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GEOGRAPHIC VARIATION IN VOCALIZATIONS AND EVOLUTION OF NORTH AMERICAN PINE GROSBEAKS

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ABSTRACT.—North American Pine Grosbeaks (*Pinicola enucleator*) vary geographically in two of their call notes. Variation is greatest in the location calls that communicate between individuals at great distances. Birds of the taiga and coastal Alaska give whistled calls, of which four categories have been identified. Western montane and Queen Charlotte Islands birds give more complex, modulated calls, which vary greatly among localities. Taiga and montane birds do not approach playback of each other's calls, though wild birds usually respond quickly to playback of their own calls. Cross-fostering experiments show that the location call can be entirely learned in the first weeks of life, suggesting that the observed variation in nature arose in association with isolation of small, possibly founder, populations. No selective agent leading to call variation has been identified, but vegetation structure is discounted as a factor.

Variation in the songs of passerines has, in recent years, received considerable attention (reviewed by Thielcke 1969, Nottebohm 1975). Variation in vocalizations other than primary song has, however, received much less attention. The Chaffinch (*Fringilla coelebs*) shows a mosaic pattern of geographic variation in one of its call notes, the "rain call" (Sick 1939; L. F. Baptista, pers. comm.). Preliminary evidence indicates similar variation in calls (*Lockrufe*) of Bullfinches (*Pyrrhula pyrrhula*; Wilkinson and Howse 1975, Schubert 1976). Alarm calls of island populations of two *Sylvia* warblers are reported to differ from those of mainland populations (Bergmann 1976). The call notes of several emberizine species with song dialects apparently do not vary (J. Mulligan, pers. comm.). Individual variation and call imitation in six species of carduline finches have been reported by Mundinger (1970, 1979). His observations suggest that upon joining a flock, a bird may change its call to match those of its new flockmates. Marler and Mundinger (1975) showed call plasticity in free-living Twites (*Acanthis flavirostris*). In these small carduelines, an isolated population could develop a distinctive call "dialect," but to my knowledge such has never been reported.

In this paper, I describe the call repertoire of North American Pine Grosbeaks (*Pinicola enucleator*) and geographic variation in certain calls. I also present an explanation for the observed variation in the light of morphological variation (Adkisson 1977) and new evidence from studies of vocal ontogeny in juveniles.

METHODS

I recorded Pine Grosbeak vocalizations at many places over much of the range of this species in North America using a Uher 4000-L or I C tape recorder and a Uher cardioid microphone mounted in a 60-cm fiberglass parabolic reflector. The sounds were analyzed with a Kay Elemetrics Co. Sonagraph, model 7029A, using the wide band setting. Calls of over 200 adult individuals were recorded in the summers of 1969–74, and of nearly 200 individuals in the winter during that period. Recordings were made in: Newfoundland, 9 localities, 16 individuals; Churchill, Manitoba, 8; Banff National Park, Alberta, 10; Togwatee Pass, Teton Co., Wyoming, 2; Smith Lake, Wind River Range, Fremont Co., Wyoming, 4; Snowy Range, Carbon Co., Wyoming, 7; Brainerd Lake, Boulder Co., Colorado, 5; White River Plateau, Garfield Co., Colorado, 10; Gothic, Gunnison Co., Colorado, 23; Grand Mesa, Delta and Mesa cos., Colorado, 37; Mirror Lake, Uinta Range, Duchesne Co., Utah, 9; Tushar Range, Beaver Co., Utah, 5; Cedar Breaks, Iron Co., Utah, 11; White Mountains, Apache Co., Arizona, 1; Echo Summit, Eldorado Co., California, 4; Red's Meadow, Madera Co., California, 9; vicinity of Fairbanks, Alaska, 7; Kenai Peninsula, Alaska, 10; Cassiar Range, B.C., 8; Queen Charlotte Islands,

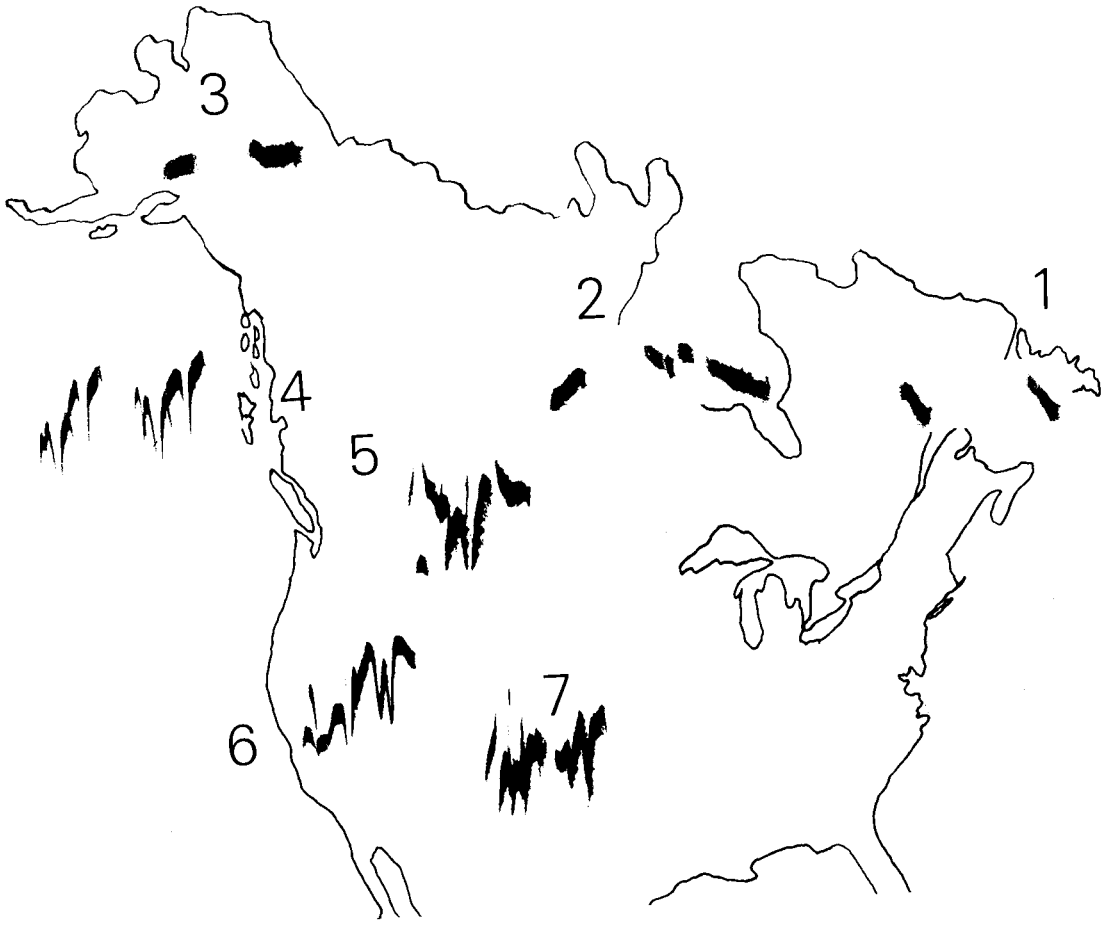

FIGURE 1. Major features in location call variation in North American Pine Grosbeaks: numbered breeding season localities and their typical calls are 1, southwestern Newfoundland; 2, Churchill, Manitoba; 3, Fairbanks, AK; 4, Queen Charlotte Islands, B.C.; 5, Banff, Alberta; 6, Madera Co., CA; 7, Grand Mesa, CO.

B.C., 15. Winter sample sizes by region are: northern New Hampshire, 38; northern New York, 5; northern Michigan, over 50; northwestern Ontario, over 50; Saskatchewan, 10; Alberta, 44.

RESULTS

THE VOCAL REPERTOIRE

Pine Grosbeaks appear to resemble several other cardueline finches in possessing a small repertoire of sounds (Marler and Mundinger 1975; Adkisson, unpubl. data). In addition to loud primary songs and "whisper songs" characteristic of breeding season males, I have found four distinctly different calls (Adkisson 1972): an alarm call (used for both flying and non-flying predators), a food-begging call in breeding-season females, and two other calls, which I have named "contact notes" and "location calls."

The location call (Figs. 1–4). The location call (Fig. 1 provides an overview of variation in this call) is the most conspicuous year-round vocalization in the species' repertoire, and is given by both sexes. It seems to be the primary means of identifying the caller as a Pine Grosbeak, and is capable of carrying this message for perhaps hundreds of meters when given loudly. In the context of flocking, this call seems to attract the birds to each other, and in the breeding season it functions similarly in paired birds. I have no evidence that it has sexual significance. The following points show the nature of this vocalization in more detail. 1) Lone, wild birds often call spontaneously. I have located at least 60 wild individuals by tracing the source of these sounds. Wild birds predictably respond to playback of this call and approach the source of the sound. 2) Lone birds approach the source of location calls, whether it be a caged bird or tape recording, and then cease calling. I have seen over 200 individuals behave in this manner. 3) Lone birds are always more responsive to playback than are pairs or flocks. The great majority of birds attracted

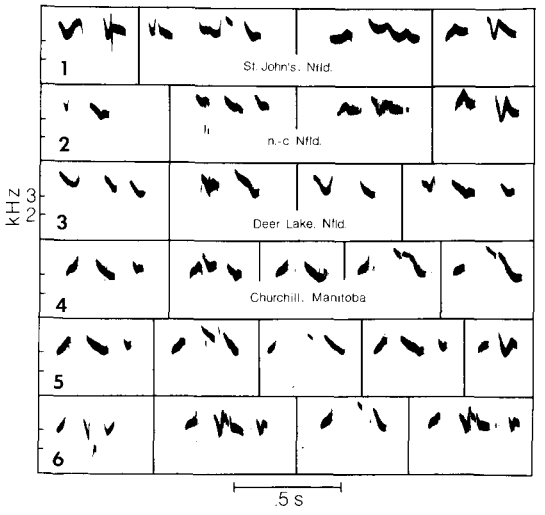

FIGURE 2. Location calls of birds from Newfoundland and Manitoba. Row 1, four birds from near St. John's, Newfoundland. Row 2, four birds from north-central Newfoundland. Row 3, four birds from near Deer Lake, western Newfoundland. Rows 4 and 5, calls of 10 birds near Churchill, Manitoba. Row 6, the first two examples are of complex calls rarely given by birds at Churchill, Manitoba. The last two are both kinds of calls given by one bird in succession, Churchill.

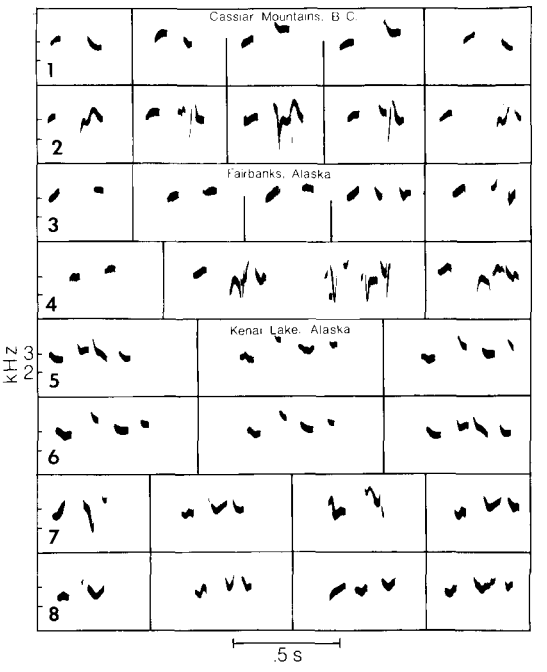

FIGURE 3. Location calls of birds from northwestern North America. Row 1, the primary, simple calls given by five birds in the Cassiar Mountains, B.C. Row 2, uncommon, complex calls of the same five birds as in Row 1. Row 3, the primary, simple calls of five birds at Fairbanks, AK. Row 4, the typical call of a sixth bird at Fairbanks, followed by three examples of uncommon, more complex calls, all at Fairbanks. Rows 5 and 6, typical four-note calls of six birds at Kenai Lake, AK. Rows 7 and 8, uncommon, more complex calls of the above six birds at Kenai Lake.

to playback in the field were apparently alone. Birds in a flock typically call in response to playback, but are less likely to approach. 4) There is much calling in travelling flocks, little or none in flocks and pairs engaged in feeding. Several authors, beginning with Price (1897) have noted that feeding or preening groups are difficult to find on account of their silence. 5) After flocks or pairs are scattered, as by a thrown object or by a shot, calling is loud and persistent, ceasing when the members once again come together. 6) Calling accompanies mobbing behavior, and in this context, could be considered an alarm call. My captives use a shortened version of location call when a cat approaches the aviary. I have never observed grosbeaks mobbing a predator, but on several occasions wild birds have fluttered around me after I captured a member of the flock. As long as the new captive continued to scream, its flockmates remained nearby uttering both location calls and alarm calls. This behavior and the greater reactivity of lone birds are similar to behavior reported for Chaffinches (Marler 1956), Bullfinches (Nicolai 1956, Schubert 1976), crossbills (*Loxia* spp.) and redpolls (*Carduelis* spp.; pers. observ.). Marler was able to distinguish four forms of the Chaffinch social call (social, mobbing, escape, and aggressive). In every sampling locality I have detected two forms of the location call and, in a few individuals, three forms. In any locality the forms are similar in structure, varying primarily in duration due to repetition of elements. I have not detected different functions for the forms of the location call except in the context of alarm, or agitation as noted above.

The location call is an integral part of the social behavior of this species, functioning, in flocking or paired birds, to keep individuals aware of the direction and distance of other members, and in lone birds, to aid in finding other conspecifics.

Contact notes. Contact notes (Fig. 5, row 4) are given almost constantly by grosbeaks when moving about. At times, in flying birds, each note seems to correspond to a wing beat. These sounds attenuate so rapidly with distance that it is difficult for an observer to determine their function. However, the calls can at times be correlated with apparent readiness to fly. On at least 200 occasions I have watched feeding flocks or pairs depart from a place. Typically, a wave of restless movement seems to sweep

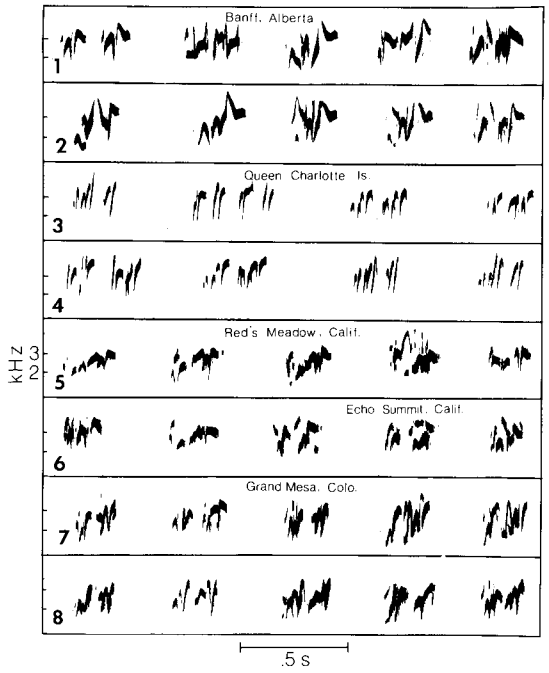

FIGURE 4. Location calls of birds of western North America south of Alaska. Rows 1 and 2, typical modulated calls of ten birds recorded at Banff, Alberta. Rows 3 and 4, typical modulated calls of eight birds recorded at Graham Is., Queen Charlotte Islands. Row 5, typical modulated calls of five birds recorded at Red's Meadow, Madera Co., CA. Row 6, typical modulated calls of two birds recorded at Red's Meadow, and three birds recorded at Echo Summit, CA. Rows 7 and 8, typical calls of 10 birds recorded at Grand Mesa, CO.

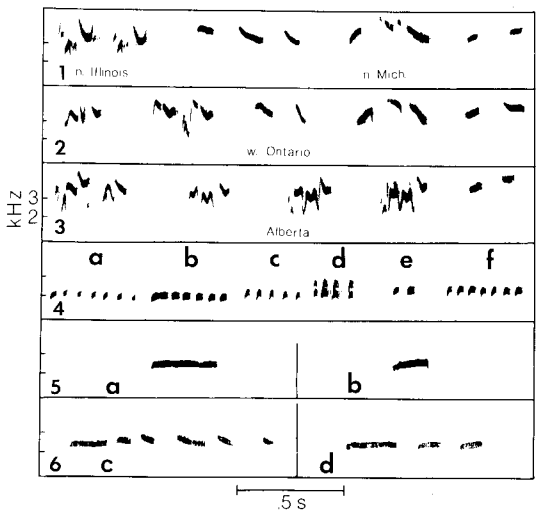

FIGURE 5. Location calls recorded in winter, contact notes, and alarm calls. Row 1, calls of one bird recorded in winter in Rockport, IL, and three birds recorded in Chippewa Co., MI. These three calls correspond to whistled call Types 1, 2, and 3, respectively. Row 2, calls of birds recorded along the Trans-Canada Highway in winter in western Ontario; the first two calls were recorded west of Kenora (both modulated) and the last three were recorded between Lake Nipigon and Marathon (1972). Row 3, modulated calls of two birds recorded in January, 1972, at Banff, Alberta, followed by modulated calls from 2 birds and a whistled call from one bird recorded at Edmonton, Alberta, January 1972. Row 4, Contact notes: a) Fairbanks, AK; b) Cassiar, B.C.; c) Graham Is., Queen Charlotte Islands, B.C.; d) Red's Meadow, Madera Co., CA; e) Grand Mesa, CO; f) St. John's, Newfoundland. Row 5, Alarm calls: a) Grand Mesa, CO; b) Churchill, Manitoba. Row 6, Alarm calls: c) Red's Meadow, CA; d) St. John's, Newfoundland.

over the group, and the birds gather in some prominent tree top for a few seconds, then suddenly fly out of sight. At these times contact notes become louder and are uttered more rapidly, reaching a peak just prior to departure. Also, contact notes replace location calls as a wild bird approaches either the source of playback or a decoy. In the latter case, both birds give location calls loudly until the wild bird has approached closely. The exact distance at which the transition takes place is difficult to estimate because wild birds usually fly from some distance to within a few meters of the captives.

Contact notes have a notable quality of seeming to originate elsewhere than the actual source; it may be as difficult for predators to locate the bird as for humans. Individuals may be assured of the continuing proximity of flockmates by participating in this chorus of contact notes.

Alarm calls. Pine Grosbeaks have an alarm call, which may be used to indicate either flying or nonflying predators (Fig. 5). My observations on captive and wild birds indicate that the call may be chiefly associated with the presence of aerial predators. On three occasions in Colorado I saw grosbeaks assume a rigid, upright posture on a perch and give this call when Swainson's Hawks (*Buteo swainsoni*) were soaring nearby. On another occasion this behavior alerted me to the presence of a Great Horned Owl (*Bubo virginianus*). R. B. Payne (pers. comm.) was recording my captives at the University of Michigan Botanical Gardens when the appearance of Red-tailed Hawks (*Buteo jamaicensis*) elicited this combination of calling and an unusual upright posture. In my experience, the quality of alarm calls makes it difficult to find calling birds. The structure of the vocalization is similar to that of alarm calls of many woodland birds, except that it is at least 4 kHz lower in pitch, around 2 kHz (Fig. 5). Once in Colorado, when I finally located the tree from which alarm calls seemed to emanate, I did not see the bird immediately because of its "unnatural" posture, suggesting that this posture also helps the birds to remain undetected.

Female food-begging vocalizations. Male grosbeaks feed their mates from early in courtship at least until the eggs hatch, and also during the ensuing week when females spend much time brooding the young. Such feedings are nearly always accompanied by loud, ringing vocalizations from the female. Twice in central Colorado in early June I witnessed females apparently being fed, all the while giving a series of these calls. The females first called, fluttered their wings in a manner reminiscent of a begging juvenile, were fed, and then continued to call. These calls bore no resemblance to any other grosbeak sound. In neither case was the pair near a known nest. In California I observed two nesting pairs for nine days in mid-June. At this locality, the males fed their mates at the nest as well as in nearby trees. In both situations, feeding was accompanied by loud calls from the females similar to those recorded from Colorado females being fed. In five out of seven instances in which one female was fed on the nest, her begging call immediately preceded the male's approach from a nearby tree. At this nest I once saw a male fly past the nest tree, and reverse direction just after a loud begging call from the female, whereupon he fed her. In most instances at these two nests the females continued to call from the nest for up to five minutes after the male's departure. I have seen courtship feeding in captives, but have never heard this call in captive or wild birds from the taiga, or in breeding captives from California and Colorado.

Vocalizations of the young. The earliest age at which I have heard vocalizations from nestlings is about five days. They utter a high-pitched "seee" when fed, the volume becoming greater as the birds grow. Nestling calls of wild Colorado and captive Newfoundland birds are similar, with a pitch of about 8 kHz. After fledging, the calls of the young are at virtually the same pitch as those of their parents (2 to 4 kHz), though they differ in a number of structural details (compare juvenile and adult calls in Fig. 6). I have observed fledging in five captive broods. In all cases the fledged birds began giving single, short (40- to 50-ms) calls at about 2.5 kHz while birds still in the nest continued to make 8-kHz sounds when fed. The later-fledging birds also uttered the lower-pitched sounds upon fledging. This change in call pitch was characteristic of all other captive-reared juvenile grosbeaks, whether reared by their genetic or by foster parents.

Vocalization develops in three gross stages in juveniles: fledging to independence 3 to 4 weeks later, when begging calls only are made (the post-fledging calls mentioned above); 4 to 15 weeks post-fledging, during which time contact, alarm, and location calls appear, the latter initially crude, variable copies of adult location calls; and after 15 weeks, by which time all calls are indistinguishable from those of the adults, and subsong appears.

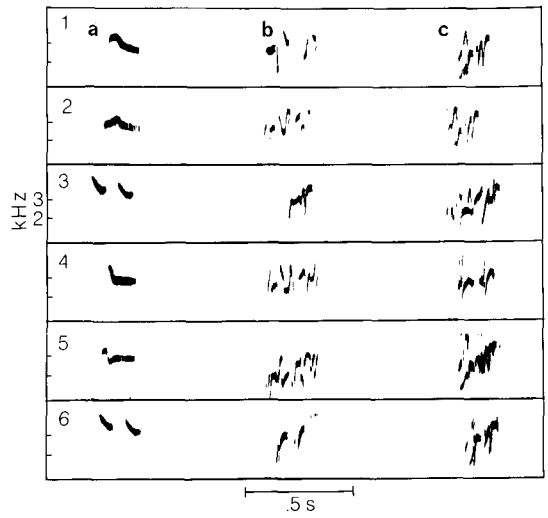

FIGURE 6. Ontogeny of location calls in juvenile Pine Grosbeaks in 1978. Row 1, calls of juvenile "White" a) one week after fledging, b) 10 weeks after fledging, c) five months after fledging. Row 2, calls of "White's" sibling "Yellow" at the above ages. Row 3, a) location calls of male parent of above juveniles. This bird was captured in winter in New Hampshire; b) and c) calls of the juveniles' foster parents from Grand Mesa, CO. Row 4, calls of juvenile "Blue" a) one week after fledging, b) 10 weeks after fledging, c) five months after fledging. Row 5, calls of "Blue's" sibling "Green" at the above ages. Row 6, Location calls of a) male parent of juveniles "Blue" and "Green" from New Hampshire, b) and c) of foster parents of these juveniles from Grand Mesa, CO.

GEOGRAPHIC VARIATION IN VOCALIZATIONS

Variation in the location call. The location call shows striking, apparently discontinuous, geographic variation (Figs. 1–4). I have detected location calls of two major categories, each of which may be subdivided: calls containing whistles (pure or nearly pure tones) between 3.0 and 4.5 kHz, and calls composed of modulated sounds of average lower pitch, between 1.8 and 4.2 kHz. I have recorded whistled location calls in the summer in the taiga (Newfoundland; Churchill, Manitoba; Fairbanks, Alaska), coastal Alaska (Kenai Peninsula, and Haines), and in the Cassiar Mountains in northern British Columbia (see Fig. 1 for overview, Fig. 2, rows 1–6, and Fig. 3, rows

1–8). In the summer, I recorded modulated calls in the Rocky Mountains north to Banff, Alberta, in California, and in the Queen Charlotte Islands (Fig. 4).

For convenience of discussion, I have arbitrarily divided whistled calls into four types. At all Newfoundland localities they were composed of one, two, or three whistles which descend in pitch between 4.5 and 3.0 kHz (Type 1). Most birds I recorded gave 2- or 3-note calls. In these calls the first and second notes are usually shorter than the third.

At Churchill, Manitoba, grosbeaks gave two kinds of location calls (Type 2). The most frequently heard (about 70%) of these calls has three elements and begins with an upslurred note at about 3.7 kHz. The second is highest in pitch, and is downward inflected between 5.0 and 4.1 kHz. The third element is also downward inflected between 4.5 and 3.0 kHz. The second type of location call at Churchill also has three elements, beginning with a whistle identical to the opening note of the first Churchill call type. The two notes following are modulated between 3.0 and 4.5 kHz (Fig. 2, rows 4–5).

Birds from Fairbanks also uttered two types of calls (Type 3) (Fig. 3, rows 3–4). One type is composed of two whistles, the second higher in pitch than the first. Both notes ascend in pitch and are of similar duration (70 ms); they span ranges of average frequencies of 3.2 and 3.8 kHz respectively. The second call type recorded at Fairbanks has three notes, the first two of which are similar to the two notes of the first call type. The third note is modulated between 3.0 and 4.2 kHz, as in Churchill birds. All birds recorded in the Kenai Peninsula of Alaska gave whistled calls slightly different from those of Fairbanks birds (Type 4).

Grosbeaks of the Rocky Mountains, California, and the Queen Charlotte Islands have no whistled notes in their location calls (see Fig. 4). The calls are complexly modulated and, within a locality, individually variable. Yet in each mountain range in the Rocky Mountains there are distinctive characteristics, such that there appear to be call "dialects" peculiar to a locality (Adkisson, unpubl. data). I have not attempted to classify modulated calls, as I did the whistled calls.

Location calls recorded in winter. My data from wintering grosbeaks, in particular those with whistled calls, suggest that variation in the location call is discontinuous, but the boundaries of the breeding season "dialects" are unknown. Over three winters I recorded location calls of many wintering birds. (I also captured 24 birds in Michigan and Ontario and kept them in captivity for up to five years.) Figure 5, rows 1–3 depict winter-recorded location calls. In New York and New Hampshire, all location calls recorded were similar but not identical to those recorded in Newfoundland in summer (Type 1). Ten individuals recorded in New Hampshire in January 1970, and 15 individuals captured there in 1976, also gave this type of location call. Of 12 birds caught in northern Michigan in November 1969, five gave Type 1 location calls, four gave Churchill type (Type 2) calls, and three gave Fairbanks type (Type 3) calls. In the ensuing three years, during which time these birds were kept in neighboring cages or in the same outdoor flight cages, I recorded more than 50 location calls from each of these birds, and heard many more; all consistently gave only one type of call.

In January 1971, I recorded location calls from at least 26 individuals in Ontario east of Lake Nipigon. Ten of these gave Type 1 calls, the remainder, Type 2 calls. I heard, but did not record, at least 50 other birds in this field trip; all but one (which had Type 3 calls) gave one of the two call types. In January 1972, the relative abundance of call types in Ontario was very different. Between English River and Thunder Bay along the Trans-Canada Highway I encountered over 50 grosbeaks. Most of these birds gave Type 3 location calls, and at least five gave modulated calls similar to those recorded in the Rocky Mountains in summer. East of Thunder Bay I found fewer grosbeaks. Six birds gave Type 2 whistled calls, and two gave Type 1 calls. In January 1972, Type 3 whistled calls, and modulated calls not similar to any recorded elsewhere, were recorded by W. B. Shepherd at Rockford, Illinois.

In February 1972, in the Lower Peninsula of Michigan, I encountered several dozen grosbeaks, all but one (which made Type 1 calls) of which gave Type 2 location calls.

In the prairie provinces of Canada I recorded both Fairbanks type (3) whistled calls and modulated calls similar to those recorded at several localities in the Rocky Mountains. In Calgary, Edmonton, and Vermilion, Alberta, I saw or heard an estimated 500 grosbeaks, and made good recordings of location calls of about 45. With grosbeaks constantly present and moving about, it was difficult to assess the relative abundance of call types. However, whistled (Type 3) and modulated call types appeared to be equally

abundant in Alberta. At Regina, Saskatchewan, I found about 50 grosbeaks in one morning, and heard and recorded only modulated location calls like those recorded in Alberta and northwestern Ontario. I heard no Type 1 or Type 2 calls in winter in the Canadian prairie provinces, although I found only Type 2 birds at Churchill, Manitoba in summer.

The structure of these modulated calls in the prairie provinces was similar but not identical to that of birds breeding or wintering at Banff National Park. The origin of these birds may have been somewhere in central or northern British Columbia, but probably not in the taiga, because I never encountered modulating birds summering there.

The remaining calls of grosbeaks vary less than the location call. My sample of female begging calls is too small to suggest any pattern of variation.

Variation in contact notes and alarm calls. Over most of the range of this species, I could detect no variation in contact notes. Each note is a short, pure tone of between 2 and 6 ms duration (average 3.4, n = 73, 30 individuals) at about 2.3 kHz (Fig. 5). Duration and pitch vary within individuals as much as among populations. Unexpected was the observation that grosbeaks of greatly differing body size have contact notes of equal pitch. Thus, contact notes of a 50-gram Newfoundland bird and those of a 70-gram Manitoba bird are indistinguishable.

California birds differ from all others recorded in having contact notes of two distinct frequencies; the lower is usually just below 2.5 kHz and the upper just above 2.5 kHz (Fig. 5). While contact notes of *P. e. californica* usually have two elements, individuals also appear to be capable of giving notes of just one frequency. The significance of this kind of variation is unknown. Contact notes in this population are also notable in that the two elements appear to vary somewhat independently. I have recorded contact notes in which the pitch of the upper element is higher, and that of the lower is lower in some utterances than in others. Such variation occurs frequently in any series of notes taken from an individual. Thus, it is likely that the birds can alter the tension of the two syringeal membranes independently. Variations in the contact notes of California birds may have communicative significance, but I have yet to detect it.

The California population aside, alarm calls show no consistent geographic variation in pitch (Fig. 5, rows 5–6). The duration and pitch of utterances vary even in individuals within the span of a few seconds. I have detected no significant differences in average duration between populations (average 1.9 kHz, n = 57, 23 individuals). Alarm calls of California birds differ from those of other populations in that they often descend in pitch. Figure 5, row 6 shows a series of utterances from one bird in which the last five are slurred downward. In alarm calls of other populations, pitch is essentially constant, or slightly down-slurred.

Variation in and the study of ontogeny in juvenile calls. I have preliminary evidence that juvenile postfledging (i.e. begging) calls vary geographically. The calls of 15 captives reared by their own New Hampshire parents averaged 0.5 kHz higher in pitch than those of two captive Rocky Mountain fledglings reared by their own parents. The New Hampshire birds also made long (average 0.25 s) calls descending in pitch, and the Colorado birds made shorter (average 0.05 s) piping calls of constant pitch. Within one week, the two Rocky Mountain birds acquired a two-note call, apparently by adding a slightly higher-pitched note to the original one. In all these captive juveniles, no additional changes in call structure occurred until after independence, but by 12 weeks they could make good copies of the calls of their parents. Further study will be necessary to show that this apparent difference in begging calls of birds from New Hampshire and Colorado is real, in view of the small sample of birds from the latter region.

In light of the great geographic variation in the location call, I performed cross-fostering experiments using freshly-laid eggs in order to determine whether the typical structure of a location call could be learned. In 1976, a juvenile of New Hampshire parents, hatched and reared by a California pair with modulated calls, and out of hearing of any other Pine Grosbeaks, made typical begging calls for four weeks after fledging. Between 8 and 15 weeks, however, its calls gradually came to match those of its foster parents. The begging call of New Hampshire birds greatly resembles the adult location call (see Fig. 6). In 1978, five more birds of New Hampshire parentage, hatched and reared by Colorado adults, showed the same ability to learn the more complex foster-parent calls. Sonograms in Figure 6 show calls of four of these juveniles at three ages, along with calls of their genetic and foster parents. Attempts to perform the alternate experiment, with Colorado juve-

TABLE 1. Results of location call playback.

Call type played	No. of birds showing positive response to playback at:			
	Grand Mesa	Red's Meadow	Banff	Churchill
Grand Mesa, CO	10	0	No test	0
Red's Meadow, CA	0	7	No test	0
Banff Natl. Park, Alberta	No test	No test	7	No test
Churchill, Manitoba	0	0	0	6

niles fostered by New Hampshire birds, have thus far failed.

My experiments show that location calls of independent juveniles gradually change until they are identical to those of adults. In the Rocky Mountain calls, at least, there is a period of about three months after fledging during which juveniles have calls of variable structure. That these sounds are incipient location calls is suggested by the observation—in both captive and wild birds—that when adults begin to call, the juveniles begin calling also.

Learning is thus crucial to normal development of location calls, but Pine Grosbeaks differ from the other cardueline finches studied by Mundinger (1970, 1979) in that their call structure does not change during prolonged contact with conspecifics (Adkisson, unpubl. data). During a two-year period (1972 to 1974) I kept New Hampshire and Colorado birds (four of each) in adjacent small cages, and two each of California, Colorado, and Queen Charlotte Islands birds in the same aviary. All of these birds showed no change in their calls, except for one New Hampshire male who was captured and exposed to foreign calls when he was about six months old. He learned to make typical Colorado calls after about five months, and continued to give calls of both types until his death two years later.

Playback experimentation in the field. Having observed a large number of wild grosbeaks approach the source of playback of location calls, I felt that the playback technique would be useful for assaying responsiveness to familiar and foreign call types. I predicted that grosbeaks would respond only to those location calls sounding like their own.

During July 1971 I conducted playback experiments with wild birds at: Churchill, Manitoba; Banff National Park, Alberta; Red's Meadow, Madera County, California; Grand Mesa, Delta County, Colorado. Only single birds were tested, because the presence of other individuals might hinder the interpretation of responses. Each test began with the subject from 50 to 100 m away from the playback source, such that its response could be observed easily. The majority of individuals tested were feeding in spruce or fir trees at the beginning of playback; the rest were preening.

The playback regime was as follows: five examples of a selected foreign location call, each separated by a 5-s interval; this series was followed by a 10-s pause, then five calls similar or identical to those of the local birds. The response of a bird was scored as positive if it approached to within 5 m of the playback source, a Uher 4000-L tape recorder. Positively responding birds typically gave location calls before and during approach.

The results of these experiments (Table 1) showed that birds with modulated location calls responded only to tapes of modulated location calls, and those with whistled calls responded only to tapes of whistled calls. At all localities some individuals responded positively to playback of their own type of location call as many as three or four times within 30 min, drifting away during playback of foreign calls (these occurrences are not included in Table 1).

The results of playback experiments at Banff and Churchill are most interesting, since grosbeaks are usually abundant in winter where the mountains meet the plains (Arbib 1972), and individuals with modulated calls may regularly encounter those with whistled calls, as happened in January 1972. In 1974 and 1976, in late December, I trapped birds in New Hampshire, often using locally-taped calls to attract small flocks to the vicinity of a live decoy. On many occasions I also tested passing flocks or individuals with playback of modulated calls, and never had a positive response.

DISCUSSION

Variation in Pine Grosbeak calls is chiefly in the location calls, which are probably homologous to the flight calls of various smaller cardueline finches (Paul Mundinger, pers. comm.). With the exception of contact notes and alarm calls, which in California birds differ from those of other populations,

I know of no other call variation in North American grosbeaks. Small samples of songs from most localities limit discussion of variation in songs, but there is surely considerable variation over the continent (Adkisson, unpubl. data). The calls recorded at all taiga localities resemble each other much more than any call recorded in the Queen Charlotte Islands or in the mountains from central British Columbia south to Arizona and California.

Certain unresolved questions about grosbeak call variation limit the application of the terms "whistled" and "modulated" in this case. For example, virtually all individuals, wherever recorded, make location calls that are somewhat modulated. In populations where the most frequent sounds are a nearly pure, unmodulated tone to my ear, individuals are also capable of uttering a second, more complex call in which certain elements are highly modulated. My application of the terms, then, is arbitrary, and could lead to oversimplification of a very complex geographic variation system. Of course, I do not know that grosbeaks hear these sounds in the same way as people. A bird might not classify all North American location calls as I have done. Nevertheless, my limited experimentation in the field shows a clear pattern of responses by wild birds both in winter and summer to playback (Table 1), which is consistent with these interpretations. At the least, in some of the "populations" most likely to come into contact in nature, individuals could treat others with foreign calls as non-conspecifics.

Furthermore, it is not known where call variation boundaries occur. The only evidence for the existence of such boundaries lies in the recordings of wintering birds. Most of these calls fall within the variation known for the breeding localities, and all whistling birds recorded in winter made only calls characteristic of a known breeding locality.

At all breeding localities I recorded at least six birds, and at most localities, more than 10. I have presented as many location calls as possible from each locality in order to show that 1) relatively little variation exists at a recording site in the "primary" or most frequent calls, and 2) there is always at least one additional call, used in similar situations. At a few localities I recorded enough of these less common calls to suggest that they also tend to be characteristic of a given area.

In attempting to understand this call variation, note that call note variation and morphological variation are associated. Comparison of these two kinds of variation may reveal the overall pattern of evolution in North American grosbeaks.

The major trends in morphological variation (condensed from Adkisson 1977) are as follows: over the apparently continuous range of the species in the taiga there is gradual clinal change. Grosbeaks in the Maritime Provinces have small bodies compared with most North American populations. Body size gradually increases northward in the Labrador Peninsula and also northwestward, reaching a maximum near Great Slave Lake. Farther west, body size decreases slightly. Beginning at the southern end of James Bay, to the northwest across the taiga, bills become shorter, the shortest-billed birds occurring in western Alaska. In the Rocky Mountain region the trends are for both smaller body size and shorter bills toward the north. Wing length and altitude of the specimen locality are highly positively correlated, in association with the occurrence of spruce-fir forests at successively lower elevations to the north. I found no geographic variation within each of the three isolated western forms: in California, the Queen Charlotte Islands, and coastal Alaska. These birds are also morphologically distinct from all other populations. In California and the Queen Charlotte Islands, body size is small, extremely so in the Queen Charlottes, and California birds have very thin, narrow bills. Coastal Alaskan birds are intermediate in body size, and have the longest bills among North American grosbeaks. I have interpreted the morphological distinctiveness of California and Queen Charlotte birds as indicating a long period of isolation from other populations of the species in possibly unique ecological circumstances.

The smallest taiga birds, breeding in the Maritime region, apparently have the whistled calls of simplest structure (Type 1), as shown by birds recorded in spring in Newfoundland and many others recorded in New England, Michigan, and Ontario in winter (compare calls shown in Fig. 2, row 3 with those in Fig. 5, row 1). Some specimens of intermediate size, which were captured or collected after recording in Michigan, made Type 2 calls spectrographically identical to those recorded at Churchill, Manitoba (compare calls shown in Fig. 2, row 4 with those in Fig. 5, row 1). Their size alone suggests that these birds could have come from north of 52°N in the Labrador

Peninsula or west of James Bay in Ontario (Adkisson 1977). Unusually large birds are reported to occur in winter in New England and New York (Sutton 1948), but their call structure is unknown. Breeding birds with Types 2 and 3 calls were recorded west of James Bay in the taiga, where body size is greatest. A large male I captured in northern Michigan made only Type 3 whistled calls and a more complex variant (as in Fig. 3 rows 1 and 2) during his three years in captivity.

Thus, I predict that adult males found in the taiga, with whistled calls, should show the following size-to-call-type associations: small birds (wing 105–112 mm), Type 1 calls; intermediate to large birds (wing 112–118 mm), Type 2 calls; large birds (wing 116–125 mm), Type 3 calls or possibly Type 2 calls (immature males and females with the above call types should be about 10% smaller than adult males; Adkisson 1977).

Coastal Alaska birds are easily distinguishable from the taiga birds using bill length; the relatively few birds I recorded in the Kenai Peninsula and at Haines gave whistled calls (designated Type 4) consistently separable, by ear or by sonogram, from western taiga birds (Fig. 3, rows 5 and 6). I have not encountered birds with calls like these elsewhere (but all birds recorded for me at Sitka, Alaska, by William L. Foster in the winter of 1976–77 made only modulated calls unlike any I have seen before (not figured).

The three populations in which only highly modulated calls are found are restricted to areas south and/or west of the taiga and coastal Alaska. They show considerable morphological variation among them, in body size as well as in proportions.

The Pine Grosbeaks occurring in the Cassiar Mountains of northern British Columbia are of uncertain systematic affinities. Specimens collected in the early 1960's indicate that this population is merely part of the Rocky Mountains cline, different in wing and bill measurements from birds of the closest taiga and wet, coastal regions (Adkisson 1977). Yet all eight birds I recorded there in mid-June 1973 had whistled calls very similar to those of Fairbanks birds (Fig. 3). This population may prove to be a morphologically distinct, whistling subspecies (perhaps an invasion from the taiga which has evolved a smaller body size since that time), though other interpretations are possible. In view of this possibility and the complex systematics of other species or superspecies of birds in this region (Remington 1968, Hubbard 1969) further field work is needed.

Since each of the major categories of location call shows morphological variation ranging from among the smallest to among the largest bodies found in this species, it is tempting to speculate on the evolution of this system. The pattern of variation suggests two alternative scenarios: 1) that highly modulated, whistled calls have persisted through considerable morphological change, or 2) that the major variations in location call have evolved independently of each other.

Cross-fostering studies have led me to reject the hypothesis that call structure is genetically based (see Fig. 6). I have found some minor differences in early fledgling calls between birds from Colorado and New Hampshire, and these differences may be genetic. But, given the learning abilities of juvenile grosbeaks, and the uncertain ontogenetic relationship between these fledgling food-begging calls and the adult location calls, one conservative interpretation is suggested: call variation in North American grosbeaks could have arisen in a manner similar to evolution of song dialects, through mistakes in learning through time, especially together with isolation of small (possibly "founder") populations (Lemon 1975). Thus, one need not invoke natural selection as leading to genetic change to account for location call variation.

Glaciation might have played a role in isolation of populations in the past, as in Mengel's accounts (1964, 1970) of the effects of Pleistocene glaciations upon speciation in several groups of birds, especially wood warblers (Parulidae). According to this scheme, there were at least two refugia of spruce forest during Wisconsin time, in the Southeast (Appalachian Mountains) and the Southwest (Great Basin, southern Rocky Mountains), with a third probably in an unglaciated part of Alaska (Flint 1971). Certainly the entire ranges of *P. e. flammula, carlottae,* and most of the ranges of *P. e. montana* and *leucura* were under ice.

It is likely that Pine Grosbeaks persisted at least in the southeastern and southwestern refugia until about 10,000 years ago, then accompanied their forests northward. Guilday et al. (1977) have found remains of this and other taiga species in Pleistocene deposits in Virginia. Mengel (1970) suggested that at the close of Wisconsin time, the eastern avifauna quickly re-occupied the northwestern taiga via a well-known forest corridor in the Mackenzie River valley

(see also Flint 1971). At this time the birds of the Southwest may have been "bottled up" by the vast Columbian glaciers. Some birds with eastern affinities (e.g., Yellow-shafted Flicker, *Colaptes auratus borealis*; Yellow-rumped Warbler, *Dendroica coronata hooveri*) breed in Alaska (the warbler reaches the coast) while western counterparts (Red-shafted Flicker, *C. a. cafer*; Audubon's Warbler, *D. coronata auduboni*) are found farther south in B.C. (the flicker also reaches coastal Alaska) (A.O.U. 1957).

Variation in calls suggests a similar distributional history for Pine Grosbeaks. If the location call was conservative through time, it is possible that the western isolates with only modulated calls are derived from one or more refugium populations, and the whistling populations from southeastern stock. Thus modern *flammula* of the coastal rain forests, with whistled calls, may be descended from taiga birds that arrived in the region ahead of the southwestern "modulators." The Queen Charlotte Islands, however, were colonized by "modulators."

Isolation surely played a role in vocal divergence, but was there selection for divergence as well? Recent studies have implicated vegetative structure in the evolution of vocalizations (Emlen 1972, Morton 1975, and Bowman 1979). It is also possible that some grosbeak habitats of the past, such as dense forest, favored modulated calls with a greater range of frequencies, while whistles were favored in the open habitats of tree line-dwelling taiga birds. But it is unlikely that one or the other of the call types has been selected for in association with the forest habitat, since neighboring populations in the Pacific Northwest (*carlottae* and *flammula*) inhabit similar forests and have very different calls.

In terms of the present distribution of grosbeaks, also interesting is the possible significance of winter encounters of birds with different location calls (see "Location calls recorded in winter," above).

The location call is the signal that attracts grosbeaks to each other. I have shown that these birds respond selectively to calls somewhat like their own in the breeding season, and that they are strongly attracted to playback of their own call type in winter. On the Great Plains, grosbeaks with different calls surely meet in some winters, as they did in January 1972. Under these conditions a bird originating near Great Bear Lake in the taiga might become incorporated into a flock of birds from the mountains for breeding. My observations of assortative flocking in Alberta suggest, however, that such mixing may be uncommon.

Grosbeaks from the northern Rocky Mountains and those of the taiga are rather similar in every measurable respect except the location call; I have no evidence of selection for the avoidance of birds with different location calls. However, by flocking with birds most like itself, an individual can make best use of the entire system of communication signals by which flocks avoid diurnal predation, find food, go to roost in the most secure places, and finally return together to the breeding grounds. That singing occurs in February and March (Grinnell 1900, and pers. observ.) suggests that pairing may begin on the wintering ground. If so, mates are likely to be chosen from within the flock. Reproductive success of a pair should be maximized if its members use similar signals and are both adapted for breeding in the same environment (Nottebohm 1975).

A definitive statement on the evolutionary significance of geographic variation in grosbeak vocalizations must await further study of the location call types and behavior in winter. Nevertheless, I speculate that "hybrid" pairs are less likely to form in late winter and subsequently reproduce than if location calls of taiga and montane birds were identical.

That I have failed thus far to find whistling birds with calls intermediate between Types 1, 2, and 3, even in winter when grosbeaks often wander widely, suggests that there are three distinct populations in the taiga. These are the birds most likely to undergo irruptive migrations, so that if each location call type proves to be specific to a region then we have an unparalleled opportunity to map the continent-wide movements of a species of bird. With better sampling of breeding season ranges, it may be possible to identify both "modulators" and "whistlers" and map their origins by matching their calls with those recorded on the breeding grounds.

SUMMARY

Pine Grosbeaks vary geographically in certain vocalizations. Alarm calls and contact notes are everywhere similar, except for distinctive variations found in California birds. Location calls show the most variation, with three distinctive local variations of whistled calls in the taiga birds, and similar calls in the birds of coastal Alaska and the Cassiar Mountains of B.C. Birds of the Queen Charlotte Islands, Rocky Mountains, and Cali-

fornia have highly modulated calls. Body size per se is not strictly related to variations in calls, but within the taiga, small birds have one type of call, birds of intermediate size have a second type, and the largest birds have a third. Among the western populations with modulated calls, body size also varies from small to large.

Regional differences in vegetation are discounted as a cause of the divergence of calls, since a population of "modulators" and one of "whistlers" are found in similar wet, coastal spruce forests. This pattern of dialectal variation may result ultimately from the interactions of imperfect call learning and isolation of breeding populations through time.

Playback experiments using location calls and brief observations of flocking winter birds suggest that wintering birds of different call types tend not to intermingle.

The patterns of call variation and morphological variation could be used to map seasonal movements of this species in North America.

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