for the Siberian subspecies. The Siberian subspecies should be deleted from the North American list since there is no unequivocal demonstration of its occurrence in that region.

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