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BICKNELL'S THRUSH: TAXONOMIC STATUS AND DISTRIBUTION

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ABSTRACT.—The southeastern population of the Gray-cheeked Thrush (*Catharus minimus*), found in southern Quebec, the Maritime Provinces, and in the higher areas of parts of the New England States, has been considered to be a subspecies (*C. m. bicknelli*) since its description in 1882. Recent information and analyses show that Bicknell's Thrush is different from the Gray-cheeked Thrush as follows (1) it has well marked morphological differences when compared to adjacent populations of the Gray-cheeked Thrush, particularly in size and coloration, (2) its breeding and wintering ranges do not overlap with the ranges of the other populations of *C. minimus,* (3) it has a different song from that of *C. minimus,* (4) it does not respond to playbacks of songs of *C. m. minimus* or *C. m. aliciae* songs presented during the breeding season in its territories, (5) it uses different habitats, particularly mixed second-growth stands in coastal and higher parts of southern Quebec and in the Maritime Provinces, (6) there is no known intergradation or hybridization between it and Gray-cheeked Thrush populations, like *C. m. minimus* and *C. m. aliciae,* and (7) it has a high level of sequence divergence in the number of its fixed fragment patterns as revealed by biochemical analyses. It is considered to be a relict taxon from a past refugium, probably located in the Sable Island area and adjacent banks. It may have diverged from an ancestral population shortly after the beginning of the Pleistocene. This hypothesis is supported by the biochemical information as well as the glacial and ecological evolution theories of northeastern North America. It is recommended that (1) the *bicknelli* population be treated as a full species, *Catharus bicknelli* (Ridgway), [1882. Proc. U.S. Nat. Mus., 4:377, *Hylocichla aliciae bicknelli*], with Bicknell's Thrush as its English name, and "Grive de Bicknell" as its French name, and (2) the other populations of the Gray-cheeked Thrush retain their current status within *Catharus minimus* (Lafresnaye) [1848, Rev. Zool., 11 (1):5, *Turdus minimus*]. *Received 20 Aug. 1992, accepted 8 Dec. 1992.*

The Gray-cheeked Thrush (*Catharus minimus*), a thrush of the boreal forest region, occurs in suitable habitats throughout its breeding range from Newfoundland to Alaska, with extensions in the northern New England states and in northeastern Siberia (A.O.U. 1983, Allen 1909,

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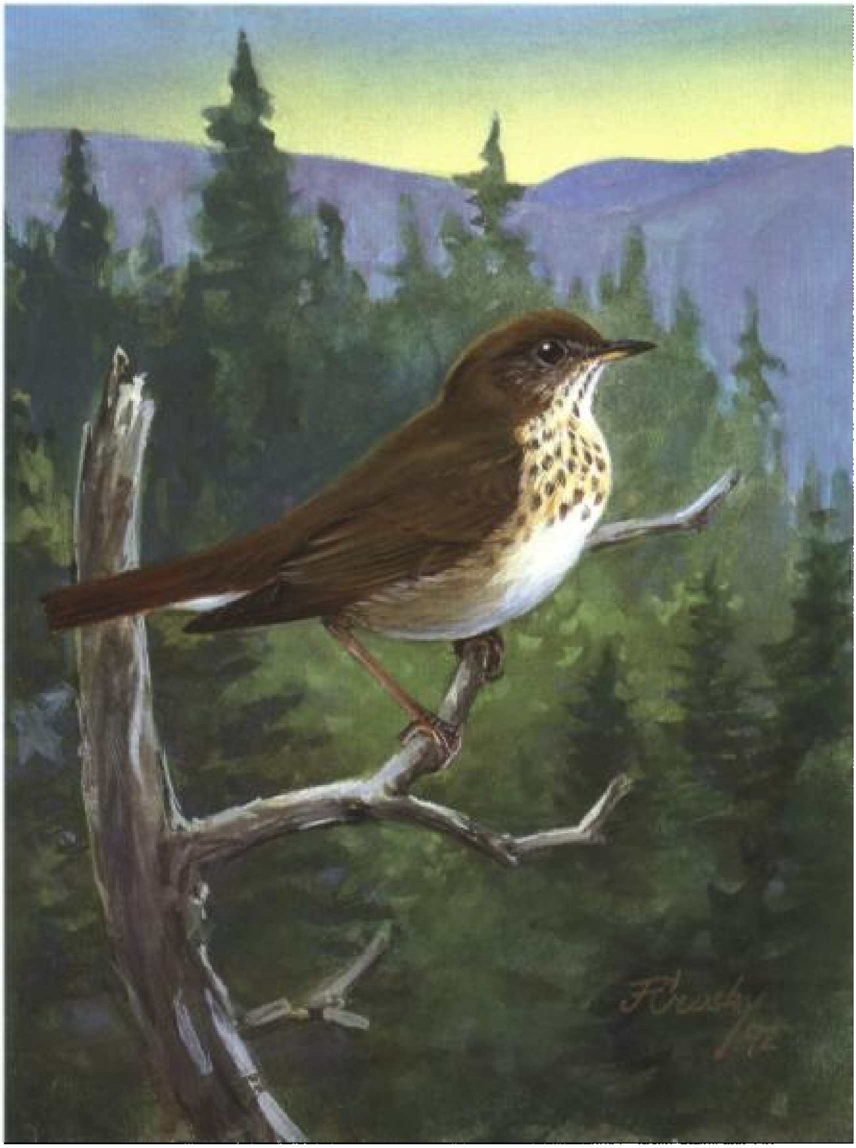

Bicknell's Thrush, *Catharus bicknelli,* in its breeding habitat in southern Quebec, a second growth coniferous stand. Original acrylic painting by John F. Crosby.

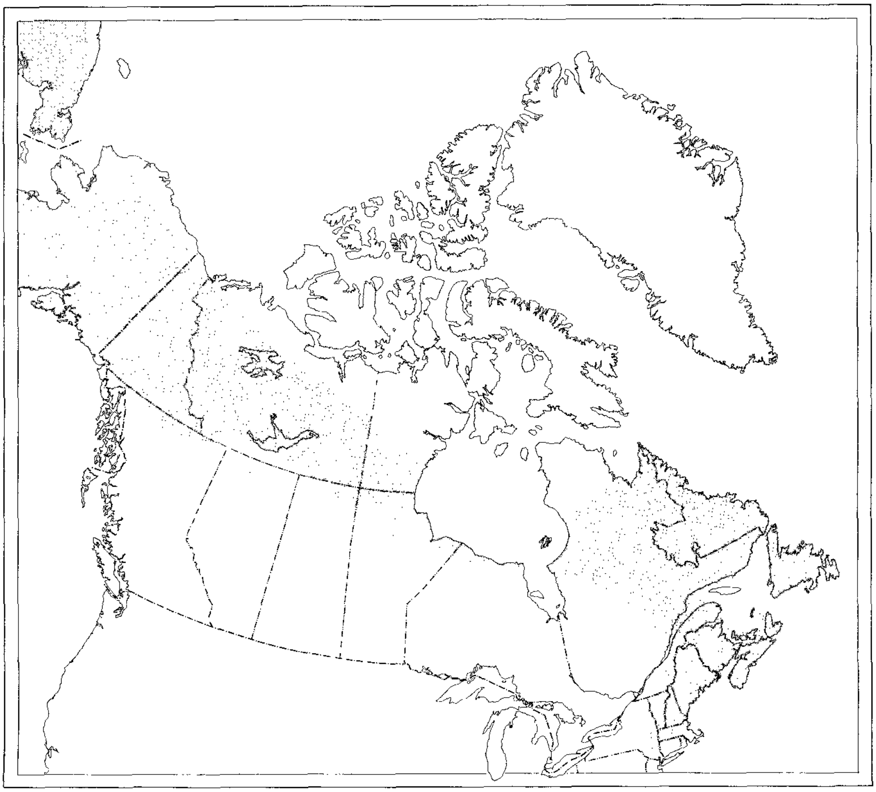

FIG. 1. Breeding distribution of the Gray-cheeked Thrush (*Catharus minimus*) based on several sources (Vaurie 1959, A.O.U. 1983, Godfrey 1986, Stepanyan 1990).

Stepanyan 1990, Vaurie 1959, Godfrey 1986; Fig. 1). Geographic variation has been known for a long time (Baird 1858, Bicknell 1882, Ridgway 1882) and has led to the recognition of three subspecies (Wallace 1939, A.O.U. 1957). One of these, Bicknell's Thrush (*Catharus minimus bicknelli*), was described on the basis of morphological differences found in specimens collected at the higher altitudes of mountainous areas in New England (Ridgway 1882). In a classic work, Wallace (1939) studied the distribution, life history, and taxonomy of this subspecies and that of the other subspecies of *Catharus minimus*. He proposed that the birds from the island of Newfoundland are different from those of the adjacent mainland and belong to the nominate subspecies. He resolved the nomenclatural problems related to the original description of the Gray-cheeked Thrush as *Turdus minimus* by Lafresnaye (1848), based on a specimen taken at Bogotá, Colombia. Finally, he dispelled the confusion resulting from subsequent nomenclatural proposals and changes (Sclater 1854; Baird 1864; Bangs and Penard 1919; Wetmore and Swales 1931; A.O.U. 1886, 1895, 1910, 1931).

Since 1957 (A.O.U. 1957), Bicknell's Thrush has been accepted generally as a subspecies of the Gray-cheeked Thrush, essentially as proposed in the original description (Ridgway 1882, 1907) and subsequent evaluation of the taxon (Wallace 1939), notwithstanding the earlier nomenclatural changes and recommendations. The song of Bicknell's Thrush was alleged to be unlike that of other Gray-cheeked Thrush populations (Gillet 1935), and variations in song were confirmed later by Wallace (1939) but ignored by Stein (1956). In the meantime, little importance was given to song differences because recordings have been difficult to acquire, preventing objective song comparisons among populations.

The winter distribution of Bicknell's Thrush remained poorly known, and much confusion persisted about the wintering ranges of subspecies until Wallace (1939) cleared the confusion related to the identification and origin of the type. However, incomplete and inaccurate information persisted in the literature, even in the fifth edition of the A.O.U. Check-list (A.O.U. 1957). The winter range of Bicknell's Thrush is still undefined for the most part and may be situated in areas subjected to environmental pressures as reported for many other species (Askins 1992, Terborgh 1989).

Todd (1963) speculated about intergradation between *C. m. bicknelli* and the northeastern population, *C. m. aliciae,* found on the north shore of the Gulf of St. Lawrence, east of Natashquan, Quebec, and in southern Labrador. Variation in the dorsal coloration of *bicknelli* was recognized by both Wallace (1939) and Todd (1963), the latter suggesting that the birds of the northern part of the range (e.g., Quebec, Labrador, and Maritime Provinces) were sufficiently different from those of New England to warrant subspecific recognition but he recognized a northern continental population which he designated as *C. m. aliciae* and restricted the nominate form, *C. m. minimus,* to the island of Newfoundland (Todd 1963). Godfrey (1986) followed that treatment.

Personal field observations, examination of specimens, and comparison of song recordings from various parts of the range of the Gray-cheeked Thrush, in eastern Canada and the United States, revealed differences among birds of southern Quebec (*C. m. bicknelli*) and birds from Newfoundland and northern Quebec (*C. m. aliciae* and *C. m. minimus*) (A.O.U. 1957, Godfrey 1986, Todd 1963), which led me to undertake a more detailed study of the eastern populations. Concurrently, I completed detailed examinations of specimens in collections and a survey of the literature since Wallace's publication (1939). Except for a discussion by

Todd (1963) of the subspecific status of the eastern populations, papers on the taxonomy and behavior of the genus *Catharus* and *Hylocichla* (Dilger 1956a, b, c), and information on the ecological relationships of the Gray-cheeked Thrush with other species occupying similar habitats (Sabo 1980, Sabo and Holmes 1983), little had been added to what Wallace (1939) had reported earlier.

MATERIALS AND METHODS

Specimens.—Specimens from breeding populations were adults of known sex in fresh or relatively fresh definitive (nuptial) plumage; badly worn or discolored specimens were not used. For migratory and wintering populations, specimens of both sexes, regardless of age or plumage condition were retained for obtaining measurements or coloration data for comparison purposes, but heavily worn or discolored individuals were rejected.

List of localities.—Locality data were obtained from specimen labels and adjusted to contemporary designations given in official atlases, gazetteers, or on maps for specimens of Canadian origin; in the other cases they correspond to the designations of road maps or international or regional atlases and gazetteers (Paynter 1982; Paynter and Traylor 1977, 1981).

At least one breeding specimen was studied from: Labrador: Assizes Harbour, Cape Charles, Groswater Bay, L'Anse-au-Clair, Makkovik, Manak Island, and south of Schefferville. Massachusetts: Granville, Mount Greylock. New Brunswick: Rivière-Verte, Popple Depot. Newfoundland: Bay of Exploits, Blow Me Down, Brigus, Connoire Bay, Corner Brook, Custlett, Deer Pond, Eddies Cove, Englee, Flat Island (St. John Bay), Fogo Island, Garnish, Glenwood, Grand Lake, Grandy Brook (45 km N Burgeo), La Scie, Lewisporte, Nicholsville, Otter Cove (Canada Bay), Pistolet Bay, Placentia, Port Saunders, Quirpon, South Brook, St. Anthony, St. George's Bay, Table Mountain. New Hampshire: Carter's Dome, Carter's Notch, Mount Madison, Mount Moosilauke, Mount Washington. New York: Big Indian Valley, Slide Mountain, Whiteface Mountain. Nova Scotia: Seal Island. Québec: Caniapiscau, Godbout (20 km north), Grand Portage (Sainte-Marguerite River), Grosse Île (Îles-de-la-Madeleine), Kuujjuaq (Fort Chimo), Lac à Pierre, Lac Élysée (Charlevoix), Lac de la Frontière (north of Schefferville), Lac Brisay, Lac Vincelotte, Lac Chaumont, Lac Stewart (near Kuujjuak), Mont Mégantic, Mont de la Table, Mont Sir-Wilfrid, Mont Jacques-Cartier, Mont-Saint-Pierre, Percé, Pointe de Natashquan, Portage-Saint-Hélier, Poste-de-la-Baleine, Rivière du Petit Mécatina, Rivière Korok, Saint-Urbain (43 km northwest), Schefferville. Saint-Pierre and Miquelon: Little Miquelon Island. Vermont: Mount Killington (Sherburne), Mount Mansfield.

Migrating or wintering specimens from Canada (Ontario, Quebec, the Maritime Provinces, Manitoba, Saskatchewan) and the United States (Illinois, Iowa, Maryland, Massachusetts, Minnesota, Montana, Nebraska, New Jersey, New York, North Dakota, South Carolina, Virginia, Wisconsin), Belize, Bermuda, Colombia, Costa Rica, Dominican Republic, Ecuador, Guatemala, Guyana, Honduras, Panama, Swan Islands (U.S.A.), and Venezuela have been examined.

Plumage coloration.—Color classes were determined on the basis of the dominant coloration of the specimens. These were grouped by sex and assigned to one of the color classes that I have recognized for various regions of the body: (1) Four dorsal coloration categories—olive, olive gray, olive brown, and brown. (2) Three tail color classes—chestnut, olive brown, and olive. (3) Four throat color classes—very light buff, light buff, medium buff, and deep buff. (4) Three ventral coloration classes—white, whitish, and buffy white.

Body measurements.—Standard measurements were taken using electronic dial calipers, and the terminology used in this work appears in square brackets when different from the longer and more exact terminology: chord of unflattened wing [wing], tail length [tail], exposed culmen [culmen], bill length from a nostril to tip [bill-nostril], tarsus length [tarsus], mass, and total length [length]. All measurements are in millimeters and are recorded to the nearest 0.1 mm, except for the mass which is in grams and is recorded to the nearest 0.1 g, and the total length in centimeters, to the nearest 0.1 cm.

Statistical treatment.—Analysis of variance (ANOVA) and multiple comparison tests based on Tukey's Honestly Significant Difference procedure (Tukey-HSD Procedure) were used for all mensural characters and were conducted with SPSS-PC. Coloration data were analyzed using a G-test (Sokal and Rohlf 1981).

Vocalizations.—My recordings were made using a Nagra 4.2 tape recorder with a Sennheiser MKH 815T shotgun microphone at a speed of 19.05 cm/sec or a Panasonic SV-250 Digital Audio Tape recorder with a Beyerdynamic MC 737 shotgun microphone. Other recordings were provided by J. T. Marshall, who used a Sony TCD-5M stereo cassette recorder and a Sony Walkman Professional stereo cassette recorder with two Sennheiser ME 80 directional microphones inserted 30 cm apart. Additional recordings from New England, Quebec, Manitoba, and Alaska were provided by Cornell University Library of Natural Sounds (recordings by P. P. Kellogg and W. W. H. Gunn). Sounds, songs and calls, were analyzed and measured on a Multigon Uniscan II sonograph. Song playbacks were presented on a Sony TC-110 cassette recorder. In 1989, a three minute recording of full songs of *Catharus minimus aliciae* from northern Quebec, *C. m. minimus* from Newfoundland (courtesy of J. T. Marshall), and *bicknelli* from southern Quebec was used, whereas a two minute tape with only songs of *bicknelli* was used in 1990.

RESULTS

Color variation in breeding individuals.—Body coloration of breeding individuals from eastern Canada and United States varies to a great extent, particularly in the dorsal and ventral regions, tail and throat. No intersexual difference was found, but the differences between the dorsal coloration classes and the geographic origin of the specimens are significant for males as well as females (♂: $G = 50.27$, $P < 0.05$, df = 6, N = 106; ♀: $G = 21.52$, $P < 0.05$, df = 6, N = 43; Fig. 2), specimens of the *bicknelli* group being more frequently 'olive brown' dorsally. 'Olive' is dominant in the *minimus* groups, whereas 'olive gray' has not been found in the breeding series of *bicknelli.*

Three classes have been recognized in the coloration of the tail (chestnut, olive brown, and olive), and no intersexual difference has been found in this character. The data for both sexes have been combined and show a significant difference in the three classes on the basis of the geographic origin of the specimens. Specimens of *bicknelli* have almost consistently a 'chestnut' tail, whereas the tail is 'olive' or 'olive brown' in the *minimus* and *aliciae* samples (♂: $G = 366.34$, $P < 0.05$, df = 4, N = 118; Fig. 3).

A noteworthy variation has been observed in the coloration of the under parts based on color classes established for the throat region, including

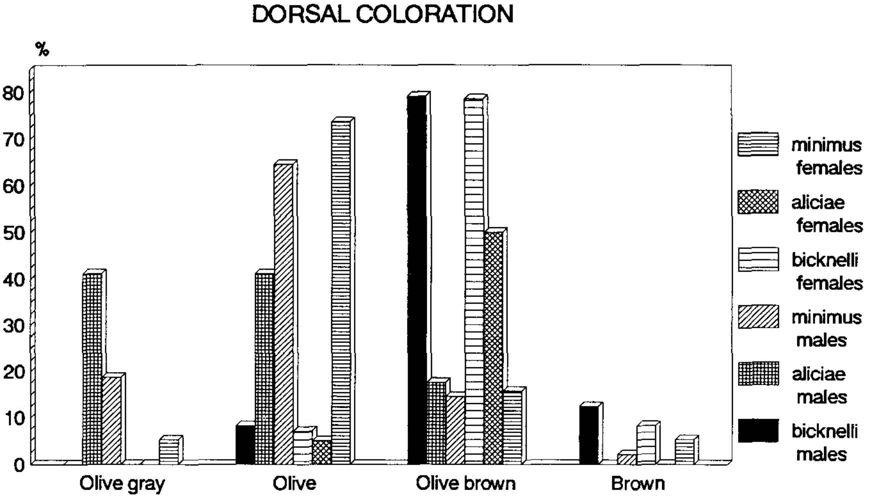

FIG. 2. Color classes of dorsal coloration, by sex, in eastern populations of *Catharus minimus*.

the upper abdomen, and the ventral region, from the upper abdomen to the under tail coverts. Differences in throat coloration among the males of the three samples proved to be significant and indicate that males of *bicknelli* have more buffy throats than those of the other two groups (*G*

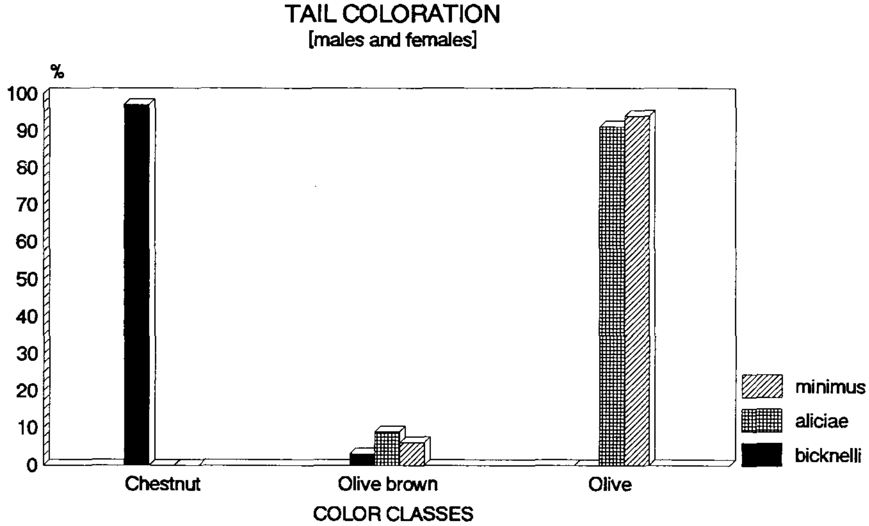

FIG. 3. Color classes of tail coloration, males and females, in eastern populations of *Catharus minimus*.

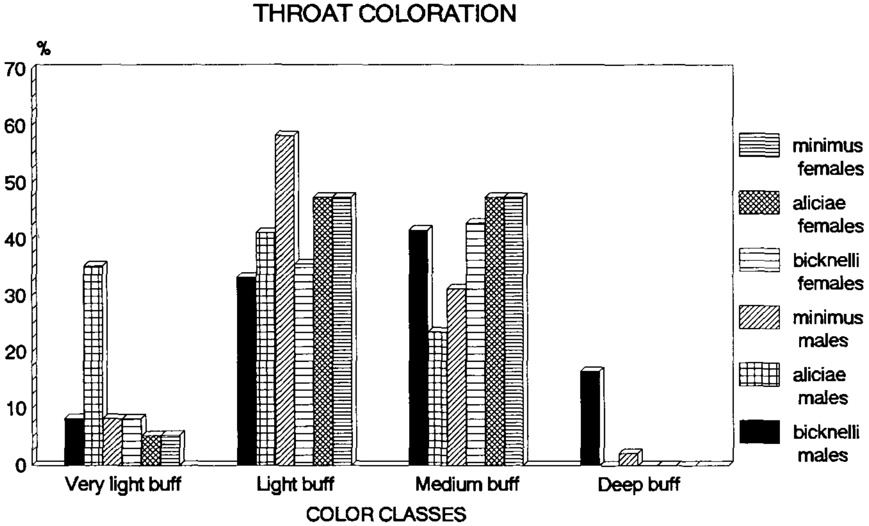

FIG. 4. Color classes of throat coloration, by sex, in eastern populations of *Catharus minimus*.

= 15.92, $P < 0.05$, df = 4, N = 89; Fig. 4). The situation is different in females, and no significant difference was found among samples (G = 8.13, $P > 0.05$, df = 4, N = 41; Fig. 4).

Significant intersexual and inter-sample differences were found in the coloration of the ventral regions (♂: G = 14.15, $P < 0.05$, df = 4, N = 87; ♀: G = 10.43, $P < 0.05$, df = 4, N = 41; Fig. 5) and indicate that the white of the under parts of the *bicknelli* sample is duller than that of the other samples, being often tinted with a grayish wash.

The soft parts colors of *bicknelli* are different from those of *minimus* or *aliciae.* The base, or proximal half, of the mandible is 'bright pale yellow' in *bicknelli,* whereas it is 'flesh' or 'yellowish flesh' in the other two populations. The dark distal area is more extensive in *aliciae* and *minimus,* thus reducing substantially the light proximal region in those populations. The maxilla varies from 'blackish brown' to 'black' in all populations. The rictal region is pale, varying from flesh to yellowish flesh in the three populations. In *bicknelli,* the color of the legs varies from 'light purplish flesh' to 'purplish flesh' and the tarsus is often pigmented with a darker brownish wash in a small number of individuals, but the toes are, in all cases, darker than the tarsi. In the other two populations, the legs have a lighter 'flesh' color heavily tinted with a 'brownish black' wash that often conceals the basal coloration, and the toes are always much darker. The soles of the feet vary from 'flesh' to 'dull pale yellow' in *bicknelli* but are of a truer and brighter 'yellow' in the other two

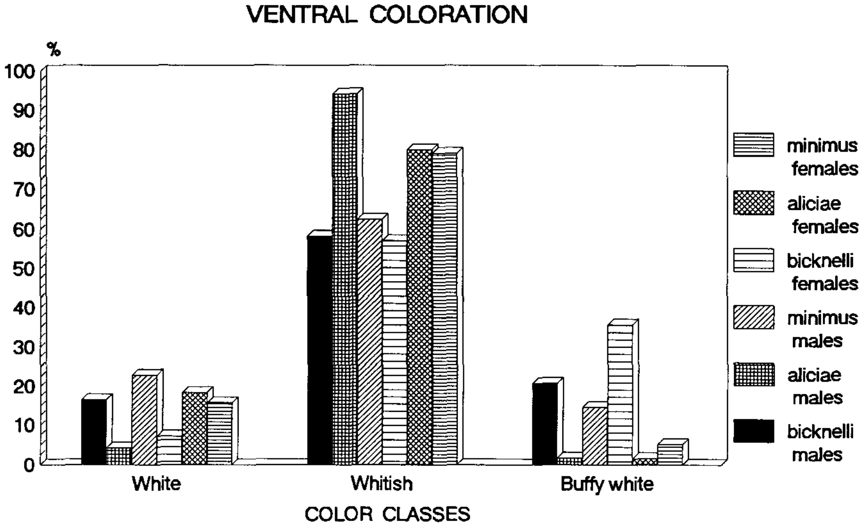

FIG. 5. Color classes of ventral coloration, by sex, in eastern populations of *Catharus minimus*.

populations, particularly in *minimus* from northern Quebec and Labrador.

Morphometrics of breeding individuals.—Body dimensions of breeding birds from eastern Canada and United States are larger in the northern part of the breeding range, as revealed by a series of linear regressions of several body measurements on latitude. Figure 6 illustrates the situation for wing length ($r = 0.52$, $N = 219$, $P < 0.0001$, $Y = 0.72x + 62.18$). The other body dimensions, such as exposed culmen ($r = 0.32$, $N = 210$, $P < 0.0001$, $Y = 0.06x + 10.22$), culmen from nostrils ($r = 0.34$, $N = 206$, $P < 0.0001$, $Y = 0.04x + 7.35$), tarsus ($r = 0.31$, $N = 212$, $P < 0.0001$, $Y = 0.07x + 26.20$), and mass ($r = 0.64$, $N = 82$, $P < 0.0001$, $Y = 0.57x + 2.50$) display the same northward increase in size. All the body dimensions of the *bicknelli* sample also follow this trend, on a smaller scale, and attain largest size in the northern part of their range.

A two-way analysis of variance (ANOVA) performed on body dimensions (chord of wing, tail, exposed culmen, culmen length from nostrils, and tarsus) indicates significant interpopulation and sexual differences among samples, with the exception of the exposed culmen and culmen length from the nostrils, for which no significant intersexual difference was detected (Table 1). Differences among samples are significant for nearly all body dimensions, but intersexual differences, where they occur, are much lower.

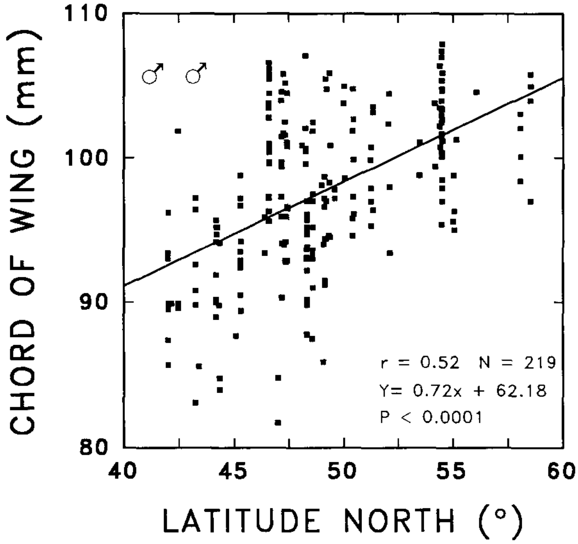

FIG. 6. Regression of wing length on latitude in eastern populations of *Catharus minimus* and "*bicknelli*".

Comparisons based on Tukey-HSD Procedure ($P < 0.05$) show that wing length is significantly different in the males of the three groups (Newfoundland, northern Quebec, *bicknelli*), being shortest in *bicknelli*; in females, it is significantly shorter only in *bicknelli*. Tail and tarsus lengths of both sexes, as well as mass (males only), are significantly smaller in *bicknelli* than in the other two populations. Bill measurements (exposed culmen, nostril-tip) are significantly shorter in males and females of *bicknelli* but no significant difference was found in this character among the other two populations.

Measurements and data pertaining to the three populations of *Catharus minimus* and *bicknelli* reveal that *bicknelli* has the smallest measurements, except for the mass of females which can probably be accounted for by the small size of the sample (Table 2). Specimens from northern Quebec, including northern Labrador, have the largest body dimensions, whereas the Newfoundland population is intermediate in size for most dimensions, although these differences are not always statistically significant between it and the individuals from northern Labrador and northern Quebec.

Vocalizations.—Songs of birds of the *minimus* group are different from those of the *bicknelli* population. Each song type can be identified in the field once it has been learned. To characterize and measure the differences observed in the song of each population, each song was broken down into

TABLE 1

ANALYSIS OF VARIANCE OF MAIN MORPHOMETRIC CHARACTERS OF THREE POPULATIONS OF *CATHARUS MINIMUS* SPECIMENS FROM EASTERN CANADA AND UNITED STATES: *MINIMUS, ALICIAE,* AND *BICKNELLI*

	N	df	*F*	*P*
Wing	230			
Main effects		3	218.563	<0.0005
Sex		1	113.654	<0.0005
Regions		2	300.219	<0.0005
Tail	230			
Main effects		3	50.023	<0.0005
Sex		1	66.627	<0.0005
Regions		2	51.526	<0.0005
Exposed culmen	230			
Main effects		3	14.916	<0.0005
Sex		1	0.182	>0.0005
Regions		2	22.283	<0.0005
Bill from nostril	230			
Main effects		3	20.409	<0.0005
Sex		1	0.025	>0.0005
Regions		2	29.881	<0.0005
Tarsus	229			
Main effects		3	33.550	<0.0005
Sex		1	24.290	<0.0005
Regions		2	43.368	<0.0005

four basic parts: Part I, a series of 3–4 introductory notes ("*chuck-chuck-chuck*"); Part II, an initial phrase with a relatively high frequency; Part III, a middle phrase where the frequency is lower than in the preceding part; and, Part IV, a final phrase, which is the most different part of the two song types.

Part I was not analyzed because it is missing in too many recordings; these introductory notes can be heard and recorded only when the recorder is near the singing bird (±10–12 m). Each part of the song has a unique pattern (Fig. 7) and characteristic values (Table 3).

The mean durations of Parts II and IV are significantly different in the two populations whereas the difference is not significant in Part III, the mean duration being longer only in Part II of *bicknelli* songs. High frequencies are higher in Parts II and IV of *bicknelli*, with a significant difference only in Part IV. The difference between the two taxa is not significant in Part III. Low frequencies are significantly and consistently

TABLE 2

MEASUREMENTS OF THREE SAMPLES OF *CATHARUS MINIMUS* (*MINIMUS*, *ALICIAE*, AND *BICKNELLI*) SPECIMENS FROM VARIOUS PARTS OF EASTERN CANADA AND UNITED STATES. MEASUREMENTS ARE IN MM BUT TOTAL LENGTH IS IN CM AND MASS IN G

Region	N	Mean	SD	SE	Minimum	Maximum	95% conf. interval
Wing							
♂♂							
Newfoundland	59	101.88*	2.9184	0.3799	94.6	107.1	101.1174–102.6385
Northern Quebec	31	103.40*	2.7819	0.4996	94.4	107.9	102.3764–104.4172
"bicknelli"	74	92.92*	2.7327	0.3155	84.8	98.8	92.3130–93.2177
♀♀							
Newfoundland	26	97.58	2.2404	0.4394	93.4	102.5	96.6720–98.4818
Northern Quebec	15	98.97	2.5758	0.6651	95.0	103.4	97.5469–100.3998
"bicknelli"	19	87.78*	3.8744	0.8888	81.7	95.2	85.9116–89.6463
Tail							
♂♂							
Newfoundland	59	72.92	3.0683	0.3995	66.7	79.6	72.1207–73.7199
Northern Quebec	31	73.62	2.5842	0.4641	68.5	80.0	72.6779–74.5737
"bicknelli"	74	68.73*	2.7907	0.3222	62.1	77.6	68.0846–69.3687
♀♀							
Newfoundland	26	69.01	3.1917	0.6259	64.0	75.5	67.7262–70.3045
Northern Quebec	15	69.53	3.0297	0.7823	64.3	75.2	67.8489–71.2045
"bicknelli"	19	65.57*	2.6098	0.5987	61.6	70.6	64.3158–66.8316
Exposed culmen							
♂♂							
Newfoundland	57	13.16	0.6894	0.0913	11.2	14.7	12.9785–13.3443
Northern Quebec	29	13.34	0.5207	0.0967	12.3	14.3	13.1468–13.5429
"bicknelli"	73	12.71*	0.7587	0.0889	10.6	16.7	12.5323–12.8869

TABLE 2
CONTINUED

Region	N	Mean	SD	SE	Minimum	Maximum	95% conf. interval
♀♀							
Newfoundland	25	13.07*	0.8106	0.1621	11.3	14.8	12.7374–13.4066
Northern Quebec	13	13.50*	0.6338	0.1758	12.6	14.5	13.1170–13.8830
"bicknelli"	19	12.56*	0.5177	0.1188	11.8	13.7	12.3136–12.8127
Culmen from nostrils							
♂♂							
Newfoundland	54	9.53	0.5297	0.0721	8.6	10.9	9.3850–9.6742
Northern Quebec	29	9.61	0.3848	0.0715	8.8	10.4	9.4640–9.7567
"bicknelli"	73	9.09*	0.4101	0.0480	8.1	10.2	8.9933–9.1847
♀♀							
Newfoundland	25	9.57	0.4440	0.0888	8.8	10.2	9.3887–9.7553
Northern Quebec	13	9.65	0.4427	0.1228	9.0	10.4	9.3786–9.9137
"bicknelli"	19	9.10*	0.4216	0.0967	8.0	9.9	8.8968–9.3032
Tarsus							
♂♂							
Newfoundland	58	30.30	0.8218	0.1079	28.7	32.3	30.0874–30.5195
Northern Quebec	30	30.48	0.8461	0.1545	28.8	32.1	30.1674–30.7993
"bicknelli"	72	29.24*	0.6885	0.0811	27.5	30.7	29.0868–29.4104
♀♀							
Newfoundland	26	29.47	1.0632	0.2085	27.4	31.2	29.0360–29.8948
Northern Quebec	15	29.89	0.6638	0.1714	28.7	31.1	29.5257–30.2609
"bicknelli"	17	28.89*	0.4981	0.1208	28.1	29.7	28.6380–29.1502

TABLE 2
CONTINUED

Region	N	Mean	SD	SE	Minimum	Maximum	95% conf. interval
Mass							
♂♂							
Newfoundland	4	34.45	3.3571	1.6785	32.1	39.4	29.1082–39.7918
Northern Quebec	27	34.18	1.7679	0.3402	28.2	36.8	33.4821–34.8808
"bicknelli"	38	28.18*	2.0222	0.3280	20.5	33.0	27.5169–28.8462
♀♀							
Newfoundland	1	40.00					
Northern Quebec	10	32.97	3.8537	1.2187	27.5	41.8	30.2132–35.7268
"bicknelli"	3	31.97	4.2712	2.4660	28.7	36.8	21.3562–42.5771
Total length							
♂♂							
Newfoundland	5	17.66			16.5	18.5	
Northern Quebec	24	18.90			18.2	19.7	
"bicknelli"	38	17.68			16.8	19.0	
♀♀							
Newfoundland	1	18.10					
Northern Quebec	5	18.08			17.2	18.8	
"bicknelli"	2	18.00			17.7	18.3	

* Indicates a significant difference at $P \leq 0.05$ (Tukey-HSD Procedure).

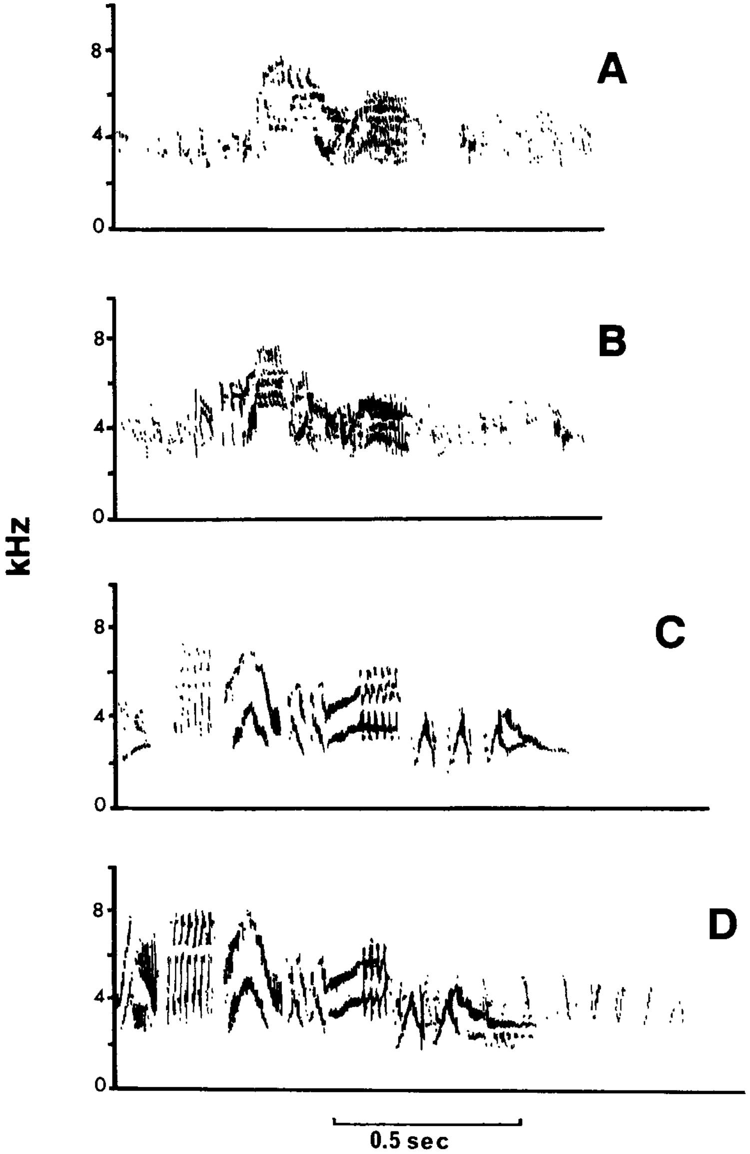

FIG. 7. Representative sonograms of songs of *Catharus* populations: A—*minimus*, Québec, Schefferville, 23 June 1977. B—*minimus*, Manitoba, Mile 17 on Twin Lake Road, Churchill, 19 June 1958 (L.N.S. No. 58380). C—*bicknelli*, Québec, Mont Mégantic, 7 June 1989. D—*bicknelli*, Québec, Charlevoix Co., 35 km north of Saint-Urbain, 14 June 1990.

TABLE 3

QUANTITATIVE CHARACTERISTICS OF SONGS FROM TWO GROUPS OF INDIVIDUALS RECORDED IN THE *MINIMUS* AND *BICKNELLI* BREEDING RANGES. PART I OF SONG WAS LEFT OUT BECAUSE OF SMALL SAMPLE SIZE. AMPLITUDE IS THE VALUE OBTAINED FROM THE DIFFERENCE BETWEEN HIGHEST AND LOWEST FREQUENCIES

	minimus song			*bicknelli* song		
	N	Mean	SE	N	Mean	SE
Part II						
Duration[a]	52	0.6063	0.0269	32	0.7713	0.0361
High kHz	52	7067.69	134.6401	32	7217.50	114.7640
Low kHz*	52	2641.15	57.9083	32	3211.87	174.3580
Amplitude*	52	4423.85	144.0316	32	3834.69	211.6925
Part III						
Duration	52	0.6227	0.0332	32	0.5639	0.0425
High kHz	52	6603.08	117.9710	32	6450.00	149.3966
Low kHz*	52	2463.08	41.4131	32	2907.81	69.5908
Amplitude*	52	4140.00	120.2887	32	3750.00	153.0655
Part IV						
Duration*	52	0.8185	0.0480	32	0.6059	0.0403
High kHz*	52	5049.62	123.4820	32	6027.50	83.9054
Low kHz*	52	2053.85	57.5296	32	2878.75	112.1412
Amplitude	52	3051.92	130.9683	32	3148.75	127.4848

* $P \leq 0.005$ (least significant differences procedure).

[a] Time in milliseconds.

higher for *bicknelli,* whereas amplitude is significantly higher for *minimus* in Parts II and III. The relationships between the high and low frequencies, and the amplitude of Part IV, indicate that the final part of the song of *bicknelli* is much different from that of *minimus,* the mean high and low frequencies of *bicknelli* being almost 1000 kHz higher in both instances. The song of *bicknelli* is consistently high in Part IV and the frequency does not fall to lower frequencies towards the end of the vocalization as in *minimus*: it remains constant or increases (Fig. 7). This difference can be detected in the field and provides an accurate means of identification.

In call notes, mean high frequency tends to be higher in *bicknelli* (5751.11 kHz, N = 29) than in *minimus* (4616.00 kHz, N = 25). The mean low frequency is statistically different in both samples (3208 kHz and 2304 kHz, N = 26), but no significant difference was found in the duration of the call notes of the two taxa (3052 msec and 2924 msec, N = 25).

Although both taxa usually sing from well-concealed perches, rarely above 6–8 m from ground level, they do sing in more open situations, sometimes fully exposed, at heights reaching 12–18 m. Songs from the

TABLE 4

REACTIONS TO PLAYBACKS OF *C. M. MINIMUS, C. M. ALICIAE,* AND "*BICKNELLI*" SONGS IN THE BREEDING RANGE OF "*BICKNELLI*" DURING THE FIELD SEASONS OF 1989 AND 1990

	Number of playbacks	Number of responses by *bicknelli*	Percent
1989	187 [*bicknelli* song]	89	47.6
	125 [*minimus* song]	0	0
1990	106 [*bicknelli* song]	49	46.2

minimus and *bicknelli* populations are usually given from perches. However, I have heard and observed flying birds in full song three times: Mont de la Table, Gaspé Peninsula, 9 June 1989, about 07:30 h; Mont Sir-Wilfrid, 21 June 1989, about 21:30 h; Saint-Urbain, Charlevoix, 15 June 1990, 21:45 h.

Reactions to song playbacks.—Songs of birds from central and southern Quebec were played back in various habitats in southern Quebec. The results of this experiment (Table 4) show that in the range of *bicknelli* no reaction was obtained from the playbacks of *aliciae* or *minimus* songs. In contrast, songs of *bicknelli* elicited reaction from *bicknelli* in over 45 percent of the playbacks during the breeding seasons of 1989 and 1990.

Biochemical analysis.—An analysis of mitochondrial DNA (mtDNA) differentiation between *Catharus minimus* and *C. m. bicknelli,* using RFLP technique (Quinn and White 1987) with 13 endonucleases, revealed sequence divergence of 1.7% between the two taxa (Seutin and Ouellet, unpublished data), greater than that observed between most avian sibling species pairs studied to date (Avise and Zink 1988). Based on the calibration of mtDNA sequence evolution proposed by Shields and Wilson (1987), this level of differentiation suggests that the taxa diverged approximately 1 million years ago.

Habitat.—The Gray-cheeked Thrush inhabits the Boreal Forest Region (Rowe 1972) and occurs primarily in coniferous stands although it also is found in tall shrubby enclaves in the taiga or above tree line, particularly in Alaska (A.O.U. 1983; Bailey 1948; Kessel 1979, 1989; Godfrey 1986), in Labrador, and in northern Quebec. The populations of Labrador, Newfoundland, and northern and central Quebec are usually found in mature coniferous stands where conditions of exposure, altitude, latitude, and plant species composition are highly variable. By comparison, southern populations or *bicknelli* in southern Quebec, the Maritime Provinces, and the New England States have traditionally been reported in altitudinal coniferous stands and "scrub spruces" up to tree line (Able and Noon 1976; Palmer 1949; Palmer and Taber 1946; Taber 1948; Wallace 1939;

TABLE 5
SUMMARY OF "*BICKNELLI*" OBSERVATIONS BY HABITAT TYPES IN SOUTHERN QUÉBEC

Location	Number of observations in traditional habitats				Number of observations in second-growth habitats			
	1967	1968	1969	1990	1967	1968	1989	1990
Percé[a]	6	1	2		2		17	
Cap Bon-Ami	2							
Mont-Saint-Pierre[b]	3	18				1	10	
Mont Jacques-Cartier	45		4					
Mont Mégantic			3	2			18	59
Mont de la Table							14	
Portage Saint-Hélier			18					
Saint-Urbain[c]			2				27	24
Mont Sir-Wilfrid							1	
Godbout[d]								1
Total	56	19	29	2	2	1	87	84

[a] In mountainous areas around Percé, above 175 m.
[b] Region south of Mont-Saint-Pierre, above 250 m.
[c] Region north of Saint-Urbain, near Zone d'exploitation contrôlée (ZEC) des Martres, above 600 m.
[d] About 10 km south of Godbout, above 250 m.

pers. obs. 1967, 1968) and exceptionally in deciduous habitats (Eaton and Curry 1926).

Observations obtained in the Gaspé Peninsula in 1967 and 1968 (Table 5), particularly in the Mont Jacques-Cartier and Gaspé areas, indicate that the birds recorded then were mostly restricted to thick stands of stunted conifers on steep mountain slopes (Percé) or near tree-line (Mont Jacques-Cartier). However, two birds were heard and seen on 6 July 1967, near Percé, in a mixed second growth area from where the original forest had been removed some 20 yr earlier. A single singing bird was recorded also in a similar situation on 22 June 1968, some 25 km south of Mont Saint-Pierre. But now, I interpret these observations as cases of extra-limital foraging because the second growth areas in which the observations were made covered areas of less than 3 km^2 and were located in the middle of traditional habitats as described above or in the literature (Forbush 1929, Wallace 1939).

In contrast, observations of *bicknelli* in southern Quebec in 1989 and 1990 (Table 5) establish that only a small number of breeding birds can be found now in traditional habitats as described above or in the literature (A.O.U. 1983, Forbush 1929, Wallace 1939). More birds were recorded then in second growth stands characterized by relatively young conifers of small size (*Abies balsamea, Picea glauca*) intermixed with a variety of deciduous species typical of second-growth regeneration (*Prunus* sp., *Betula* sp., *Amelanchier* sp., *Acer spicatum, Populus* sp.) following forest fires

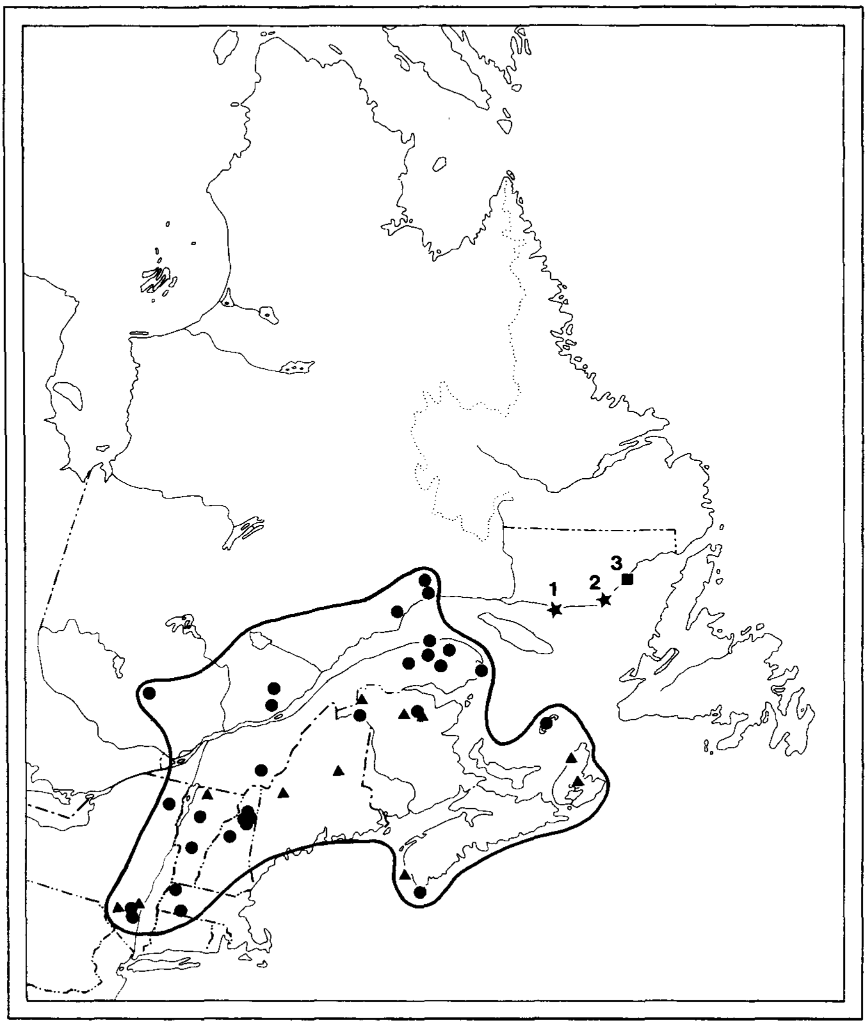

FIG. 8. Breeding distribution of Bicknell's Thrush (*Catharus bicknelli*) is delimited by thick line. Boundary is approximate because breeding distribution is dependent on suitable habitats. FULL CIRCLES = specimen localities and TRIANGLES = locality records from the literature. Other symbols [stars = *C. bicknelli*; full square = *C. m. minimus*] are as follows: 1 = Pointe Natashquan (50°11'N, 61°45'W), 2 = Rivière du Petit Mécatina (50°38'N, 59°26'W), 3 = La Tabatière (50°50'N, 58°58'W).

or clear cutting. The trees there, coniferous or deciduous, have small diameters (4–15 cm) and seldom exceed ten meters in height. Their density is relatively high but one can progress with relative ease in such habitats as the distance between trees is seldom less than one m.

In southern Quebec *bicknelli* is found at altitudes ranging from approximately 175 to 1160 m in the Gaspé Peninsula, in Charlevoix County, and in the southwestern part of the province (Eastern Townships, Mont Sir-Wilfrid). The number of birds observed in the second growth habitats indicates that a shift in habitat selection appears to have taken place and that *bicknelli* now occupies a different habitat resulting from human activity. It is more numerous in this habitat than in the habitat considered until now to be typical of the taxon.

Breeding distribution.—The present breeding distribution of Bicknell's Thrush may be more restricted than it was in the past because it is relatively difficult to identify this bird in the field unless its song is heard and known by the observer. Some of the observations reported in the literature are considered as hypothetical unless supported by specimens or unless they fall within the range of *bicknelli* as defined in the present study. The distribution of Bicknell's Thrush presented here (Fig. 8) is based on specimens in collections, on published data recorded south of the St. Lawrence River, and on fully documented observations obtained by myself and my associates during the breeding seasons of 1967, 1968, 1989, and 1990.

It is difficult to determine with certainty the past distribution of Bicknell's Thrush at the northern periphery of its range. Recent specimens taken in the Strait of Belle Isle are similar in size and coloration to birds from Newfoundland and have thus been referred to the nominate subspecies. In addition, the comparison and study of songs recorded in 1953 at La Tabatière on the lower north shore of the Gulf of St. Lawrence by P. P. Kellogg of the Laboratory of Ornithology, Cornell University, indicate that those songs are virtually identical to songs from central Quebec and Manitoba and very different from songs recorded in southern Quebec, the Gaspé Peninsula, and the New England states. The range of *minimus* thus appears to have reached the middle north shore of the Gulf of St. Lawrence at that time, at least as far south as La Tabatière, which is only some 100 km southwest of Middle Bay (Quebec). At the latter locality, at Pointe-des-Belles-Amours, and at L'Anse-au-Clair (Labrador) over 18 individuals of *minimus* were recorded from 7 to 14 July 1981.

Although the breeding range of Bicknell's Thrush may have been more extensive in the past, particularly along the north shore of the Gulf of St. Lawrence, as shown by specimens collected on the St. Margaret River and near Natashquan during the nesting season, there is no evidence to confirm breeding along the southern part of the north shore of the Gulf of St. Lawrence at present. It continues to be present in the interior highlands of New Brunswick (Squires 1976, *fide* A. J. Erskine), in Vermont (Laughlin and Kibbe 1985, Spear 1976, Perkins and Howe 1901), and in New York State (Bull 1974, Andrle and Carroll 1988, Merriam 1884). It is probably also present in the highlands of northwestern Maine, northern New Hampshire, and northern Vermont, adjacent to southern Quebec, because the habitats of these regions display strong similarities.

Non-breeding distribution.—The migration patterns of Bicknell's Thrush are poorly known but specimens in various collections indicate that it has occurred during migration in the following states and provinces: Connecticut, New Jersey, New York, South Carolina, Virginia, New Brunswick, Nova Scotia, Quebec, Ontario, and the Bahama Islands (Bond 1956, Cory 1891). An extralimital specimen was found on Bermuda (Paget East, 23 November 1957, female immature, A.M.N.H. No. 789068). In spite of difficulties related to its identification in the field and the spottiness of records, Bicknell's Thrush probably occurs more frequently during migrations along the eastern coast of North America from Quebec to Florida, than is revealed by the known records.

The winter range of Bicknell's Thrush appears to be restricted to islands in the Caribbean region but little information is available on its winter distribution on the islands and population (Bond 1979). It has been recorded in the Dominican Republic (Santo Domingo, 27 December 1906, male immature, A.M.N.H. No. 448949; Wetmore and Swales 1931, Bent 1949—Puerto Plata, Sánchez, Aguacate, Santo Domingo), Cuba (A.O.U. 1957, Garrido 1975), Haiti (Wetmore and Swales 1931, Bent 1949—Morne Malanga), Puerto Rico (Faaborg and Arendt 1985, Norton 1989, Phillips 1991, Raffaele 1983), and St. Croix (Sladen 1988).

The collections examined revealed no specimens of Bicknell's Thrush taken anywhere in Central or South America. I have identified in various collections migrating and wintering specimens of *C. m. minimus* and *aliciae,* from 9 October to 11 May, in the following countries: Belize, Brazil, Colombia, Costa Rica, Ecuador, Guatemala, Guyana, Guadeloupe (*fide* E. Benito-Espinal), Honduras, Mexico, Panama, Swan Islands (U.S.A.) (Paynter 1956), and Venezuela. In addition, there are reports of *C. minimus* from Brazil (Peres and Whittaker 1991), Trinidad (Worth and Aitken 1965), and Curaçao (Voous 1983). Dorsal coloration and wing length permitted the subspecific determination of the specimens that I have examined. Dorsal coloration of the Central and South American wintering and migratory populations is similar to that found in the *aliciae* and *minimus* samples from the breeding grounds. Wing length (Table 6), as well as dorsal coloration, indicate a double origin for the wintering spec-

TABLE 6

MEASUREMENTS OF CHORD OF WING OF SPECIMENS FROM WINTERING GROUNDS IN CENTRAL AND SOUTH AMERICA. SPECIMENS WERE ASSIGNED TO THE TWO SUBSPECIES OF *CATHARUS MINIMUS* (*MINIMUS* AND *ALICIAE*) ON THE BASIS OF THEIR DORSAL COLORATION

	N	Mean	SD	SE	Range
♂♂					
minimus	18	101.31*	3.1407	0.7403	95.6–105.9
aliciae	48	103.13	2.5917	0.3741	98.0–108.3
♀♀					
minimus	30	97.36**	3.1553	0.5761	90.0–103.5
aliciae	37	99.91	2.1574	0.3547	95.0–103.8

* $t = 2.4036$, $df = 64$, $P < 0.05$.
** $t = -3.9105$, $df = 65$, $P < 0.05$.

imens in Central and South America. These characters show that no individual in the samples can be referred to *bicknelli.*

DISCUSSION

Data presented here show that the population of thrushes referred to as *Catharus minimus bicknelli* (A.O.U. 1957), currently a subspecies of the Gray-cheeked Thrush, is indeed different from other populations of *C. minimus.* Its overall coloration, particularly that of the upper parts, differs from that of adjacent populations in Newfoundland, along the eastern north shore of the Gulf of St. Lawrence, and in northern Quebec, being distinctly browner (Fig. 2). The throat is markedly more buffy (Fig. 4), and the white of the ventral region is duller than in the other samples (Fig. 5). The tail is uniquely pigmented with various amounts of chestnut (Fig. 3), a feature absent in other populations. On the basis of coloration alone, including that of the soft parts, this population can be distinguished from adjacent populations. Size differences are strong in all body dimensions (Table 2).

Vocalizations of the *bicknelli* population differ (Table 3) from those of birds immediately to the north and west of its breeding range, and the negative reactions obtained from playbacks of *aliciae* and *minimus* songs (Table 4) are particularly revealing.

Differences in habitat selection are strong and consistent. *Catharus m. minimus* and *C. m. aliciae* are primarily birds of mature northern coniferous stands, although they are found in other boreal forest and taiga habitats, particularly in Alaska (Kessel 1979). Although *bicknelli* has been generally considered to inhabit stunted altitudinal coniferous forests of eastern Canada and United States, it has been recorded in deciduous stands in Vermont since the mid-1920s (Eaton and Curry 1926). In New Hampshire, *bicknelli* occurs in forest stands with a 68% conifer dominance (Sabo 1980, Sabo and Holmes 1983). It is important to note that it is now found in larger numbers in mixed second growth stands in many parts of southern Quebec during the breeding season than in the 'original' habitat and that it is no longer restricted to stunted altitudinal or coastal conifer stands. This habitat selection, previously unreported, is probably not a new adaptation following the extensive logging that has taken place in many parts of its breeding range. Indeed, enormous forest fires have seriously modified in the past the vegetation in its breeding range. These were followed by vegetal successions, similar to those in which Bicknell's Thrush now occurs in greater numbers than in the 'traditional' or original habitats. It may have been overlooked for years in these mixed second growth habitats because, since its description in 1882, it has always been associated with altitudinal stunted coniferous forests and krummolz stands. The consequences of *bicknelli* being more numerous in this habitat in Quebec and the Maritime Provinces (*fide* A. J. Erskine) can be very important for the conservation of the taxon. However, recent reports indicate that it has disappeared in parts of its known range, notably from Seal Island and Cape Forchu (*fide* J. T. Marshall), Nova Scotia, where it formerly was known to breed in good numbers (Tufts 1986) as late as 1954, when it was very scarce (Erskine 1955). Its slow decline and eventual disappearance from Seal Island is attributed to the presence of numerous cats and dogs on the island (Erskine 1955).

Analysis of mtDNA shows marked differences among *bicknelli* and adjacent populations and indicate a level of divergence greater than what has generally been observed in most avian sibling species pairs (Avise and Zink 1988). These data also suggest that the taxon has diverged from an ancestral population about one million years ago.

Data on present and past distribution indicate that the *bicknelli* population is not known to have occurred in sympatry with *C. m. aliciae.* Sympatry could likely have taken place in the northern part of its range or with *minimus* at the extreme northern limit of its distribution along the north shore of the Gulf of St. Lawrence. The breeding ranges of these populations have apparently never overlapped or met with that of *bicknelli.* At best, they were adjacent to it. Currently, the breeding range of *bicknelli* appears to be totally distinct and separated from that of the other taxa by a discontinuity (Fig. 8), thus creating a situation of total allopatry.

There is no phenotypic evidence for gene flow between *bicknelli* and the other breeding populations of eastern North America because there is no specimen in collections suggesting intergradation or hybridization.

Hybrids or intergrades could be recognized by their intermediate measurements as well as by the coloration of the dorsal regions where small amounts of chestnut and brown should appear in the plumage. Such birds, if they exist, could reliably be identified with comparative material on hand.

A specimen taken during the breeding season at Percé, Québec (N.M.C. No. 8298, adult male, 14 June 1915, wing 101.0 mm) has been referred to *C. m. minimus* on the basis of its dorsal coloration and measurements. I propose that this bird is not an intergrade nor a hybrid and that it is either a late migrant or an individual that has failed to reach its breeding grounds in Newfoundland or southeastern Labrador. Migrating specimens of *C. m. minimus* have been recorded as late as 6 June as far south as Louisiana (*fide* J. V. Remsen).

Specimens taken at Point Natashquan on 2 June 1928 (Carnegie Museum No. 102539) and at Rivière du Petit Mécatina on 27 June 1928 (Carnegie Museum No. 102637) are valid *bicknelli* on the basis of their measurements and coloration (Fig. 8). Although Todd (1963) extended the distribution of what he considered an undescribed race along the north shore of the Gulf of St. Lawrence, from about Sept-Iles to the eastern extremity of the Strait of Belle Isle, it seems unlikely that there was ever a distinct population in that region. It can be argued that these specimens represent breeding individuals of a population that occupied a more extensive breeding range in the past. However, the presence of *bicknelli* so far to the northeast can be interpreted as extralimital records of birds that have strayed beyond their regular breeding grounds during the spring migration. In either case, there is no definite evidence that *bicknelli* was ever sympatric with *minimus* or *aliciae.* La Tabatière (±60 km to the north of Petit Mécatina River) is the southernmost locality along the St. Lawrence north shore where *minimus* is known to occur during the breeding season (Fig. 8).

Specimens in collections show that *bicknelli* is mainly restricted during migrations along the eastern part of North America, between southern Quebec and South Carolina. It may be found in Florida as well, but I have not seen specimens from that state. The other taxa have been recorded during migrations in almost every province and state as well as in Mexico (Ramos 1988) and Central and South America. During winter, *bicknelli* is restricted to a few Caribbean islands and has not been recorded anywhere in Central or South America.

The distinguishing characteristics of the *bicknelli* population are as follows: (1) strong morphological differences from adjacent populations of closely related taxa, (2) allopatric breeding and wintering ranges, (3) a different song from *C. minimus,* (4) no response to playbacks of *C. m.*

minimus or *C. m. aliciae* songs, (5) use of different habitats, (6) no known intergradation or hybridization with other populations, such as *C. m. minimus* and *C. m. aliciae,* and (7) a high level of sequence divergence in the number of fixed distinct fragment patterns.

I propose that *bicknelli* be treated as a relict taxon from a past refugium, probably located in the Sable Island area and adjacent banks (Howden et al. 1970), that diverged from an ancestral population shortly after the beginning of the Pleistocene (Fulton 1989). This hypothesis is compatible with the biochemical information provided in the current study and with glacial and ecological evolutionary theory of northeastern North America (Pielou 1991).

TAXONOMIC CONCLUSION AND RECOMMENDATION

The data presented in this work demonstrate that the *bicknelli* population, heretofore considered to be a subspecies of the Gray-cheeked Thrush (*Catharus minimus*), is in fact significantly different from it and that it meets all the criteria necessary for its recognition as a species. The debate about species concepts is still actual but the *bicknelli* population qualifies as a species under any species concept (Mayr 1970, Cracraft 1983, McKitrick and Zink 1988). Aspects of its affinities with other *Catharus* species are still unclear, but *bicknelli* is undoubtedly closely related to *C. minimus* from which it appears to have diverged during or before the Pleistocene. On the other hand, *bicknelli* and *minimus* may have evolved from a common ancestor, also a close relative of other *Catharus* species, such as *C. guttatus* or *swainsoni* and other Neotropical taxa. Similarly, its affinities with other northern Neotropical *Catharus* species such as *C. fuscescens* remain uncertain pending additional biochemical studies. I therefore recommend that (1) the *bicknelli* population be treated as a full species, *Catharus bicknelli* (Ridgway), 1882. Proc. U.S. Nat. Mus., 4:377, *Hylocichla aliciae bicknelli,* with Bicknell's Thrush as its English name, and Grive de Bicknell as its French name, and (2) the other populations of the Gray-cheeked Thrush remain as they are within *Catharus minimus* (Lafresnaye), 1848, Rev. Zool., 11 (1):5, *Turdus minimus.*

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COLOR PLATE

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