

# MORPHOLOGICAL VARIATION IN NORTH AMERICAN PINE GROSBEAKS

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The Pine Grosbeak (*Pinicola enucleator*) is a resident of the taiga of North America from Newfoundland to the Bering Sea, and southward in the western mountains to California, Arizona, and New Mexico. Within this range it shows geographic variation in size (Jenks 1938). The breeding range of one population in California and another in the Queen Charlotte Islands are isolated from the other populations. The limits of the forms described from the taiga are only approximately known.

In this paper I present an analysis of morphological geographic variation in this species. In another paper I will describe the geographic variation in calls and songs, and attempt to use data from morphological and vocal variation to draw some conclusions about the patterns of evolution in North American Pine Grosbeaks.

## METHODS

I analyzed morphological variation using measurements of 9 characters from study skins: wing length (chord); upper mandible length (distal end of nostril to tip); lower mandible length (1, middle of ramus fork to tip; 2, exposed proximo-lateral notch at the corner of mouth to tip); lower mandible width at widest point; bill depth; tarsus length (outer side of proximal joint to the base of the toes); and tail length (base of the central pair of rectrices to tip of the longest rectrix). Weight was used in the analysis when available from specimen labels.

In addition to these measurements, age, sex, plumage color, and comments of the collector were recorded. Only breeding-season adults were used in the analysis. Those taken before 1 May and after 15 August were excluded on the grounds that they might be migrants.

Data were collected from 487 specimens from throughout the species' range in North America and analyzed with analysis of variance and regression programs written by the Statistical Research Laboratory of the University of Michigan. Regression analysis and scatter plots were used to test for clinal variation. In addition, product-moment correlation coefficients were computed to test for possible concordance in all characters.

## RESULTS

Data are presented for 9 morphological characters of birds within the following regions: the taiga from Newfoundland to western Alaska; coastal Alaska; the Queen Charlotte Islands; California; and the Rocky Mountains to northern British Columbia (Fig. 1, Table 2). I subdivided the range of the species to correspond to previously described subspecies' ranges. Each of these regions appeared to contain separate, isolated populations, judging by

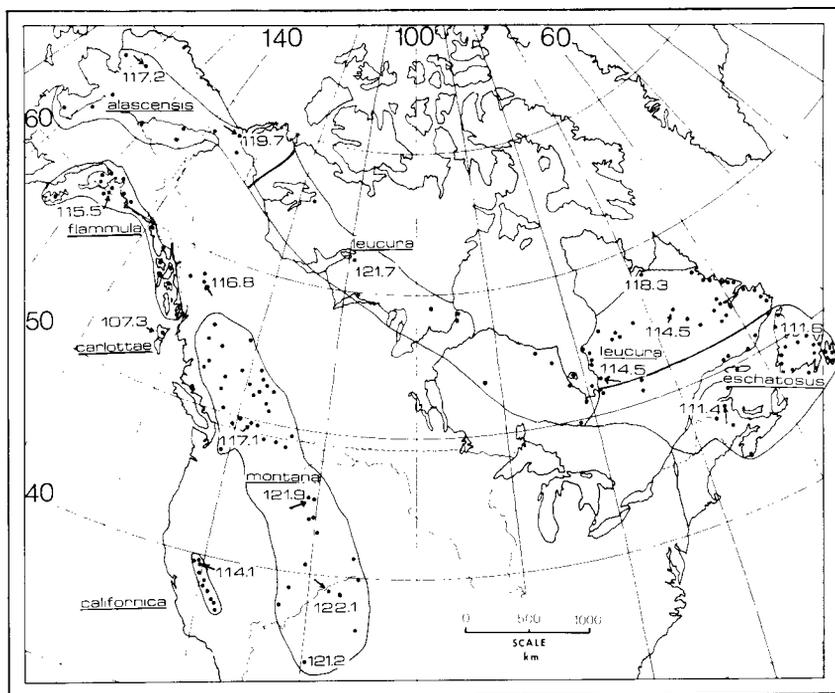


FIG. 1. Map of the breeding range of North American Pine Grosbeaks. Dots indicate localities where birds used in this study were collected. Wing lengths are included for several isolated localities and for certain 2° blocks (arrows point to locality in center of the block). The wing length average for Newfoundland includes 5 neighboring 2° blocks. Subspecific names and ranges (delineated by lines) are from the A.O.U. Check-List (1957).

the literature (Cowan 1939, Rand 1946, A.O.U. 1957) and by the geographic origin of available specimens. In addition I divided the species' range into 2-degree blocks, and computed character means for each block containing 5 or more birds, making it possible to look for trends in variation over large areas. This technique proved of only limited use, since few of the blocks contained enough birds. Wing length means for some blocks are included in Fig. 1.

Analysis of variance for the above regions shows significant geographic variation for all 9 characters (all  $p < .0001$ ). Linear product-moment correlation coefficients of the means of each population indicate that variations in wing and tail lengths are positively correlated, as are the bill measurements. Table 1 gives a correlation matrix for the large Newfoundland sample. Weight data from most areas are unavailable. Only the Rocky Mountain sample has

TABLE 1  
CORRELATION MATRIX FOR 8 SIZE CHARACTERS IN PINE GROSBEAKS  
FROM NEWFOUNDLAND

	Tail	Tarsus	Upper Mand.	Lower Mand. 1	Lower Mand. 2	Mand. Width	Bill Depth
WING	.787*** (100) <sup>1</sup>	.111 (101)	.149 (98)	.220* (99)	.205* (99)	.233* (99)	.176 (55)
TAIL		.004 (100)	.098 (97)	.138 (98)	.119 (98)	.217* (98)	.149 (54)
TARSUS			.104 (98)	.031 (99)	.105 (99)	.215* (99)	.138 (55)
UPPER MAND.				.572*** (97)	.522*** (97)	.314** (96)	.159 (53)
LOWER MAND. (1)					.697*** (97)	.403*** (97)	.047 (53)
LOWER MAND. (2)						.268** (97)	.221 (54)
MAND. WIDTH							.328** (55)

\*, \*\*, \*\*\* Significance levels for correlation coefficients: .05, .01, .001, respectively.

<sup>1</sup> Sample sizes in parentheses.

a sufficient number of weights for correlation analysis, and in this population weight and wing length are positively correlated ( $r = .341$ ,  $n = 31$ ,  $p < .058$ ).

Pine Grosbeaks vary clinally in the Rocky Mountains and in the taiga. Nevertheless it is useful for comparisons to provide sample statistics, for subregions of the taiga as well as for the other regions, for each of the 4 least correlated size characters used in this study (Table 2). From these data the following generalizations can be made. The longest bills are found in coastal Alaska, the shortest in the Alaskan taiga. The narrowest bills are found in the California population followed by those of the eastern taiga and the Queen Charlottes. Bill depth and width are greatest in the taiga west of Hudson Bay and least in California and the Queen Charlottes. Wing length is greatest in the western taiga and the Rocky Mountains, and least in the Queen Charlottes and eastern Maritime provinces. The tarsus is longest in coastal Alaska birds, closely followed by that of some birds from the taiga and Rocky Mountains, and is the shortest in birds from the Queen Charlottes. The populations of the Maritime provinces, California, Queen Charlottes, and coastal Alaska are all very distinct. Birds from the coast of Alaska in turn can be distinguished from those of the interior region using all size characters except bill width and depth.

TABLE 2  
PINE GROSBEAK SIZE DATA FOR 8 NORTH AMERICAN REGIONS

	Wing Length (ad. males) (mm)			Tarsus length (mm)		
	N	$\bar{x}$	S.D.	N	$\bar{x}$	S.D.
Maritime Provinces	70	111.68	2.298	134	22.30	0.600
Labrador Peninsula	31	115.16	3.072	73	22.51	0.780
Taiga, Ont. to NWT	17	119.57	3.305	40	22.50	0.630
Alaskan Taiga	16	118.66	2.673	24	22.37	0.712
Coastal Alaska	6	115.23	2.331	25	22.54	0.803
Rocky Mountains	56	118.00	3.395	124	22.44	0.802
Queen Char. Islands	7	107.53	3.333	23	21.39	0.706
California	15	114.19	1.354	30	22.08	0.821

	Upper Mand. Length			Lower Mand. Width		
	N	$\bar{x}$	S.D.	N	$\bar{x}$	S.D.
Maritime Provinces	130	11.37	0.484	132	9.35	0.340
Labrador Peninsula	73	11.40	0.505	70	9.78	0.340
Taiga, Ont. to NWT	40	11.69	0.647	37	10.04	0.369
Alaskan Taiga	25	10.96	0.622	25	10.19	0.318
Coastal Alaska	25	12.08	0.544	25	10.14	0.353
Rocky Mountains	124	11.83	0.633	122	9.66	0.307
Queen Char. Islands	22	11.36	0.402	22	9.50	0.286
California	29	11.45	0.418	28	8.70	0.352

The most interesting patterns of variation occur in specimens from the taiga from Newfoundland to western Alaska, and the northern Rocky Mountains. Birds taken from the Maritime provinces and the Gaspé Peninsula of Quebec form a homogeneous population for each of the size characters. Comparison of 2° block means from this area shows no differences. Wing length of birds from this area is among the smallest for the species. However, on the Labrador Peninsula small birds indistinguishable from those of Newfoundland, and much larger birds, have been collected. The largest and smallest adult males differ in wing length by 15%. Most of the birds taken on the Labrador Peninsula north of about 54°N are inseparable from those of the taiga population west of Hudson Bay, while most of those taken from near the St. Lawrence River to about 52°N are inseparable from Maritime provinces birds. Regressions on latitude for wing and tail lengths in adult males are significant ( $p < .001$ ). Figure 2 reveals no evidence of discontinuities in the cline of wing length in the Labrador Peninsula sample. There is no well-defined pattern of variation in other size characters, nor is there any east-west variation in the birds of the Maritimes, Labrador, and Quebec.

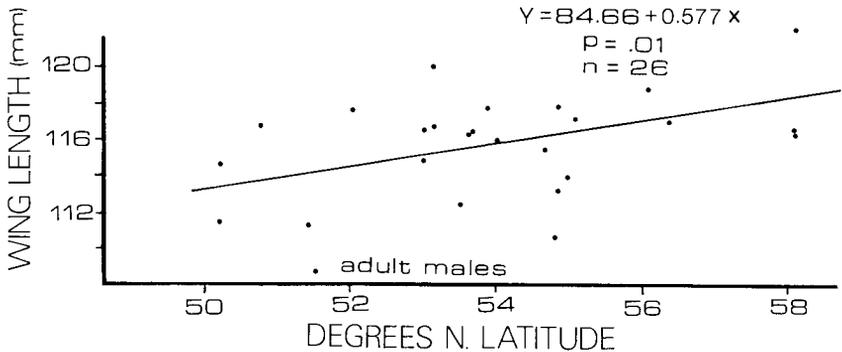


FIG. 2. Plot of wing length on latitude in Quebec and Labrador.

West of Hudson Bay, the Pine Grosbeaks are among the largest in this species. The region from Moosonee, Ontario, to Great Slave Lake is poorly collected, but a trend toward larger body size appears to begin in northwestern Ontario (Ft. Albany). The longest-winged birds were taken near Great Slave Lake ( $110^{\circ}\text{W}$ ), and from there to western Alaska ( $160^{\circ}\text{W}$ ), there is a trend toward shorter wings. While there is little variation in tarsus and bill width measurements, regressions of wing length, and bill length and depth on longitude from Great Slave Lake to western Alaska are significant ( $p < .05$ ,  $p < .001$ ). Figure 3 contains plots of wing length and bill length on longitude. The change in bill length in the western half of the taiga is on the order of 10%. There is less than 3% change in bill depth and wing length. Thus, birds taken along the Kobuk River in western Alaska average shorter bills ( $p < .05$ ) than birds taken at Great Slave Lake, but many intermediate birds have been taken between these localities.

Pine Grosbeaks of the Rocky Mountain region also show clinal variation. Regression of size characters on latitude for the entire Rocky Mountain region revealed decreasing size northward in wing, tail, and tarsus lengths, and in bill length, width, and depth. Figure 4 contains plots of wing (adult males), tarsus, and upper mandible lengths, and lower mandible width on latitude. The wing length cline appears not to be a simple linear function, since it levels out around  $48^{\circ}\text{N}$ . Within B.C. there is little change in wing length, and bill width and depth increase slightly (slopes not significant) to the north. Specimens from the southwestern localities in B.C. (Lyttou, Lillouet, Rossland) have shorter wings than are found anywhere else in the Rocky Mountain region (Fig. 4, specimens with wing lengths  $< 116.0$  mm,  $48^{\circ}$ – $51^{\circ}\text{N}$ ).

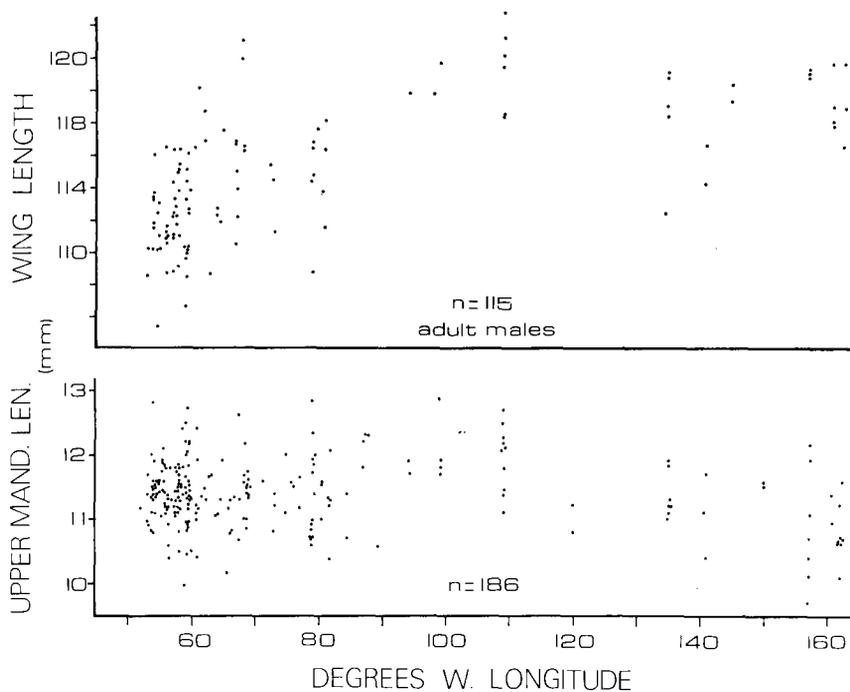


FIG. 3. Plots of wing length and upper mandible length on longitude in the taiga from Newfoundland to Alaska.

The northern part of British Columbia presents an especially interesting problem since Pine Grosbeaks appear (Fig. 1) to breed from the montane region throughout coastal Alaska. Five birds taken along the Stikine River near Telegraph Creek were reported (Swarth 1922) to resemble those of coastal Alaska. These specimens are indeed inseparable from birds taken on Chichagof Island or in Prince William Sound, and differ from recent specimens from Dease Lake, just 60 km to the east, in having shorter wings, longer bills, and darker plumage. Similarly, birds from Cassiar and Dease Lake differ from coastal Alaska birds in having longer wings ( $p < .01$ ,  $n = 21$  females and gray males) and shorter bills ( $p < .001$ ,  $n = 33$  of both sexes). As stated above, Cassiar area birds do not differ significantly in any of the size measurements from birds collected in the southern half of B.C. and Alberta.

*Age and sex variation.*—There is secondary sexual dimorphism in size in all populations examined. Analysis of variance for size characters in Maritime

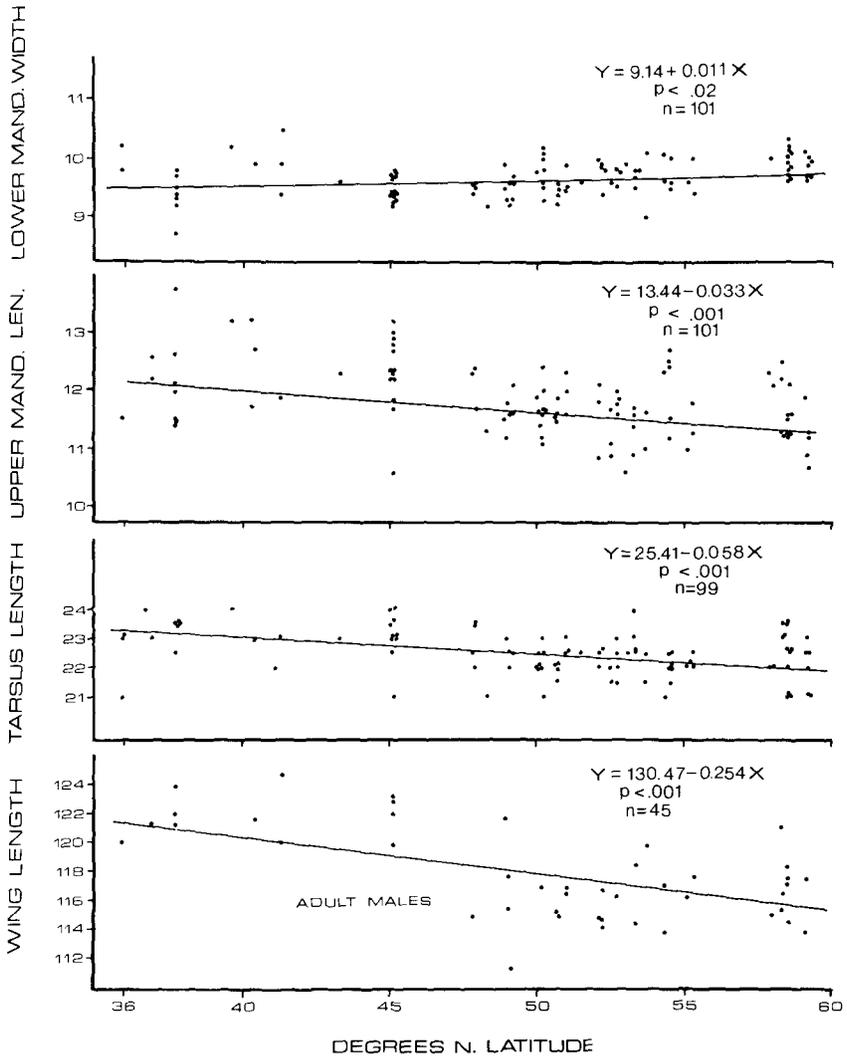


FIG. 4. Plots of wing length, tarsus length, upper mandible length, and lower mandible width on latitude in the Rocky Mountains, New Mexico to northern British Columbia.

provinces birds, the largest sample in this study, showed that of 8 skin characters, adult males and females differed only in wing and tail lengths. In the U.S. Rocky Mountains sample, which contains weight data adequate for comparisons, males were consistently heavier than females ( $p < .01$ ,  $n = 26$ ).

Age and sex variation in plumage color is well known in this species. Adult males have red body plumage, and first year males are usually indistinguishable from females in possessing gray body color with yellow crown and rump. In addition, a few gray males and females of unknown age have bronze or reddish crown and rump color.

In addition, there is a pronounced age dimorphism among males. First year, gray-plumaged males have shorter wings and tails than adult red males ( $p < .001, n = 97$ ) by an average of 3% in the Maritime sample. There are no differences in the other characters. Other regions, though less well sampled, are similar in this respect. Thus yearling males and females are very similar in all characters.

*Geographic variation in plumage color.*—Adult male body color within each population is highly variable, and is sufficient to swamp out differences claimed by Todd (1963) and others to exist between most continental populations. For example, a sample of 56 adult males from Newfoundland varied in color between yellowish-orange and dark red. I have noticed similar variation in wild birds of the taiga and Rocky Mountains. Pine Grosbeaks molt in August and September and sometimes disperse immediately toward the wintering grounds. Adult male specimens taken in fall and winter in Quebec, Ontario, Michigan, and the Great Plains are decidedly pinker than those collected anywhere on the breeding grounds. Microscopic examination of feathers shows that the difference in hue arises from wear of the pigmentless barbules at the tips of the red feathers. Attempts to establish the subspecific identity of winter specimens using plumage color (Gabrielson and Jewett 1940, Jewett et al. 1953) apparently failed to take feather wear into account.

There are, however, 2 populations in which this plumage is consistently distinctive. On the Queen Charlotte Islands males are a dark brick red in contrast to the lighter carmine red of most populations. In males from the Alaska panhandle, the plumage contains more orange than is found in that of interior Alaska birds. Curiously, adult males from Anchorage and the Kenai Peninsula, otherwise similar to Alaska panhandle birds, have red plumage similar to Rocky Mountain and taiga birds (5 specimens, pers. observ. in the field, and photographs). In addition, adult males from California appear to have more orange in their plumage than is found in males from most other regions. Average population differences in hue of red among the populations might be revealed with spectographic techniques, but hue of red can be of limited use in identifying the origin and population affinities of a given specimen.

As noted, female and first-year male plumages are very similar within all

populations, but Queen Charlotte Islands and coastal Alaska birds of this plumage are also distinctive. In the former there is a pronounced olive-green cast to the plumage, and in the latter, except in Kenai Peninsula birds, the gray is much darker than in the interior population. Microscopic examination of individual feathers from these populations showed that dark gray feathers have more pigment granules in the barbules. The greenish cast in the plumage of Queen Charlottes birds is due to the presence of a pale yellow pigment in the feather barbs, and in males the darker red is the result of a concentration of a dark pigment in the barbules at the feather tips. In other populations there is no pigmentation in these barbules.

#### DISCUSSION

The Pine Grosbeaks of the taiga vary clinally, but unevenly. Throughout the Maritime provinces the birds are uniform in size and proportions. North of the St. Lawrence River the only change is toward larger body size (longer wings and tail) in the north. Both Griscom (1934) and Todd (1963) insisted on the occurrence of 2 distinct populations, *P. e. leucura* and *P. e. eschatosus* in the Labrador Peninsula, despite Austin's (1932) observation that the birds merely increase gradually in size to the north. I examined specimens seen by previous workers, and many more collected since 1950, and agree with Austin that it is impossible to separate birds of the region into 2 populations. Todd (1963) argued that the southern limit of the large grosbeaks extended from the Straits of Belle Isle to southern James Bay, a boundary fitting closely the one between dense boreal forest and the sparse transitional zone between forest and tundra described by Rowe (1957). In the absence of breaks in the body size cline, however, any effect of this described difference in the forest on Pine Grosbeaks is at best hypothetical. Either of 2 explanations may account for the observed clinal change in body size: natural selection has favored greater body size in the north, or there is secondary contact between previously isolated populations, with considerable intergradation in this region. In the latter case, small birds adapted to thick boreal forest may have invaded the peninsula from the south and east, with large birds moving from the northwest around James Bay to occupy sparse forest in northern Quebec and Labrador. That body size also appears to increase over the same latitudinal range to the northwest, between James Bay and Great Slave Lake, supports the former explanation. Variation in vocalizations, to be discussed in another paper, is consistent with a theory of 2 colonizations of the peninsula after the last glacial recession (Adkisson 1972).

As noted above, only wing length varies in the poorly-collected region

between James Bay and Churchill, Manitoba, increasing to the west. Between the central taiga (95° to 115°W) and the Mackenzie delta, wing length increases, but varies little further to the west. Over this region bills become notably shorter. This region is so poorly collected that one cannot determine how gradually or abruptly these changes occur. From a taxonomic point of view, it is interesting that the cline for smaller bodies and shorter bills is first noticeable well within the described range of *P. e. leucura*.

Both of the clines of increasing wing length of taiga Pine Grosbeaks begin in northern Ontario and Quebec near the tip of James Bay. But the clinal decrease in bill length to the northwest is not repeated to the north on the Labrador Peninsula. In both examples, clinal variation in this measure of body size is consistent with Bergmann's rule, and the trend for shorter bills to the northwest, with Allen's rule. Indeed, colder average January temperatures (1945 to 1971) are found to the west in Canada (Ottawa, -10.9°C; Moosonee, Ont., -20.2°C; Churchill, Man., -27.6°C; Yellowknife, NWT, -28.6°C; Aklavik, NWT, -32.1°C; Hare and Thomas 1974). Fort Yukon, Alaska, averaged -28.1°C for January between 1931 and 1952 (U.S. Weather Bureau 1953). The lack of bill variation in the northeastern taiga is consistent with data indicating that winters are milder here than in the Northwest. For example, the January mean temperature at Sydney, N.S., is -4.4°C; at Natashquan and Quebec, P.Q., -11.8°C; at Goose Bay, Labrador, -16.3°C; and at Ft. Chimo, P.Q., -23.4°C. Thus, winters are colder to the north in the Labrador Peninsula, but not as cold as in the Northwest Territories (Hare and Thomas 1974). The decrease in wing length between Great Slave Lake and Alaska similarly implies a milder climate, yet the shortest bills are found in the westernmost populations, and winters in interior Alaska are similar to those at Yellowknife, NWT.

Clinal variation in the Rocky Mountains may have a different explanation. Clines of decreasing weight, and wing, tail, and tarsus lengths approximately parallel the decreasing altitudes toward the north at which the preferred Pine Grosbeak habitat is found. In Colorado and southern Utah, Engelmann spruce (*Picea engelmanni*) and subalpine fir (*Abies lasiocarpa*) occur between 2400 m and tree line at about 3000 m. The birds, in my experience, are most abundant above 2500 m in moist valleys, and on forested mesas. All New Mexico specimens were taken at 2500 m or above. At Togwatee Pass in northwestern Wyoming, I found the birds to be common at 2100 m to 2300 m. In Alberta, at Banff National Park, I found grosbeaks at 1500 m near Moraine Lake. Specimens from central and northern B.C. were taken at less than 1000 m.

While the trend of decreasing wing length to the north is uneven, the data

points apparently not fitting a sample linear regression on latitude (Fig. 4), there is a strong association with breeding locality altitude. Those Rocky Mountain specimens with altitude data show a strong positive correlation with altitude for weight, and wing, tail, tarsus, and bill lengths (all  $p < .02$ ). Wing length and altitude are correlated in a sample of 31 females and young males ( $r = .7522$ ,  $p < .001$ ) and 19 adult males ( $r = .6695$ ,  $p < .001$ ) from this region.

For intraspecific comparisons wing length tends to become greater at higher altitudes (Hamilton 1961, James 1970). Two prevalent theories seek to explain this effect: cold winter temperatures would favor larger bodies for heat conservation (in the original sense of Bergmann's rule; see James' discussion); and reduced air pressure selects for greater wing surface (Moreau 1960). James (1970), however, showed that wing length in 8 species of birds is most highly correlated with wet bulb temperatures, which combine both temperature and humidity effects. James points out that the known increase in evaporative water loss at higher altitudes could account for altitudinal changes in bird bodies. My own data support her argument. I have no data on winter temperature in grosbeak habitats in the Rocky Mountains, nor do I know exactly where the birds winter, but I suggest that the altitudinal limit of the spruce-fir forest is related to climate, and that Pine Grosbeaks in this forest throughout the Rockies face similar weather conditions. The most parsimonious explanation for the association of body size and altitude is that increased evaporative water loss at higher altitudes selects for larger bodies at all seasons. Analysis of measurements from other sedentary Rocky Mountain species, and of weather from high altitude localities, would help clarify further the relationship between altitude and body size in homeotherms.

In the other isolated western populations, there is no evidence of intra-population variation. In California, for example, there is no hint of latitudinal variation in the north-south oriented Sierra Nevada. It is possible, however, that larger samples from more localities could reveal some variation. The morphology of California birds bears no obvious relation to trends in populations from the Rocky Mountains or elsewhere. Rocky Mountain birds are at least 10% larger than any California birds, and the narrowness and shallowness of the bill in California birds is unique within this species. If California birds were more widespread we might find variation as in Rocky Mountain birds, but they are apparently largely restricted to the red fir (*Abies magnifica*) forest (ca. 1700 m) over a distance of 500 km in the Sierra Nevada, mainly on the western slope (Ray 1912, pers. obs.). In 1970 I observed at least 6 pairs near Devil's Postpile National Monument (Madera

Co.) for 10 days. In a mixed forest of red fir, Jeffrey pine (*Pinus jeffreyi*), and lodgepole pine (*P. contorta*), I found the birds virtually ignoring the pines, only perching in them occasionally, while using the firs constantly for food, nesting, and during maintenance activities. There are no spruces in the range of the California form (Little 1971). In view of its unique bill proportions, a comparison of its food habits with those of other populations seems justified. In summary, therefore, it is not possible now to predict or fabricate its morphology by extending any known cline from any other part of the species' range. My preliminary explanation for the small size of this form, by comparison with Rocky Mountain birds, is that it is found at much lower elevations, at similar latitudes, in a generally warmer mountain range.

Similarly, the Queen Charlotte population is morphologically homogenous, and seems isolated in its own unique environment. With the exception of one winter specimen from southwestern B.C., no grosbeaks of the nearby mainland approach Queen Charlotte birds in any characteristic, nor are there known clines, which if extended, could predict its extreme smallness and darkness. Newfoundland birds, also occupying a cold, moist island habitat, approach the size of Queen Charlotte birds, but less than 10% of a sex or age class are as small, and none is as dark. In spite of reports that "*carlottae*" breeds on the mainland and Vancouver Island (Rand 1943), the specimens ( $n = 3$ ) on which these speculations are based fall within the color and size ranges of Alaska panhandle birds, and may be birds that bred following a winter irruption.

In forested coastal Alaska, many areas where the birds should occur have never been sampled, and sample sizes from several localities are small. However, there is no evidence of intraregional variation. Nor is there evidence of continuous distribution and clinal variation between (1) coastal and interior Alaska north of the Alaska Range, and (2) coastal Alaska and interior B.C. Swarth's (1922) birds from Telegraph Creek, B.C., may represent either an unusual occurrence or possibly a logical extension of the breeding range of *flammula*. In the latter case, at most 40 km would separate 2 very different populations, as I noted earlier. Possibly there is introgression in this region, but in the absence of specimens I suggest that coastal Alaska and northern B.C. birds have allopatric ranges.

In light of the known morphological variation in Pine Grosbeaks, past confusion over the subspecific identity of birds collected in winter (see comments and citations in Sutton 1948) is understandable. In most years there is a limited movement to the south from the taiga. In nearly all winters they are common around Canadian cities and in northern New England

(Godfrey 1966, Forbush 1927). At irregular intervals they move south in large numbers as far as New Jersey, Ohio, and Kansas, but not all populations irrupt in the same winter. There is little concordance between northeastern and northwestern irruptions. Support for this statement has appeared in many issues of *American Birds*. For example, in the winter of 1973-74 the northwestern U.S. and British Columbia experienced an irruption of unprecedented size, while the birds were scarce in the central provinces and in the northeast (Arbib 1974). Montane populations apparently undergo only a slight altitudinal migration. In California, Pine Grosbeaks have never been recorded outside the Sierra Nevada (Grinnell and Miller 1944), and in Colorado they are seldom seen below the limits of pine forest (Bailey and Niedrach 1965). Specimens of Pine Grosbeaks taken in winter in Kansas and Missouri have been referred to the taiga form, *P. e. leucura* (Ely 1961, Rising 1965).

In order to understand more fully the movements of this species, specimens and tape recordings should be obtained from every irruption. A combination of morphological and vocal characters should make it possible to determine the approximate geographic origin of the birds in most instances (Adkisson, unpublished data).

Even if trinomial classification is retained as a convenience, defining the limits of the subspecies is arbitrary in many cases (Mayr 1963, Simpson 1961; see also discussion in Lidicker 1962). Whether or not one believes subspecies to be incipient species, to recognize them where there is neither isolation nor evidence of discontinuous variation serves neither taxonomy nor evolutionary biology. I follow Mayr (1963) in allowing subspecific distinction for any isolated population differing in certain morphological characters from others. The geographical isolates of *P. enucleator* considered here already have this status. I attempted to apply the 97% rule (Amadon 1949) and found that single-character comparisons among the isolates failed. In fact, only the longest-winged (western taiga) and shortest-winged (Queen Charlotte Islands) populations can be separated using the formulas in Amadon's paper. However, I find that specimens of each of the isolates can easily be identified using all characteristics described in this paper. I have less success separating all specimens of the Rocky Mountain and taiga populations in this way.

Each of the isolates possesses a unique combination of characteristics. The western-most ones (*californica*, *carlottae*, and *flammula*), occupy relatively small ranges, and I detect no intrapopulation variation (except color of adult males in *flammula*). Rocky Mountain birds (*montana*) are clinally variable, and there appears to be a hiatus in range between northern B.C. and central

Yukon Territory and Alaska. In my opinion, each of these 4 populations should continue to have subspecific status.

In the taiga, however, the birds appear to occur continuously from coast to coast. *P. e. alascensis* was originally separated from other taiga grosbeaks mainly on the basis of a shorter bill and larger body (Ridgway 1898). However, I have shown that these characters vary clinally in the taiga, and recommend that *alascensis* be considered a synonym of *leucura*.

*P. e. eschatosus*, described on the basis of small size (Oberholser 1914), can be applied to birds from the Maritime provinces of Canada. But equally small birds also occur in southern Quebec, and from there to tree line, wing and tail lengths increase gradually. On this basis I suggest that *eschatosus* be synonymized into *leucura* also. I prefer to adopt the system of Owen (1963) in which clinal variation is acknowledged, as opposed to arbitrary subspecific categories.

Accordingly, *P. e. leucura* should be applied to all Pine Grosbeaks in the taiga, from Newfoundland to western Alaska. Future checklists should contain a note on its variation, in the manner described in Owen's paper. We thus recognize that, in the absence of geographical barriers, regional variation in selection pressures can give rise to continuous morphological variation, and the different characters need not vary concordantly. In fact, *montana*, recognized since 1898, is nearly as variable as the newly-defined *leucura*. The distinctiveness of *flammula*, *carlottae*, *montana*, and *californica* may be related to their being set apart in apparently different environments.

#### SUMMARY

There is significant morphological variation in North American Pine Grosbeaks. Variation in wing length and bill length in birds of the taiga is clinal. Beginning in the southern Labrador Peninsula, body size increases to the north and to the northwest. Variation in all characters is clinal in the Rockies. Body size becomes smaller to the north, and is highly correlated with the altitude of breeding localities. There is no evidence of clinal variation elsewhere.

The largest birds occur in the taiga of northern Quebec and Labrador, and west of Hudson Bay to western Alaska, and in the southern Rocky Mountains. Small birds occur in the Canadian Maritime provinces, and in California, but the smallest are in the Queen Charlotte Islands. Bills of western taiga birds are short, deep, and wide, especially in comparison with the long, wide bills of coastal Alaska birds, and the extremely narrow bills of California birds.

It is suggested that there is no basis for the recognition of 3 subspecies in the taiga, and that one name, *P. e. leucura*, should be applied to the clinally variable, continuously distributed form.

#### ACKNOWLEDGMENTS

The cooperation of many persons and institutions made this investigation possible. For the loan of specimens in their care I am grateful to the following: Dean Amadon

of the American Museum of Natural History, Richard C. Banks of the Bureau of Sport Fisheries and Wildlife, Raymond A. Paynter of the Museum of Comparative Zoology, Ned K. Johnson of the Museum of Vertebrate Zoology, Kenneth C. Parkes of the Carnegie Museum, Jon C. Barlow of the Royal Ontario Museum, W. Earl Godfrey of the National Museum of Canada, Victor Lewin of the University of Alberta Museum of Zoology, R. Wayne Campbell of the University of British Columbia, C. J. Guignet of the British Columbia Provincial Museum, and Hugh Smith of the Alberta Provincial Museum and Archives. I am indebted to R. W. Storer for his interest and advice for the duration of this study, to H. B. Tordoff for encouragement in earlier phases of the study, and to R. B. Payne and F. C. James for advice and constructive criticism of the manuscript. This paper is derived from part of a dissertation submitted in partial fulfillment of the requirements for the Ph.D. in zoology at the University of Michigan.

The study was supported in 1969 and 1973 by grants to me from the Frank M. Chapman Fund of the American Museum of Natural History, and throughout the years 1970–1972 by National Science Foundation grants (GB 13104 and 25986) to N. G. Hairston at the University of Michigan for research in Systematic and Evolutionary Biology.

#### LITERATURE CITED

- ADKISSON, C. S. 1972. An analysis of morphological and vocal variation in North American Pine Grosbeaks, *Pinicola enucleator* (Aves). Ph.D. dissertation, Univ. Michigan, Ann Arbor.
- AMADON, D. 1949. The seventy-five percent rule for subspecies. *Condor* 51:250–258.
- AMERICAN ORNITHOLOGISTS' UNION. 1957. Check-List of North American birds. 5th ed. Baltimore, Am. Ornithol. Union.
- ARBIB, R. S. (Ed.) 1974. Seventy-fourth Christmas bird count. *Am. Birds* 28:145–585.
- AUSTIN, O. L., JR. 1932. The birds of Newfoundland Labrador. *Mem. Nuttall Ornithol. Club*, No. VII.
- BAILEY, A. M., AND R. J. NIEDRACH. 1965. Birds of Colorado. Denver Museum of Nat. Hist., Denver.
- COWAN, I. McT. 1939. The vertebrate fauna of the Peace River district of British Columbia. *Occ. Pap. B.C. Prov. Mus.* No. 1.
- ELY, C. A. 1961. Cassin Finch and Pine Grosbeak in west-central Kansas. *Condor* 63:418–419.
- FORBUSH, E. H. 1929. The birds of Massachusetts and other New England states. Mass. Dept. of Agriculture, Norwood Press, Norwood, Mass.
- GABRIELSON, I. N. AND S. G. JEWETT. 1940. Birds of Oregon. *Studies in Zoology*, No. 2. Oregon State College, Corvallis.
- GODFREY, W. E. 1966. Birds of Canada. *Natl. Mus. Canada Bull.* 203. Queen's Printer, Ottawa.
- GRINNELL, J. AND A. H. MILLER. 1944. The distribution of the birds of California. *Pac. Coast Avifauna* 27:1–608.
- GRISCOM, L. 1934. The Pine Grosbeaks of eastern North America. *Proc. New England Zool. Club* 14:5–12.
- HAMILTON, T. H. 1961. The adaptive significance of intraspecific trends of variation in wing length and body size among bird species. *Evolution* 15:180–195.
- JAMES, F. C. 1970. Geographic size variation in birds and its relationship to climate. *Ecology* 51:365–390.

- JENKS, R. 1938. A new subspecies of the Pine Grosbeak from Arizona with critical notes on other races. *Condor* 40:28-35.
- JEWETT, S. G., W. P. TAYLOR, W. T. SHAW, AND J. W. ALDRICH. 1953. Birds of Washington State. Univ. of Wash. Press, Seattle.
- JOHNSON, N. K. AND R. C. BANKS. 1959. Pine Grosbeak and Lawrence Goldfinch in Nevada. *Condor* 61:303.
- LIDICKER, W. Z., JR. 1962. The nature of subspecies boundaries in a desert rodent and its implications for subspecies taxonomy. *Syst. Zool.* 11:160-171.
- LITTLE, E. C. 1971. Atlas of United States trees. U.S. Dept. Agric. Special Publ. 1143.
- MAYR, E. 1963. Animal species and evolution. Harvard Univ. Press, Cambridge, Mass.
- MOREAU, R. E. 1960. Climatic correlations of size in *Zosterops*. *Ibis* 102:137-138.
- OBERHOLSER, H. C. 1914. Four new birds from Newfoundland. *Proc. Biol. Soc. Wash.* 27:43-54.
- OWEN, D. F. 1963. Variation in the North American Screech Owl and the subspecies concept. *Syst. Zool.* 12:8-14.
- PRICE, W. W. 1897. Description of a new Pine Grosbeak from California. *Auk* 14:182-186.
- RAND, A. L. 1943. On some British Columbia birds. *Can. Field-Nat.* 57:60-63.
- . 1946. List of Yukon birds and those of the Canol road. *Bull. Can. Natl. Mus.* 105:1-76.
- RAY, M. S. 1912. The discovery of the nest and eggs of the California Pine Grosbeak. *Condor* 14:157-187.
- RIDGWAY, R. 1898. New species of American birds. *Auk* 15:319-324.
- RISING, J. D. 1965. Townsend's Solitaire and Pine Grosbeak in Missouri. *Auk* 82:275.
- ROWE, J. S. 1957. Forest regions of Canada. *Bull.* 123, Forestry Branch, Dept. North Affairs and Nat. Res. Ottawa.
- SIMPSON, G. G. 1961. Principles of animal taxonomy. Columbia Univ. Press, New York.
- SUTTON, G. M. 1948. Small Pine Grosbeaks collected in Tompkins County, New York. *Auk* 65:125-126.
- SWARTH, H. S. 1922. Birds and mammals of the Stikine River region of northern British Columbia and southeastern Alaska. *Univ. Cal. Publ. Zool.* 24:125-314.
- TODD, W. E. C. 1963. The birds of the Labrador Peninsula. Univ. of Toronto Press, Toronto, Ontario.
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