GEOGRAPHIC VARIATION OF YELLOW WARBLERS KILLED AT A TV TOWER

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ABSTRACT.—Prairie and aspen parkland Yellow Warblers are brighter in color and larger in bill length than those from the boreal forest. Yellow Warblers from the MacKenzie River Delta near the arctic coast terminate clines of birds with smaller bill length to the north and darker plumage in forested or coastal habitats. Statistically significant differences in color and bill and wing length among Yellow Warblers killed at a TV tower in western Minnesota conform to patterns of geographic variation and demonstrate that individuals of this species originating from perhaps as far apart as 3,220 km (2,000 mi) were migrating southward together.—*Minnesota Museum of Natural History, University of Minnesota, Minneapolis, Minnesota 55455. Present address of first author: Division of Wildlife and Fisheries Biology, University of California, Davis, California 95616.* Accepted 13 May 1976.

DESCRIPTIONS of subspecies for most bird species commonly killed at TV towers during migration are inadequate for confident estimation of areas of their origin, and only a few attempts at racial identification have been made (Tordoff and Mengel 1956, Johnston and Haines 1957, Stoddard 1962, Raveling 1965). A sample of 74 Yellow Warblers (*Dendroica petechia*) was obtained from a TV tower kill at Westport, Stearn's County, Minnesota on the night of 9–10 September 1962 (see Kemper et al. 1966). Obvious differences in bill length and coloration of adults within the sample suggested that birds from different populations were migrating over this location on the same night. We analyzed geographic variation of Yellow Warblers in the midcontinent north of the TV tower from museum specimens and compared results to variation recorded among the TV tower killed birds.

METHODS

Only adults collected during June and July were used for determining geographic variation. A set of standard specimens was selected to represent the different shades of yellow and green exhibited by Yellow Warblers. Each individual was compared to these standards for assignment to a color group. Our color terminology and standard specimens are: **Males: Green back and green head**—Carnegie Mus. No. 129401; **Intermediate back**—Nat. Mus. of Canada Nos. 13479 and 36909; **Intermediate head**—Nat. Mus. of Canada No. 36909, Carnegie Mus. Nos. 129557 and 136423; **Yellow back and yellow head**—Minn. Mus. Nat. Hist. Nos. 9120 and 19251.

Specimens in series reveal a gradation in back, nape, and crown color. What we termed yellow back is actually a much lighter and brighter green than the intermediate or green categories, so that in comparison they appeared yellow.

The intermediate head color included birds with some yellow on the forehead and crown and individuals with much yellow throughout, but which also had heavy red streaking that imparted a brownish cast to the head (e.g. Carnegie Mus. No. 136423). In birds with an intermediate or green back, the yellow on the forehead and crown (if present) contrasted abruptly with the nape color. These were termed intermediate heads, even though this terminology in many cases reflects the nape color while the yellow on the forehead and crown was as bright as those classified as yellow heads.

The differentiation between intermediate and green backs was a qualitative, and often difficult, judgment. Birds that had heavy dorsal red streaking or were dirty, or showed much feather wear were darker than specimens with a smooth-appearing back. In all cases, however, the intermediate and green back classes were readily distinguished from those in the yellow back category.

Females: Females were classified in three ways: (1) **Dorsal surface color—Class I**—head a definite yellow or yellow-green; back as in the male intermediate category (U.S. Nat. Mus. No. 239450, Minn. Mus. Nat. Hist. Nos. 108 and 5353); **Class II**—head a bright olive-green; back more green than Class I (Nat. Mus. of Canada No. 35690 and Minn. Mus. Nat. Hist. No. 18927); **Class III**—head dull green,

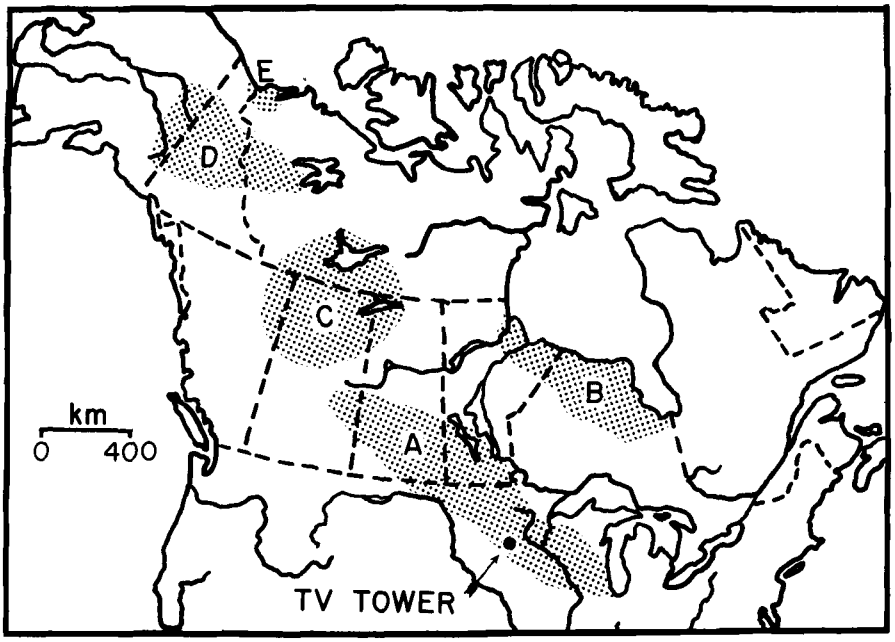

Fig. 1. Locations of June and July collected adult Yellow Warblers examined for geographic variation (A–E, refer to text).

brown-green, or grey-green; back grey-green (Carnegie Mus. Nos. 129404 and 129405). (2) **Ventral surface color—Pale**—light yellow or brownish cast (Carnegie Mus. No. 129404); **Intermediate**—some yellow, but dull overall appearance (Minn. Mus. Nat. Hist. No. 18927); **Bright**—distinct, bright yellow (U.S. Nat. Mus. No. 239450). (3) **Red streaking on ventral surface—Distinct**—heavy streaking (Carnegie Mus. No. 129404); **Faint**—sparse streaking or limited to a few spots (Minn. Mus. Nat. Hist. No. 18927); **None**—(U.S. Nat. Mus. No. 239450).

Bill length from the anterior edge of the nostril to the tip and tail length from the base of the central tail feathers to the tip were measured with dividers to the nearest 0.1 and whole mm, respectively. Wing length (flat) was measured to the nearest mm on a wing gauge. Weight of the TV tower killed birds was recorded to the nearest 0.1 g on a triple beam balance.

GEOGRAPHIC VARIATION

Collection localities of museum specimens examined are indicated on Fig. 1. Yellow Warblers from Alberta south of Edmonton and from the Overflowing River and Delta, Manitoba in the aspen (*Populus* spp.) parklands were indistinguishable from specimens collected in Minnesota, North and South Dakota, and the entire sample was combined.

Color—males (Table 1).—There was a clinal gradation in color from yellow prairie birds to intermediate, more green birds from the boreal forest to the darkest specimens from the MacKenzie River Delta. Almost 90% of the males from the prairie were readily distinguishable on the basis of back and head color from males from all other samples. From 81 to 95% of males from the boreal forest (B, C, D, Fig. 1) were designated as intermediate in head color and intermediate or green-backed, and proportions from these three geographic areas did not vary significantly ($\chi^2 = 5.19$, 6 d.f., $P > 0.5$). One half of the males from the MacKenzie River Delta were classified as green back-green head, and the difference in proportions in color classes varied significantly compared to the boreal forest samples ($\chi^2 = 17.95$, 3 d.f., $P < 0.005$).

TABLE 1
COLOR VARIATION OF ADULT MALE YELLOW WARBLERS COLLECTED IN JUNE AND JULY

Location[1]	Color category				
	Green back and head	Green back, inter. head	Inter. back and head	Inter. back, yellow head	Yellow back and head
A. Northern prairie (N = 63)	1.6%	—	7.9%	1.6%	*88.9%*
B. Hudson Bay Lowlands (N = 23)	17.4%	30.4%	*52.2%*	—	—
C. Northern Alberta (N = 18)	5.6%	*50.0%*	44.5%	—	—
D. Yukon (N = 16)	12.5%	*43.7%*	37.5%	6.3%	—
E. MacKenzie Delta (N = 18)	*50.0%*	*50.0%*	—	—	—

[1] See Fig. 1.

The dorsal surface coloration of males after the postnuptial molt becomes darker and more even colored, and the yellow cap is less intense or even absent. Prairie males are still lighter and brighter than birds from the boreal forest. Insufficient specimens in fresh fall plumage preclude conclusions on possible differences between boreal forest birds and those from the MacKenzie River Delta, but we would predict a cline of continuing darker appearance as exhibited in the breeding plumage specimens.

Color—females (Table 2).—As in males, prairie females were more yellow on both dorsal ($\chi^2 = 43.21$, 6 d.f., $P < 0.005$) and ventral ($\chi^2 = 15.48$, 6 d.f., $P < 0.025$) surfaces compared to boreal forest specimens (MacKenzie Delta specimens excluded from these tests because of sample size). The northernmost specimens were consistently dark on the back and least bright ventrally. There was not a significant difference in proportions of females in the dorsal ($\chi^2 = 2.08$, 1 d.f., $P > 0.10$) or ventral ($\chi^2 = 4.41$, 2 d.f., $P > 0.10$) color categories between birds from the Hudson Bay Lowlands and northern Alberta, Saskatchewan, and southern MacKenzie areas (B and C, Fig. 1). Difference in proportions of females exhibiting ventral red streaking was not significant among prairie, Hudson Bay Lowlands, and northern Alberta specimens ($\chi^2 = 1.96$, 4 d.f., $P > 0.5$), but Yukon, northern MacKenzie specimens did differ from the combined samples farther south ($\chi^2 = 4.12$, 1 d.f., $P < 0.05$).

TABLE 2
COLOR VARIATION OF ADULT FEMALE YELLOW WARBLERS COLLECTED IN JUNE AND JULY

Location[1]	Dorsal color[2]			Ventral color[2]			Red streaking[2]		
	I	II	III	Bright	Inter.	Pale	Distinct	Faint	None
A. Northern prairie (N = 14)	*57.1%*	42.9%	—	*71.4%*	21.4%	7.1%	*64.3%*	21.4%	14.3%
B. Hudson Bay Lowlands (N = 18)	—	27.8%	*72.2%*	11.1%	*61.1%*	27.8%	*50.0%*	38.9%	11.1%
C. Northern Alberta (N = 11)	—	*54.5%*	45.5%	*45.5%*	36.4%	18.2%	*63.6%*	18.2%	18.2%
D. Yukon (N = 12)	—	—	*100.0%*	25.0%	33.3%	*41.7%*	25.0%	*50.0%*	25.0%
E. MacKenzie Delta (N = 3)	—	—	*100.0%*	—	33.3%	*66.7%*	33.3%	33.3%	33.3%

[1] See Fig. 1.
[2] See text.

TABLE 3

MEASUREMENTS (MM) OF ADULT YELLOW WARBLERS COLLECTED DURING JUNE AND JULY

Locality[1]	Sex	Bill length N	Bill length $\bar{x} \pm SE$	Bill length Range	Wing length N	Wing length $\bar{x} \pm SE$	Wing length Range
A. Northern prairie	Male	60	8.02 ± 0.04	7.3–8.8	61	64.2 ± 0.27	59–68
	Female	22	7.89 ± 0.05	7.3–8.6	24	61.1 ± 0.30	59–64
B. Hudson Bay Lowlands	Male	21	7.82 ± 0.08	7.2–8.8	23	62.4 ± 0.25	60–64
	Female	17	7.58 ± 0.06	7.2–7.9	17	59.4 ± 0.32	56–61
C. Northern Alberta	Male	14	7.79 ± 0.06	7.3–8.1	17	62.7 ± 0.30	59–66
	Female	12	7.68 ± 0.09	7.2–8.1	12	59.5 ± 0.45	56–61
D. Yukon	Male	15	7.43 ± 0.08	6.9–7.9	15	62.4 ± 0.36	60–65
	Female	12	7.35 ± 0.10	6.9–8.0	12	58.8 ± 0.48	56–61
E. MacKenzie R. Delta	Male	16	7.50 ± 0.07	7.0–7.9	18	61.9 ± 0.36	60–65
	Female	3	7.40	7.1–7.8	3	58.0	57–59

[1] See Fig. 1.

Measurements (Table 3).—There was a cline of progressively smaller bill lengths to the north in conformance with Allen's Rule. Bill lengths of prairie males were significantly different from those of boreal forest males (vs. northern Alberta, $t = 2.65$, 79 d.f., $P < 0.02$), which were in turn significantly different from MacKenzie River Delta males ($t = 3.01$, 28 d.f., $P < 0.01$). The same pattern was exhibited by females (vs. northern Alberta, $t = 2.15$, 32 d.f., $P < 0.05$; northern Alberta vs. Yukon, $t = 2.37$, 22 d.f., $P < 0.05$).

Bills of southern birds are also obviously deeper and more massive than those of boreal forest or more northern specimens, but bill depth was not measured because of differences in methods of preparing study skins.

A small but significant difference appeared in male wing length between prairie and boreal forest birds (Hudson Bay Lowlands, $t = 3.21$, 82 d.f., $P < 0.001$). Boreal forest specimens were nearly the same in wing length and not different from MacKenzie River Delta birds (vs. northern Alberta, $t = 0.98$, 31 d.f., $P > 0.30$). The same pattern was exhibited in females (prairie vs. northern Alberta, $t = 3.00$, 34 d.f., $P < 0.01$; northern Alberta vs. Yukon, $t = 1.06$, 22 d.f., $P = 0.30$).

Tail lengths were relatively uniform throughout all samples and averaged 45.1 mm for males and 43.3 mm for females.

VARIATION AT THE TV TOWER

Location of the TV tower at Westport, Minnesota is indicated on Fig. 1. Fresh fall plumage specimens cannot be placed in the same color categories as breeding specimens because of differences produced by the complete postnuptial and partial prenuptial molts, and feather wear. Of the 57 adults in the sample 35 were prepared as

TABLE 4

MEASUREMENTS (MM) OF ADULT MALE YELLOW WARBLERS KILLED AT A TV TOWER DURING AUTUMN MIGRATION

Color category	Bill length N	Bill length $\bar{x} \pm SE$	Bill length Range	Wing length N	Wing length $\bar{x} \pm SE$	Wing length Range	Weight (g) N	Weight (g) $\bar{x} \pm SE$	Weight (g) Range
Yellow	6	8.02 ± 0.16	7.4–8.5	7	65.7 ± 0.42	65–68	7	11.10 ± 0.34	9.9–12.3
Intermediate	6	7.82 ± 0.13	7.3–8.2	6	65.3 ± 0.42	64–67	6	10.83 ± 0.39	9.3–12.0
Green	15	7.40 ± 0.08	6.9–7.9	15	63.7 ± 0.36	61–66	14	10.18 ± 0.16	9.3–11.5

TABLE 5

MEASUREMENTS (MM) OF ADULT FEMALE YELLOW WARBLERS KILLED AT THE TV TOWER DURING AUTUMN MIGRATION CHARACTERIZED BY WEIGHT CATEGORIES[1]

Weight group[1]	Weight (g)			Bill length			Wing length		
	N	$\bar{x} \pm SE$	Range	N	$\bar{x} \pm SE$	Range	N	$\bar{x} \pm SE$	Range
>10 g	14	10.86 ± 0.04	10.1–11.8	14	7.71 ± 0.08	7.3–8.1	14	61.9 ± 0.28	60–63
<10 g	15	9.46 ± 0.07	9.1–9.9	15	7.37 ± 0.12	6.8–8.4	15	61.1 ± 0.33	59–63

[1] See text.

study skins for future reference (Appendix A). We did not categorize the small sample (17) of immatures.

Males.—The 28 adult males in the sample were classified as yellow, intermediate, and green in dorsal surface color. Again, all are tones of green or yellow-green, but the yellow category specimens were distinctly lighter and brighter than the other categories. The green category was best described as a dark olive-green, and the differentiation between green and intermediate was more difficult than between yellow and intermediate.

Bill and wing length, and weight were analyzed for each color category (Table 4). Data on tail lengths are excluded from this report because we found no significant differences among the geographic or TV tower samples. Small samples of the yellow and intermediate color categories make confident estimation of differences difficult. While not statistically different ($t = 0.96$, 10 d.f., $P > 0.30$) the mean bill lengths of yellow vs. intermediate birds corresponded almost exactly to prairie and boreal forest breeding specimens. The mean bill length of green fall birds was significantly different from intermediate birds ($t = 2.78$, 19 d.f., $P < 0.02$) and they corresponded to the most northern breeding specimens (Table 3).

Wing length showed a similar pattern with no statistically significant difference between yellow and intermediate categories ($t = 0.67$, 11 d.f., $P > 0.5$), but the difference between intermediate and green birds was significant ($t = 2.54$, 19 d.f., $P = 0.02$).

Body weight of yellow birds did not differ significantly from intermediate birds ($t = 0.52$, 11 d.f., $P > 0.5$), but did from green birds ($t = 2.81$, 19 d.f., $P < 0.02$). The difference between the mean weights of intermediate and green birds approached significance ($t = 1.86$, 18 d.f., $P = 0.08$).

Females.—The color of 29 adult females killed at the TV tower ranged from a drab gray-green back and head and dull tan ventral surface to individuals that were bright yellow ventrally and yellow-green dorsally. While the brightest colored individuals were almost certainly prairie birds, the overlap in color categories among females originating from different zones (Table 2) led us to conclude that we could not separate females by color with the confidence desired to indicate geographic origin for the majority of the sample. Females in fresh fall plumage rarely contain red streaking, and too few museum specimens were available to document geographic variation in this plumage.

We categorized TV tower-killed females by weight to detect possible differences in geographic origin, because male weights corresponded to documented geographic variation. We arbitrarily split the sample equally into females weighing more ($N = 14$) and less ($N = 15$) than 10 g (Table 5) and tested for differences in bill and wing lengths. The differences were significant for bill length ($t = 2.38$, 27 d.f., $P < 0.05$) and approached significance for wing length ($t = 1.83$, 27 d.f., $P = 0.08$).

Bill and wing lengths of the two weight groups corresponded closely to differences from south to north in breeding specimens as they did for males. Wing (and tail) measurements of birds in fresh fall plumage were longer than for June-July specimens because of abrasion.

DISCUSSION

The yellow-backed, long and thick-billed Yellow Warblers of our southernmost sample were mostly from within the described range of *D. p. aestiva*, while all of the remaining samples were from the described range of *D. p. amnicola* (American Ornithologists' Union 1957). Birds fitting the description of *aestiva* were found slightly farther north of the limit established in the checklist. The aspen parklands contained Yellow Warblers indistinguishable from birds from the northern prairies.

Males from the boreal forest regions from east-central Alaska to Hudson's Bay were relatively uniform in coloring. Yukon (D in Fig. 1) females differed in color, and both males and females from this region had significantly shorter bill lengths than other boreal forest samples. A cline toward darker, less distinct coloring and smaller extremities to the north culminated rather sharply near the arctic coast at the MacKenzie River Delta, as exhibited in the male sample.

MacKenzie River Delta males seem to fit more closely the description of *D. p. rubiginosa* (see Godfrey 1966) that breed on the south coast of Alaska to western British Columbia. We have not examined specimens from the range of *rubiginosa*.

The type locations for *amnicola* (Newfoundland) and *aestiva* (Quebec City) may contain specimens differing from our descriptions of midcontinent Yellow Warblers. Newfoundland *amnicola* resemble *aestiva* more closely than they resemble MacKenzie River Delta birds (K. C. Parkes, *in litt.*) and the type locality of *aestiva* is apparently in an area of intergradation (W. E. Godfrey, *in litt.*). We defer nomenclatural suggestions with respect to MacKenzie River Delta birds until more comparative study clarifies nomenclatural confusion and geographic variation throughout the range of the species. We conclude that Yellow Warblers between the prairie and arctic coast form a greater than 3,840 km (2,200 mi) continuous breeding population that exhibits classical clines of smaller extremities in progressively higher latitudes and darker coloration in more forested and in more humid coastal habitats.

We conclude that the significant differences in color and bill and wing lengths of males, and bill lengths of females of different weights killed at the TV tower demonstrate that Yellow Warblers originating from as much as 3,220 km (2,000 mi) apart were migrating on the same night. Massive waves of warbler migration in autumn occurring over broad fronts and many different species (e.g. see Kemper et al. 1966) are apparently responding to the same migration cues. Within these massive movements are far northern breeding birds migrating at the same time and over the same area as progressively more southern populations.

The more northern birds might be expected to be larger in body size in conformance with Bergmann's Rule as well as conforming to Allen's Rule. The lighter weights of TV tower killed specimens that conformed to morphological patterns of Yellow Warblers of more northern origin suggest that they had traveled farther and had not replenished fat stores (cf. Raveling and LeFebvre 1967). In comparison, the heavier weights of prairie origin warblers might be near their maximum as they were probably undertaking their first night's major migration when killed in west-central Minnesota.

Analysis of variation in morphological characters as well as of age and sex ratios and species composition of kills of passerines at TV towers should be continued, for it is certain to add greatly to our understanding of many species and their migration at a time of year when study by other means has been most difficult if not impossible.

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Appendix A

Yellow Warblers killed on 9–10 September 1962 at the Westport, Minnesota TV tower that are deposited in the Minnesota Museum of Natural History:

Males.—**Yellow**—MMNH Nos. 18930, 18931, 18933, 18935, 19017, 19025, 19026; **Intermediate**—MMNH Nos. 18928, 19009, 19013, 19021, 19022, 19024; **Green**—MMNH Nos. 18929, 18932, 18934, 19010, 19011, 19012, 19014, 19015, 19016, 19018, 19020, 19023, 19027.

Females.—> **10 g**—MMNH Nos. 19003, 19006, 19008, 19028; < **10 g**—MMNH Nos. 19000, 19002, 19004, 19005, 19007.