

PLUMAGE, MORPHOMETRIC, AND SONG VARIATION IN MOURNING (*OPORORNIS PHILADELPHIA*) AND MACGILLIVRAY'S (*O. TOLMIEI*) WARBLERS

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ABSTRACT.—Mourning (*Oporornis philadelphia*) and MacGillivray's (*O. tolmiei*) warblers are currently recognized as distinct species (AOU 1983). The specific status of these taxa, however, has been questioned based on morphological similarity and reports of hybridization in central Alberta (Cox 1973). I investigated the distinctness of these taxa by comparing plumage, skeletal, and primary song characters from fresh collections and recent tape recordings from the allopatric portions of their breeding ranges and the potential contact areas. The plumage analyses revealed overlap in characters originally used to diagnose these taxa; however, the incidence of extreme specimens was low. Separate multivariate analyses of morphological and song characters showed that the taxa are essentially distinct in multivariate space with little or no overlap. The Mourning Warbler was larger for most skeletal characters and had lower song frequencies. Plumage characters originally used to diagnose these taxa separate a majority of specimens, but they are ineffective for distinguishing extreme variants or hybrids. Song type proved 100% reliable in discriminating between taxa. I found no hybrid contact between these taxa. Furthermore, specimens collected near the potential contact zones were as variable morphologically as specimens from the allopatric portions of the breeding ranges. I believe these taxa should continue to be considered distinct species. Received 10 May 1989, accepted 9 September 1989.

MOURNING (*Oporornis philadelphia*) and MacGillivray's (*O. tolmiei*) warblers form an east-west species complex, whose breeding ranges meet in the northern Great Plains (*sensu* Rising 1983). The Mourning Warbler is the eastern taxon; it breeds in boreal forest from Newfoundland to northeastern British Columbia and south to West Virginia, parts of Michigan, Wisconsin, Minnesota, and North Dakota. MacGillivray's Warbler breeds in riparian habitat and disturbed second growth in the Rocky Mountains from northern Arizona to Alaska. Both taxa were described as separate species by Baird (1858) and are still considered separate (AOU 1983). Difficulty in identifying intermediate specimens, however, has caused some ornithologists (Chapman 1917, Phillips 1947, Hofslund 1962, Mengel 1964, Mayr and Short 1970) to speculate that these taxa are eastern and western subspecies. Accounts of hybrid contact (Cox 1973, Salt 1973) have cast doubt on their specific status.

The doubts are based on the equivocal nature of plumage characters originally used to diagnose these taxa (Table 1). Characters used in diagnoses are presumed to be unique to a given taxon and provide 100% discrimination of spec-

imens. Further examination of Mourning Warbler specimens from different parts of its breeding range revealed the presence of intermediate specimens that possessed either dark lores, eye-arcs, absence of black bibs, or some combination of these (Chapman 1917, Hall 1979). Lanyon and Bull (1967) acknowledged the equivocal nature of plumage characters and used an external measurement (Wing minus Tail: $W - T$) to separate 98% of Mourning and MacGillivray's warbler specimens. Their results, however, were based exclusively on samples from the allopatric portions of the breeding ranges. Kowalski (1983) found much more overlap in $W - T$, using specimens near the potential contact zones. This result suggests hybrid contact between the taxa.

Cox (1973) collected some Mourning Warblers with "MacGillivray's-like" characters in central Alberta and concluded that the taxa hybridized there. Taverner (1919) collected a suspected mixed pair (Mourning male and MacGillivray's female) in Nevis, Alberta; but, based on the $W - T$ measurement, this female falls into the range of the Mourning Warbler (Hall 1979). Hall (1979) was also not convinced

TABLE 1. Plumage characters used to diagnose adult Mourning and MacGillivray's warblers.

Character	Mourning Warbler	MacGillivray's Warbler
Lores ^a	Absent	Dark in males
Eye-arc ^a	Absent in adults, present in immatures	Present in adults and immatures
Black bib ^a	Concentration of black feathers on lower throat and upper breast, present in males only	Diffuse black feathering on throat and upper breast of males, absent in females
Wing-minus-tail ^b measure	≥10 mm	≤11 mm

^a Baird 1858, Coues 1903, Hall 1979.

^b Phillips 1947, Lanyon and Bull 1967.

that all intermediate specimens reported by Cox and others (Patti and Meyers 1976, Beimborn 1977) were hybrids because he found intermediate specimens of Mourning Warblers from the allopatric portions of its breeding range. These extreme variants from eastern Canada raise the question whether the intermediate nature of these specimens is due to hybridization or falls within the normal range of variability of either taxon.

My goal was to clarify the specific limits of these warbler taxa based on the distinctness of each taxon. I concentrated my analysis on males for two reasons: intermediate males show "hybrid characters" better than females and their singing behavior can be recorded and compared. I collected and compared fresh specimens from the allopatric portions of the breeding ranges and from the hypothetical contact areas, and I evaluated the range of variability and overlap in traditional plumage characters used to diagnose these taxa. I added two new suites of skeletal and behavioral characters to the analysis, and determined if specimens of these taxa occupy different "morphological or song space" based on principal components analyses (PCA) of morphological and song characters. Finally, I evaluated song syllable sharing by these taxa.

MATERIALS AND METHODS

Field methods.—Adult males were collected during the breeding season, between 6 June and 15 July from 1983 to 1986 (Fig. 1). In 1985 I concentrated my efforts in the potential contact areas in western Canada. Specimens were prepared in the field as flat skins and skeletons. All materials are at the American Museum of Natural History.

Whenever possible, I made tape recordings of *Oporornis* songs before collection. Not all specimens were recorded, however, nor were all recorded birds col-

lected. Recordings were made with a Uher-4000 Report Stereo and Dan Gibson E. P. M. 300 microphone. At least 10 songs per male were recorded before collection. At most localities, ≥30 songs were recorded from at least one male.

Morphology.—Because of the close morphological resemblance of these taxa and the paucity of plumage characters useful for diagnosis, hybrid indices were not considered appropriate. I scored all study skins for the presence or absence of eye-arcs and dark lores. Flattened wing measurements were made with a wing ruler (nearest 0.1 mm) and tail measurements were made with Max-cal Calipers (nearest 0.1 mm) according to Lanyon and Bull (1967). I also counted the number of males with $W - T$ measurements that fell within the intervals of $(W - T) < 8$ mm, 8 mm $< (W - T) < 9$ mm, 9 mm $< (W - T) < 10$ mm, 10 mm $< (W - T) < 11$ mm, 11 mm $< (W - T) < 12$ mm, 12 mm $< (W - T) < 13$ mm, $(W - T) > 13$ mm. I used histograms to display the frequency of Mourning vs. MacGillivray's warbler specimens with these characters. The song type of each specimen was also noted.

Analyses of skeletal characters provide an independent test of results obtained from plumage analyses (Troy 1985). Morphometric analyses of skeletal characters have been used successfully to discriminate sibling taxa of meadowlarks (*Sturnella*; Rowher 1972) and wood-pewees (*Contopus*; Rising and Schueler 1980). I used 25 skeletal dimensions from Robbins and Schnell (1971): premaxilla length (PRL), bill depth (BDEP), nasal bone width (NASW), interorbital width (INORW), skull width (SKW), skull length (SKL), mandible length (MANL), mandible depth (MAND), coracoid length (CORL), scapula width (SCAPW), sternum length (STERL), keel length (KEEL), keel depth (KEED), minimum synsacrum width (SYNMW), maximum synsacrum width (SYNW), femur distal end width (FEDW), femur length (FEL), tibiotarsus length (TIBL), tarsometatarsus length (TARL), tarsometatarsus depth (TARD), humerus trochanter length (HTRL), humerus distal end width (HDEW), humerus length (HURL), ulna length (ULNL), carpometacarpus length (CARPL). Skeletal dimensions were measured with Max-cal Calipers to the nearest 0.1 mm and entered

directly into a NEC Portable Computer (PC8201A) using Lessoft (version 1.0, Marcus 1982).

Song.—Song recordings were analyzed on a Kay Elemetrics 6061 Sona-Graph using wide band filter. Terminology of components and physical parameters follows Shiovitz (1975) and Baptista (1977). A *song note* is any continuous sound tracing on a sonograph. A *syllable* is a collection of notes, and a *song* is a collection of syllables. The different parts of primary song (I, II, III) in these taxa contained a unique single syllable type repeated several times. Songs were either *monosyllabic* (part I only), *disyllabic* (parts I and II), or *trisyllabic* (parts I, II, III).

Species differences in primary song most often occur in syllable/note morphology and/or frequency parameters (Becker 1982). I visually inspected syllables from each song and cataloged them based on differences in gross morphology (syllable catalogs in Pitocchelli 1988). I then compared syllables from both catalogs to determine the amount of syllable sharing between these taxa.

I analyzed differences between these taxa in the number of parts per song based on different syllable types (NPSO), number of syllables per song (NSSO), duration of song (DUR), minimum song frequency (MINS), maximum song frequency (MAXS), number of notes of the first syllable from part I of the song (NNA), number of notes of the first syllable from part II of the song (NFA), maximum frequency of the first syllable from part II of the song (MAFA), and maximum frequency of the second syllable from part II of the song (MAFB). Sonographs were measured with Max-cal Calipers to the nearest 0.1 mm and entered into a NEC Portable Computer-PC8201A (Marcus 1982). These measurements were later converted into kilohertz and seconds. I paid special attention to the songs of intermediate specimens (based on plumage or skeletal materials) of both taxa.

Statistics.—Multivariate analyses reorganize the total variation among correlated variables to a new set of uncorrelated variables. Several multivariate approaches have been applied in phenetic analyses involving the discrimination of operational taxonomic units (OTUs) (Sokal and Sneath 1963, Thorpe 1976). I used principal components analysis (PCA) to investigate the distinctness of these taxa in multivariate space based on external study skin measurements, skeletal measurements, and physical parameters of song. The following variables were used in these analyses: external measurements—Wing, Tail, Wing minus Tail ($W - T$); skeletal measurements—NASW, MANL, CORL, KEEL, FEL, ULNL, HUML; and song parameters—NPSO, NSSO, DUR, MINS, MAXS, NNA, NFA, MAFA, MAFB. Analyses of these data sets were conducted using PROC PRINCOMP in SAS (version 5.16, 1985). Raw data were \log_{10} -transformed prior to each multivariate analysis. I extracted PC scores for each specimen along the first three principal component axes from a variance-covariance matrix. I plot-

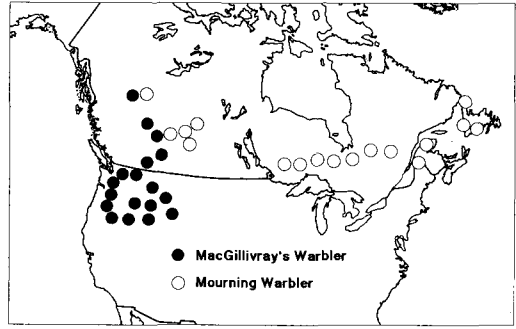


Fig. 1. Sampling localities of Mourning and MacGillivray's warblers (precise localities are available from the author).

ted the principal component (PRIN) scores in three dimensional space along the PRIN1, PRIN2, and PRIN3 axes. I rotated the plots along the x , y , and z axes using MACSPIN (version 2.0, 1988) until maximum separation of Mourning and MacGillivray's OTUs was achieved.

RESULTS

Studies of hybridization in birds have included samples from pure populations for comparisons with specimens from the contact zones (Rising 1983). I made collections and tape recordings of Mourning and MacGillivray's warblers from pure, well-marked populations in the allopatric regions of their breeding ranges and from the potential contact areas in Alberta and British Columbia. Mourning Warblers from Ontario, New York, and Quebec represented the allopatric portion of their breeding range. Allopatric samples of MacGillivray's Warblers came from south-central British Columbia, Washington, Oregon, California, Idaho, Nevada, Montana, and Wyoming. I collected 534 males of both taxa for plumage and skeletal analyses. The allopatric samples contained 218 Mourning and 236 MacGillivray's warblers. In 1985, I sampled contact areas previously reported by Erskine and Davidson (1976) in northeastern British Columbia, and by Cox (1973) and Salt (1973) in central Alberta. I collected and recorded birds along the Alaska Highway from the Liard River Hot Springs to Fort Nelson in northern British Columbia. In Alberta, I sampled from Lesser Slave Lake through Whitecourt, Obed, Brazeau Reservoir, Battle Lake, Red Deer to the Sheep River. This transect also included the sites studied by Cox

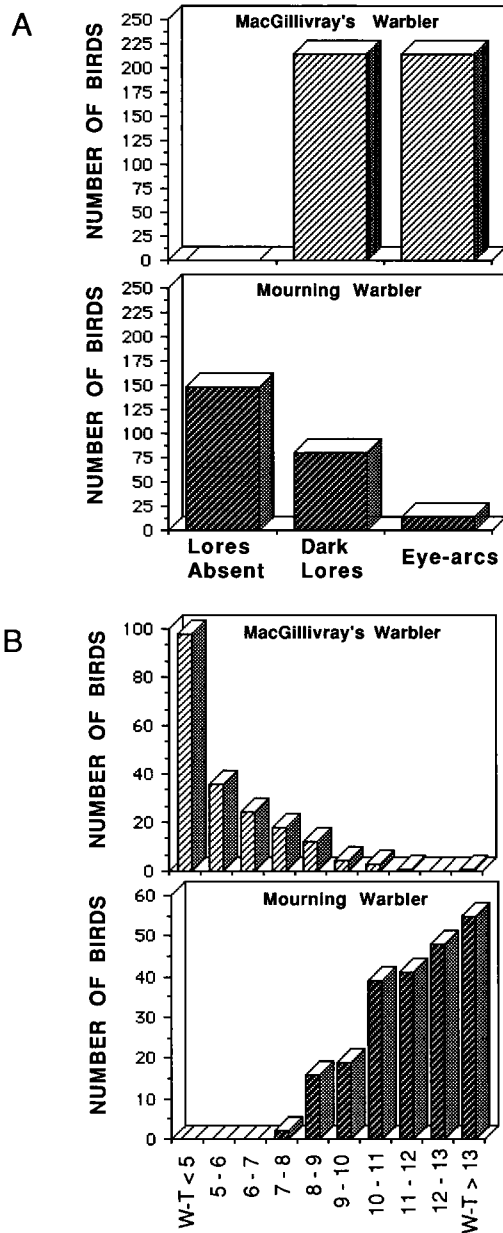


Fig. 2. Histograms of MacGillivray's and Mourning warbler specimens with traditional characters used to diagnose these taxa. (A) Frequency distributions of eye-arcs and dark lores. (B) Frequency distributions of specimens with wing-minus-tail ($W - T$) measurements (mm) falling in specified intervals.

(Rocky Mountain House, Caroline, Kananaskis) and Salt (Pigeon Lake) in 1973. I collected 49 Mourning Warblers and 29 MacGillivray's Warblers from these potential contact areas.

I taped singing males from the same localities. I recorded 137 Mourning Warblers from eastern Canada and 58 males from the contact areas. MacGillivray's males (116) were recorded in the northwestern United States and southern British Columbia. I recorded 19 males near the potential contact areas.

MORPHOLOGICAL CHARACTERS

External characters.—There was some overlap in plumage characters (Fig. 2). MacGillivray's Warblers were not variable for dark lores or eye-arcs. Extreme MacGillivray's Warblers resembled Mourning Warblers only in the wing-minus-tail ($W - T$) measurement. Extreme MacGillivray's Warblers were found in the allopatric parts of the breeding range and potential contact areas in Alberta and British Columbia. Four of these birds were from the allopatric regions (southern British Columbia, Washington, and Oregon) whereas two came from near the contact areas. All these extreme specimens sang only MacGillivray's song. Plumage characters of Mourning Warblers were more variable (Fig. 2). These birds either had dark lores, eye-arcs, ($W - T$) < 11 mm, lacked a black bib, or some combination of these characters. Although most Mourning Warblers lack dark lores, males with lores were found in small numbers throughout the breeding range. Extreme birds with eye-arcs were also uncommon (Fig. 2). There was no segregation or increase in intermediate specimens near the contact areas. For instance, there were higher incidences of males with eye-arcs in some Ontario localities (Dorion: 11.1% males with eye-arcs; Geraldton: 14.2%; and Cochrane: 16.6%) than in the potential contact areas in central Alberta (5.2%). All extreme Mourning Warbler specimens sang Mourning Warbler songs (Fig. 3: A, C). Although these external characters will work for most specimens, they are equivocal for extreme specimens.

MacGillivray's Warblers averaged longer tails than Mourning Warblers, which accounts for the smaller $W - T$ measurements (Table 2). Principal components analyses of external measurements (W , T , $W - T$) revealed little overlap in multivariate space (Fig. 4: A). Wing-minus-tail measurement had the highest loading on PRIN1 and contributed most to the separation along the PRIN1 axis (Table 3). PRIN1 accounted for 99% of the variance. In most morpho-

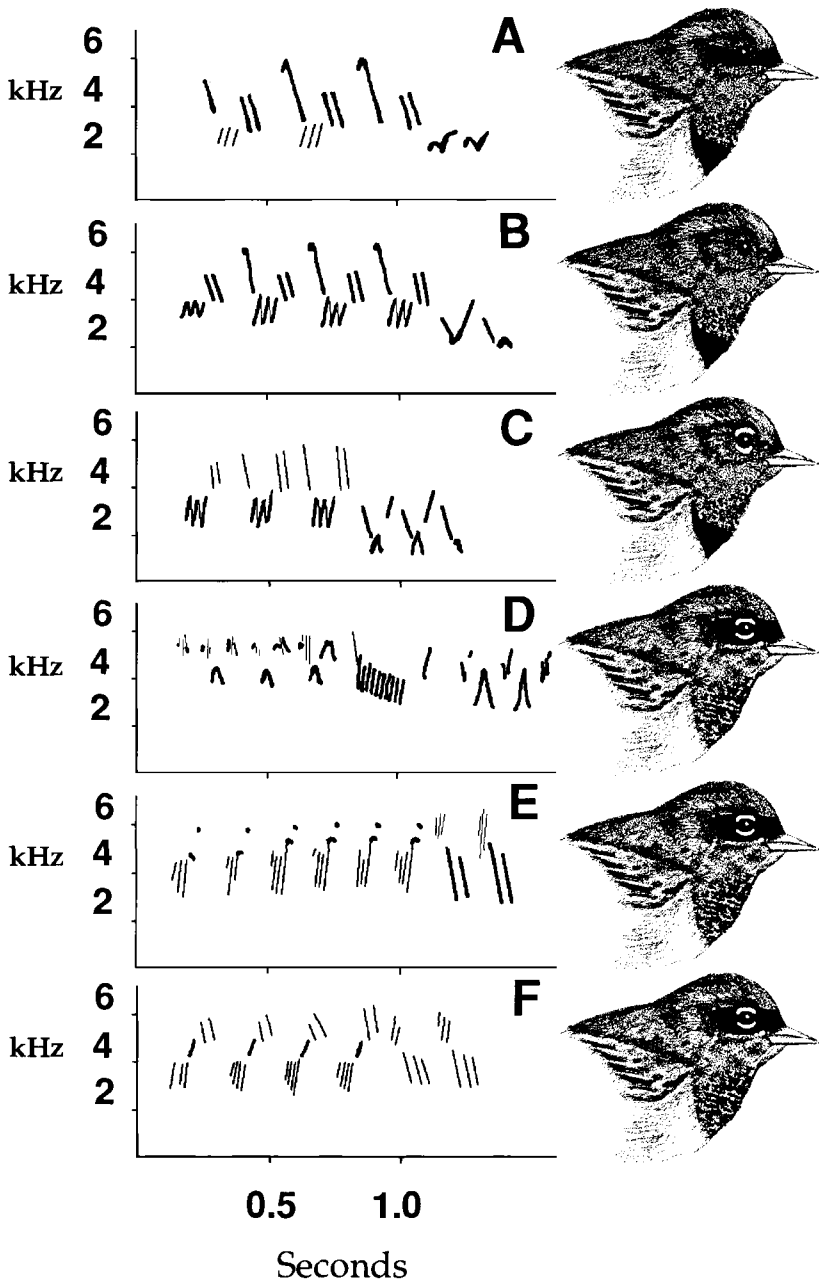


Fig. 3. Sonograms of Mourning and MacGillivray's warbler songs. (A) Ontario Mourning Warbler male (AMNH 13365) with dark lores; (B) Maine Mourning Warbler male (AMNH 13263) lacking eye-arcs or dark lores; (C) Quebec Mourning Warbler male (AMNH 13333) with eye-arcs; (D) MacGillivray's Warbler male (AMNH 14358); (E) MacGillivray's male (AMNH 14362); (F) MacGillivray's male (AMNH 14363). The three MacGillivray's males (D-F) were neighbors from Jarbidge, Nevada. AMNH refers to American Museum of Natural History skeletal specimen catalog numbers. Warbler sketches by Ken Davignon and Jay Pitocchelli.

TABLE 2. Elementary statistics of *Oporornis* skeletal and external characters.

Character ^a	Mourning Warbler		MacGillivray's Warbler	
	<i>n</i>	Mean (SD)	<i>n</i>	Mean (SD)
PRL	230	13.72 (0.62)	176	13.43 (0.54)
BDEP	245	1.12 (0.11)	180	1.06 (0.12)
NASW	249	5.95 (0.33)	170	5.62 (0.28)
INORW	240	3.03 (0.24)	165	2.66 (0.18)
SKW	221	13.35 (0.31)	121	13.38 (0.25)
SKL	194	30.74 (0.73)	122	30.42 (0.60)
MANL	235	22.32 (0.62)	167	21.89 (0.54)
MAND	252	1.51 (0.08)	187	1.39 (0.08)
CORL	238	14.59 (0.36)	184	13.81 (0.37)
SCAPW	251	1.94 (0.18)	191	1.78 (0.14)
STERL	222	16.44 (0.52)	165	15.37 (0.54)
KEEL	222	14.71 (0.60)	171	13.58 (0.66)
KEED	225	6.32 (0.34)	172	5.84 (0.34)
SYNMW	220	8.90 (0.27)	152	8.79 (0.29)
SYNW	235	5.04 (0.26)	168	4.99 (0.24)
FEDW	242	2.61 (0.08)	188	2.53 (0.08)
FEL	232	15.48 (0.44)	171	14.76 (0.39)
TIBL	156	28.14 (0.71)	44	27.51 (0.65)
TARL	189	20.57 (0.62)	146	20.60 (0.60)
TARD	229	2.21 (0.23)	174	2.07 (0.17)
HTRL	249	3.64 (0.15)	164	3.48 (0.10)
HDEW	244	3.30 (0.14)	151	3.24 (0.11)
HUML	236	14.50 (0.30)	136	13.93 (0.37)
ULNL	187	16.53 (0.50)	129	16.03 (0.41)
CARPL	159	9.46 (0.36)	135	9.20 (0.29)
WEIGHT	239	12.27 (0.67)	139	11.17 (0.73)
WING	270	61.56 (1.95)	211	60.15 (2.10)
TAIL	263	49.32 (2.01)	202	54.78 (2.99)
W - T	261	12.21 (2.00)	202	5.37 (2.72)

^a All measurements except WEIGHT (g) are in mm.

metric studies with PCA, PRIN1 has been interpreted as a "size" axis when all the character loadings on PRIN1 are positive (Zink 1988). Because Tail had a negative loading on PRIN1, it is unclear whether PRIN1 is a size axis in this analysis. Inclusion of W - T in the PCA is probably responsible for this negative loading. Tail and Wing contributed most to the separation of these taxa on the PRIN2 and PRIN3 axes. PRIN2 and PRIN3, however, accounted for only 0.67% of the variance (Table 3).

Skeletal characters.—Overall, the average Mourning Warbler is larger than the MacGillivray's Warbler for all skeletal characters except skull width and tarsometatarsus length (Table 2). Results of the PCA of skeletal characters show that these taxa are essentially distinct in multivariate space (Fig. 4: B). All seven skeletal characters had positive loadings on PRIN1 which indicates that PRIN1 is a "size" axis (Table 3). PRIN1 accounted for 58.5% of the

TABLE 3. Eigenvectors of principal component analyses (PCA) of external, skeletal, and song characters.^a

Character	PRIN1	PRIN2	PRIN3
External character			
WING	0.019	0.626	0.779
TAIL	-0.103	0.776	-0.621
W - T	0.994	0.068	-0.080
% of total variance	99.2	0.6	0.07
Skeletal character			
NASW	0.507	-0.830	0.078
MANL	0.174	-0.116	-0.036
CORL	0.360	-0.135	0.214
KEEL	0.593	0.334	-0.713
FEL	0.313	0.274	0.411
ULNL	0.239	0.235	0.422
HUML	0.273	0.190	0.299
% of total variance	58.5	18.4	8.4
Song character			
NPSO	0.079	-0.035	0.076
NSSO	0.170	-0.097	0.318
DUR	0.145	-0.017	0.229
MINS	0.210	-0.155	0.318
MAXS	0.122	0.072	0.166
NNA	0.057	0.956	0.248
NFA	0.788	0.104	-0.595
MAFA	0.348	-0.091	0.324
MAFB	0.371	-0.161	0.435
% of total variance	44.0	31.0	11.7

^a Three separate PCAs (external, skeletal, and song analyses) were performed on specimen and song data.

variance. KEEL length and NASW had the highest loadings on PRIN1. They provided the best separation of specimens along this axis. NASW contributed the most to separation of specimens along PRIN2. PRIN2 accounted for 18.4% of the variance. KEEL had the highest loadings on PRIN3 which accounted for 8.4% of the total variance.

SONG CHARACTERS

Although males of both taxa sang univalent song repertoires, differences exist in the syllable repertoire and the pattern of geographic variation in these syllables. There were five MacGillivray's syllables which remotely resembled Mourning syllables. They were not exact duplicates, differing in syllable morphology, frequency, and duration parameters. Geographic variation in Mourning Warbler song is conservative compared with that of MacGillivray's Warbler. The breeding range of the Mourning Warbler is dominated by three regional dialects.

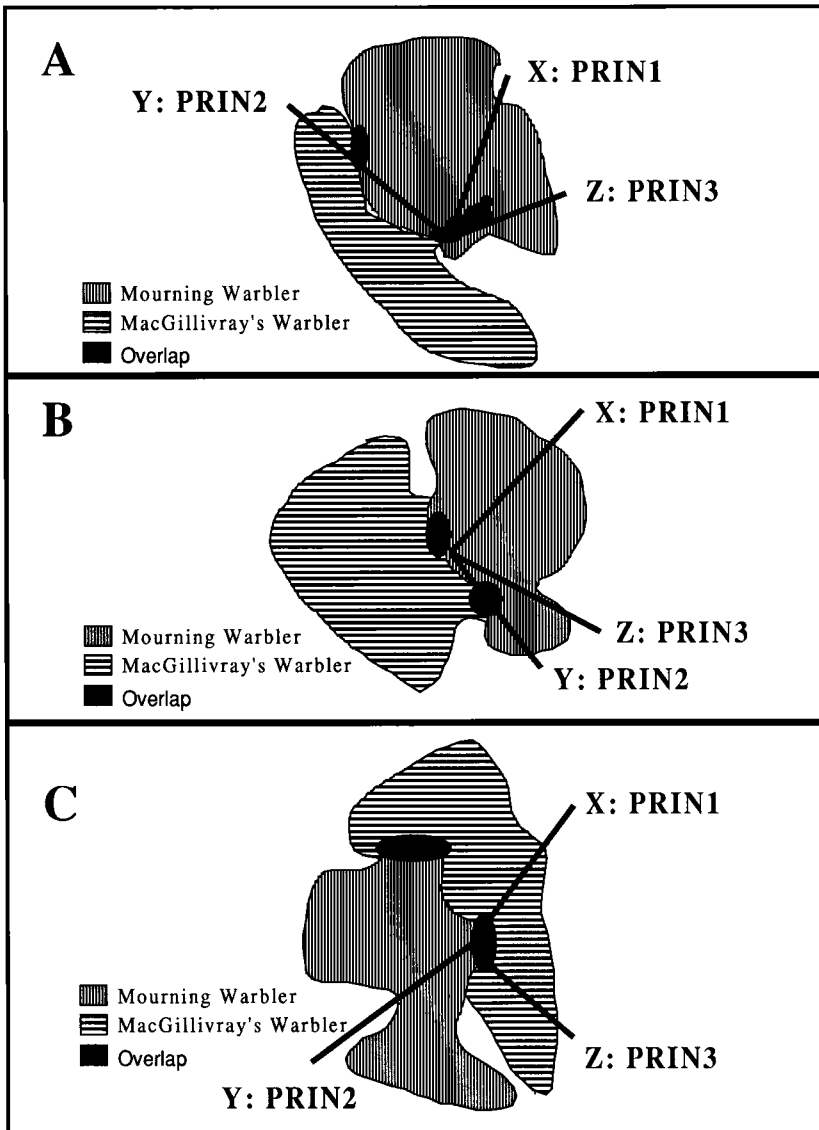


Fig. 4. Plot of specimens and songsters on principal component axes I, II, III, showing minimal overlap between taxa. Shaded areas represent clouds of points occupied by individuals in multivariate space. (A) Plots based on analysis of Wing, Tail, and W - T measurements; (B) plots based on analysis of seven skeletal characters; (C) plots based on analysis of nine song parameters.

In these dialect systems all birds sing the same song type, differing primarily in the number of syllables and/or physical parameters. In contrast, almost every male MacGillivray's Warbler sang a different song type (Fig. 3: D, E, F). The total number of syllables encountered versus the number of birds sampled was higher for MacGillivray's Warblers compared with Mourning Warblers (Fig. 5).

Mourning Warblers sang lower frequency songs on average compared with MacGillivray's males (Table 4). Mourning Warblers also sang less complex songs. MacGillivray's males sang two- or three-part songs, which contained two or more syllable types. In contrast, most western Mourning Warblers sang one-part monosyllabic songs, whereas most eastern males sang two-part songs. MacGillivray's songs averaged more

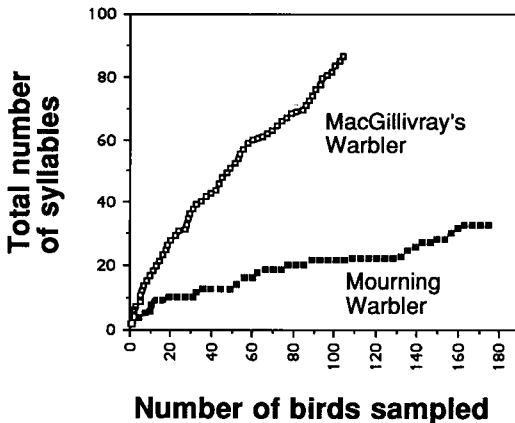


Fig. 5. Number of new syllables encountered with each new songster sampled for Mourning and MacGillivray's warblers.

NFA and NSSO (Table 4). Principal components analysis of song parameters revealed good separation of these taxa in multivariate space (Fig. 4: C). Loadings of parameter variables on PRIN1 were all positive (Table 3). The NPSO and NFA provided most of the separation of songsters along PRIN1. PRIN1 accounted for 44.0% of the variance. NNA contributed to the separation of songsters along PRIN2, which accounted for 31.0% of the variance. PRIN3 accounted for only 11.7% of the variation. Contributions from NFA and MAFB were largely responsible for separation along this axis.

HYBRID CONTACT

Contact between these taxa is different from other east-west species pairs (e.g. flickers, towhees, orioles, buntings), which hybridize in broad zones across the Great Plains (for review, see Rising 1983). Mourning and MacGillivray's warblers meet irregularly in British Columbia and Alberta. In Alberta, Mourning Warblers breed north of Kananaskis in disturbed second growth throughout the province (Salt 1973). MacGillivray's Warblers are limited to the Cypress Hills in southeastern Alberta and the Rocky Mountain region from Kananaskis south in southwestern Alberta and along the Red Deer River. In British Columbia, MacGillivray's Warblers are much more common than Mourning Warblers. They are found throughout British Columbia, whereas the Mourning Warbler is restricted to the northeastern corner of British

Columbia at the edge of the boreal forest (Erskine and Davidson 1976).

Cox (1973) and Salt (1973) observed contact in central Alberta. Cox (1973) described "contact points" in central Alberta that involved one or two individuals from one taxon mixing with many individuals from the other taxon. On the Bow River near Kananaskis, he collected a single Mourning female mixed in with MacGillivray's Warblers. I collected seven MacGillivray's Warblers in Kananaskis, but I did not collect or observe any Mourning Warblers. Cox also mist-netted four intermediate (but see Hall 1979) specimens 9 km west of Rocky Mountain House and 27 km west of Caroline near Red Deer. I did not find intermediates or members of either taxon at the Caroline or Rocky Mountain House locations. I also found neither the pure Mourning Warbler populations near Red Deer nor the pure MacGillivray's Warbler populations at Trochu reported by Cox (1973).

Salt (1973) found a single MacGillivray's male singing among several Mourning Warblers at Pigeon Lake, south of Edmonton, but I found only Mourning Warblers at Pigeon and Battle lakes. I collected both taxa west of Edmonton along the Athabasca River. I tape-recorded one MacGillivray's male and collected another near Hinton. The closest Mourning Warblers were 50 km east of Hinton, north of Obed. This was the closest these taxa came to one another during the summer of 1985. The Mourning Warbler does not occur in the foothills of the Rocky Mountains, and MacGillivray's Warblers rarely enter into the foothills from the mountains. The dry lodgepole pine forest of the foothills does not provide the dense undergrowth for breeding required by these taxa. The rare spillover of MacGillivray's Warblers into the foothills and beyond, in combination with the destruction of boreal forest for farming and ranching in central Alberta, limits contact between these taxa.

Erskine and Davidson (1976) and British Columbia Hydro (1981, MS) reported similar contact between these taxa in north-central British Columbia at Liard River Hot Springs. I sampled along the Alaska Highway from Liard River east to Fort Nelson. I collected individuals with MacGillivray's plumage and song types at Liard River. The closest Mourning Warblers were ca. 200 km east of Liard River at Steamboat, Kledo Creek, and Fort Nelson. Erskine (pers. comm.) pointed out that previous accounts of Mourning Warblers at Liard River probably refer to mi-

TABLE 4. Elementary statistics of physical parameters of *Oporornis* song.

Character	Mourning Warbler		MacGillivray's Warbler	
	<i>n</i>	Mean (SD)	<i>n</i>	Mean (SD)
NPSO	188	1.72 (0.45)	116	2.04 (0.62)
NSSO	186	5.68 (1.05)	115	6.99 (1.56)
DUR ^a	182	1.11 (0.17)	112	1.29 (0.22)
MINS ^b	187	1,933.24 (301.04)	111	2,416.05 (334.50)
MAXS ^b	180	5,458.81 (699.44)	107	5,953.18 (648.48)
NNA	174	4.58 (1.36)	100	4.38 (1.42)
NFA	133	2.54 (0.83)	95	4.34 (1.80)
MAFA ^b	132	3,975.13 (558.52)	95	5,437.49 (801.62)
MAFB ^b	122	3,744.93 (615.41)	85	5,388.10 (788.62)

^a Duration variables in seconds.

^b Frequency variables in Hz.

grants or vagrants but not to breeders. For 200 km between Fort Nelson and Liard River Hot Springs, there is a dry lodgepole pine forest that lacks suitable breeding habitat for either taxon. This acts as a barrier to contact between these taxa.

Further contact between these taxa seems unlikely. In British Columbia, the breeding ranges do not come close together. Agricultural practices in Alberta have been largely responsible for widening the gap between Mourning and MacGillivray's warblers. Beneath the foothills of the Rocky Mountains, farming and ranching are destroying suitable breeding habitat for Mourning Warblers and thus pushing the breeding range of the Mourning Warbler eastward and northward away from any potential contact.

DISCUSSION

Species limits.—These taxa overlap in plumage characters, but the incidence of overlap is low. Very few MacGillivray's Warblers resemble Mourning Warblers, and then only for the wing-minus-tail ($W - T$) character. Although many more Mourning Warblers possess eye-arcs, dark lores, or $(W - T) < 11$ mm, none of the intermediate Mourning specimens I studied possessed all three MacGillivray's characters. In contrast to plumage, PCA of the external and skeletal measurements show separation of these taxa (Fig. 4: A, B). Because these taxa do not hybridize in large zones, the intermediacy of problem specimens cannot be due to hybridization events. Intermediate individuals simply fall within the normal range of variability for each taxon.

Bush (1975) emphasized the importance of bird song as an example of a prezygotic isolat-

ing mechanism. Vocal characters have proved to be useful tools for evolutionary biologists (Lanyon 1969). Studies of *Empidonax* (Stein 1963, Johnson 1980) and *Myiarchus* flycatchers (Lanyon 1978) have shown the value of song characters in delimiting sibling taxa. Major differences in primary song also occur between Mourning and MacGillivray's warblers. Although there is geographic variation in song in both taxa, there is no syllable sharing between these taxa, and the pattern of geographic variation in these syllables is different in each taxon. Almost every MacGillivray's male sang a unique song. In contrast, the breeding range of the Mourning Warbler was dominated by three major dialect systems (Pitocchelli 1988). Furthermore, there is evidence of song displacement in these taxa. The western dialect system of Mourning Warbler males is dominated by one-part monosyllabic songs, whereas MacGillivray's male sing two- and three-part songs. Two-part songs dominate the eastern dialect systems of the Mourning Warbler. Based on principal component analyses of physical parameters of song, operational taxonomic units (OTUs) of each taxon occupy a unique portion of "song space." Mourning males with two-part songs use different syllables and occupy separate song space from MacGillivray's males with two-part songs (Fig. 4: C). Song differences are strong and consistent throughout the ranges of these taxa. Song types of eastern and western Mourning Warbler specimens that were intermediate for plumage characters were similar to "normal" plumage neighbors. Mourning Warbler males with eye-arcs or dark lores sang the same songs as Mourning Warblers that lacked these characters (Fig. 3: A, B, C). MacGillivray's Warblers which resembled Mourning Warblers

for the W – T measurement did not have songs with Mourning Warbler syllables. This problem is similar in other sibling species where behavioral differentiation may have proceeded faster than morphological characters. Although these communications systems appear unique to each taxon, the role of learning versus the influence of behavior on song has not been investigated.

The central question of my study was whether to ascribe specific status to these taxa or combine them into a single taxon as two subspecies. Traditionally, interbreeding has been the most important criterion for making this judgment (Mayr 1969), but some authors stress genotypic and phenotypic distinctness over the ability to interbreed (Cracraft 1983, McKittrick and Zink 1988). In my opinion, Mourning and MacGillivray's warblers should continue to be considered separate species, based on the distinctness of their primary song and skeletal differences. Although their plumages are similar, operational taxonomic units of these taxa occupy different portions of morphological and song space. The different patterns of geographic variation in primary song—conservative in Mourning Warblers versus highly variable in MacGillivray's Warblers—also point to separate evolutionary histories. These taxa are also still essentially allopatric, and hard evidence of assortative mating is unattainable. Results of preliminary playback experiments simulating sympatry between these taxa revealed that males of both taxa can discriminate conspecific from experimental song types (Salt 1973, Pitocchelli 1988). Only 1 of the 25 Mourning and MacGillivray's warblers was unable to discriminate between song types. This supports the importance of the distinctness of primary song in these taxa and also points to positive assortative mating if and when these taxa come back together.

Identification of extreme specimens.—Identification of extreme specimens continues to be a problem for this complex. Except for song type, no single character distinguishes these taxa 100% of the time, and song is useless for females and migrants. Although W – T appears to be the best morphological character, my results and Kowalski's (1983) have shown that it is equivocal for separating some extreme specimens. Most problem specimens have been Mourning Warblers that resemble MacGillivray's Warblers for one but usually not all plumage characters. Combinations of these characters are useful for identifying extreme specimens. Full eye-arcs contain thick layers of white feathers above and

below the eye. Eye-arcs in Mourning Warblers are usually weak, but some extreme specimens may resemble full eye-arcs of MacGillivray's Warblers. If, in spring, males east of the Rocky Mountains do not possess eye-arcs and dark lores, then they are Mourning Warblers. If they possess both, then refer to the song type (if possible) and the W – T measurement. Although I collected females, the sample sizes were much lower than in Lanyon and Bull (1967). Therefore, for identification of females, refer to the quality of the eye-arc (thick versus weak) and Lanyon and Bull's W – T measurement for separation.

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LITERATURE CITED

- AMERICAN ORNITHOLOGISTS' UNION. 1983. Check-list of North American birds. Sixth ed. Washington, D.C., Am. Ornithol. Union.
- BAIRD, S. F. 1858. Pacific Railroad Surveys, vol. 9, part 2. Washington, Beverly Tucker Printers.
- BAPTISTA, L. F. 1977. Geographic variation in song dialects of the Puget Sound White-crowned Sparrow. *Condor* 79: 356-370.

- BECKER, P. H. 1982. The coding of species-specific characteristics in bird sounds. Pp. 214-252 in *Acoustic communication in birds*, vol. 1 (D. Kroodma and E. H. Miller, Eds.). New York, Academic Press.
- BEIMBORN, D. 1977. Possible MacGillivray's × Mourning warbler hybrid. *Passenger Pigeon* 39: 257-258.
- BUSH, G. L. 1975. Modes of animal speciation. *Annu. Rev. Ecol. Syst.* 6: 339-364.
- CHAPMAN, F. M. 1917. *The warblers of North America*. New York, Dover Reprint Ed. (1968).
- COX, G. W. 1973. Hybridization between Mourning and MacGillivray's warblers. *Auk* 90: 190-191.
- COUES, E. 1903. *Key to North American Birds*. Boston, Dana Estes and Co.
- CRACRAFT, J. 1983. Species concepts and speciation analysis. Pp. 159-187 in *Current ornithology*, vol. 1. (R. F. Johnston, Ed.). New York, Plenum Press.
- ERSKINE, A. J., & G. S. DAVIDSON. 1976. Birds in the Fort Nelson lowlands of northeastern British Columbia. *Syesis* 9: 1-11.
- HALL, G. 1979. Hybridization between Mourning and MacGillivray's warblers. *Bird-Banding*. 50: 101-107.
- HOFSLUND, P. B. 1962. The genus *Oporornis*. *Flicker* 34: 43-47.
- JOHNSON, N. K. 1980. Character variation and evolution of sibling species in the *Empidonax difficilis-flavescens* complex. *Univ. Calif. Publ. Zool.* vol. 112.
- KOWALSKI, M. P. 1983. Identifying Mourning and MacGillivray's warblers: geographic variation in the MacGillivray's Warbler as a source of error. *North American Bird Bander* 8: 56-57.
- LANYON, W. E. 1969. Vocal characters in avian systematics. Pp. 291-310 in *Bird vocalizations* (R. A. Hinde, Ed.). Cambridge, Cambridge Univ. Press.
- . 1978. Revision of the *Myiarchus* flycatchers of South America. *Bull. Am. Mus. Nat. Hist.* 161: 429-621.
- , & J. BULL. 1967. Identification of Connecticut, Mourning and MacGillivray's warblers. *Bird-Banding* 38: 187-194.
- MACSPIN. 1988. Graphical data analysis and decision support software (version 2.0). Austin, D² Software, Inc.
- MARCUS, L. 1982. A portable, digital printing caliper. *Curator* 25: 223-226.
- MAYR, E. 1969. *Principles of systematic zoology*. New York, McGraw-Hill Book Co.
- , & L. L. SHORT. 1970. Species taxa of North American birds. *Publ. Nuttall. Ornithol. Club*. 9.
- McKITRICK, M., & R. M. ZINK. 1988. Species concepts in ornithology. *Condor* 90: 1-14.
- MENGEL, R. M. 1964. The probable history of species formation in some northern wood warblers (Parulidae). *Living Bird* 3: 9-43.
- PATTI, S. T., & M. L. MEYERS. 1976. A probable Mourning × MacGillivray's warbler hybrid. *Wilson Bull.* 88: 490-491.
- PHILLIPS, A. R. 1947. The races of MacGillivray's Warbler. *Auk* 64: 296-300.
- PITOCHELLI, J. 1988. Character variation in the *Oporornis philadelphia-Oporornis tolmiei* complex. Ph.D. dissertation. New York, City University of New York.
- RISING, J. D. 1983. The Great Plains hybrid zones. Pp. 131-157 in *Current ornithology*, vol. 1. (R. F. Johnston, Ed.). New York, Plenum Press.
- , & F. W. SCHUELER. 1980. Identification and status of Wood Pewees (*Contopus*) from the Great Plains: what are sibling species? *Condor* 82: 301-308.
- ROBBINS, J. D., & G. SCHNELL. 1971. Skeletal analysis of the *Ammodramus-Ammospiza* grassland sparrow complex: a numerical taxonomic study. *Auk* 88: 567-590.
- ROHWER, S. A. 1972. A multivariate assessment of interbreeding between the meadowlarks, *Stur-nella*. *Syst. Zool.* 21: 313-338.
- SALT, W. R. 1973. Alberta vireos and wood warblers. *Publ. 3, Prov. Mus. Arch. Alberta*.
- SAS Institute. 1985. *SAS user's guide: statistics* (version 5.16). Cary, SAS Institute Inc.
- SHIOVITZ, K. A. 1975. The process of species-specific song recognition by the Indigo Bunting, *Passerina cyanea*, and its relationship to the organization of avian acoustical behaviour. *Behaviour* 55: 128-179.
- SOKAL, R. R., & P. H. A. SNEATH. 1963. *Principles of numerical taxonomy*. San Francisco, W. H. Freeman Co.
- STEIN, R. C. 1963. Isolating mechanisms between populations of Trail's Flycatchers. *Proc. Am. Phil. Soc.* 107: 21-50.
- TAVERNER, P. A. 1919. The birds of the Red Deer River, Alberta. *Auk* 36: 1-21, 248-265.
- THORPE, R. S. 1976. Biometric analyses of geographic variation and racial affinities. *Biol. Rev.* 51: 407-452.
- TROY, D. M. 1985. A phenetic analysis of the Redpolls *Carduelis flammula flammula* and *C. hornemanni exilipes*. *Auk* 102: 82-96.
- ZINK, R. M. 1988. Evolution of Brown Towhees: allozymes, morphometrics and species limits. *Condor* 90: 72-82.