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GEOGRAPHIC VARIATION IN SIZE OF THE EASTERN KINGBIRD

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ABSTRACT.—We analyzed geographic variation in 12 (female) and 14 (male) morphometric characters of 428 (264 male and 164 female) Eastern Kingbirds (*Tyrannus tyrannus*) from North America. There is significant sexual dimorphism in the Eastern Kingbird: males have longer tails, wing-tips, and bills than females. This perhaps reflects the aerial courtship displays and aggressive territorial defense performed principally by males. There appears to be little difference in size between the sexes. There is no geographic variation in the degree of sexual dimorphism, indicating either that the extent of dimorphism is not influenced by interspecific competition (as predicted by the niche variation hypothesis) or that such competition is not significant for *T. tyrannus*. Although there is significant geographic variation in both sexes for all variables measured, the amount of this variation is slight and not clearly ordered in a geographic pattern. Eastern Kingbirds, for example, do not seem to show variation that conforms to Bergmann's Rule. In both sexes, there is a northwest-to-east trend of decreasing size for most characters measured, but a posteriori tests delimit few, and broadly overlapping, statistically homogeneous sets. There is no indication of character displacement in size in populations where *T. tyrannus* is sympatric with congeners even though their ecology and habits are similar. *Received 3 Sept. 1991, accepted 25 April 1992.*

The Eastern Kingbird (*Tyrannus tyrannus*) breeds from north-central British Columbia, northwest Saskatchewan, central Manitoba, central Ontario, southern Quebec, Prince Edward Island, and Nova Scotia south to northeastern California, northern Nevada, northern Utah, northeastern New Mexico, the Gulf coast of the United States, and southern Florida (A.O.U. 1983, Fig. 1). The species is migratory and winters in South America. Although the Eastern Kingbird is widespread and one of the commonest North American breeding birds, there has been no comprehensive study of geographic variation of the species (Zink and Remsen 1986). Here we describe patterns of geographic variation in size and sexual dimorphism on the basis of measurements of specimens taken from virtually throughout the species' range, and test hypotheses about the evolution of geographic variation.

MATERIALS AND METHODS

Populations.—We measured 428 specimens (see Acknowledgments) collected between May and August, when the birds are breeding, and thus all probably breeding individuals. At that time of year, all individuals are to some extent worn, but we omitted from analyses birds that were judged to be damaged excessively. We examined (264 males, 164 females)

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FIG. 1. The distribution of Eastern Kingbirds (*Tyrannus tyrannus*).

specimens from most parts of the species' range; unfortunately Florida was excluded because of small sample size. We analyzed sexes separately, and initially sorted both sexes into 10 geographic populations, from regions of approximately equal size (5° latitude and 10° longitude), each containing at least 17 males and 10 females (Fig. 2). These samples were used to quantify sexual dimorphism. After finding significant size dimorphism, we sorted specimens into 18 populations of males and 10 populations of females for analyses of geographic variation (Tables 1 and 2). These samples are of somewhat unequal geographic size, but each contains approximately the same number of individuals. This enabled us to increase the extent of geographic coverage. We identify regions by the name of a province or state prominently included in the samples.

Characters.—Following Baldwin et al. (1931), MacKenzie measured the following 12 features on each study skin with dial calipers to the nearest 1.0 mm for feathers, and to the nearest 0.1 mm for bill and tarsus: *wing length* (*WL*), the cord of the unflattened, closed wing from the farthest anterior point on the anterior edge of the wrist joint to the tip of the longest primary feather; *wing-tip to 10th* (*T10*), *wing-tip to 5th* (*T5*), *wing-tip to 4th* (*T4*), and

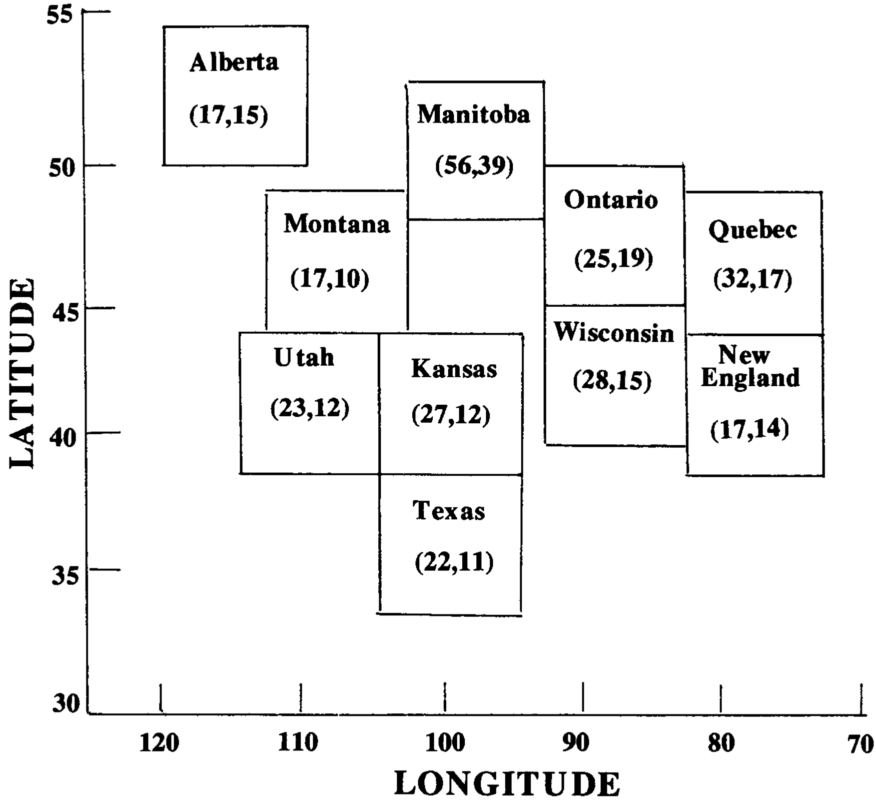

FIG. 2. Geographical positions of the samples used to determine patterns of sexual dimorphism in Eastern Kingbirds. Numbers of males and females are in parentheses. Each sample includes areas outside the area of the sample name. For example, the sample named Utah includes birds from parts of Idaho, Utah, Wyoming, and Colorado, and the sample named Texas includes birds from parts of Colorado, New Mexico, Kansas, Oklahoma, and Texas.

wing-tip to secondary (*TSC*), the distance on the closed wing from the tip of the longest primary to the tip of the 10th, 5th and 4th primary feathers, and to the longest secondary feather; *outer tail length* (*OTL*) and *inner tail length* (*ITL*), the distance from a point between the insertions of the two middle rectrices to the tip of the longest outer and longest inner tail feathers; *tarsus length* (*TRL*), the diagonal distance from the middle posterior point of the joint between the tibiotarsus and tarsometatarsus, to the lower anterior edge of the lowest undivided scute of the junction of the tarsometatarsus with the base of the middle toe; *total culmen length* (*CLL*), the chord of the bill from the point where the integument of the forehead meets the horny covering of the bill to the tip of the culmen; *culmen length* (*from nares*) (*CLN*), the chord of the bill from the anterior margin of the nares to the tip of the culmen; *culmen width* (*CLW*), the distance between the two cutting edges of the bill, at the anterior end of the nares; and *culmen depth* (*CLD*), from the upper edge of the culmen to

TABLE 1
SAMPLES OF FEMALE EASTERN KINGBIRDS: NAMES AND COORDINATES

Sample location	Latitude (°N)	Longitude (°W)
British Columbia (BC)	47–57	113–122
Saskatchewan (SK)	46–54	104–112
Manitoba (MB)	46–54	95–101
Northern Ontario (NO)	46–55	79–88
Southern Ontario (SO)	43–45	80–86
Pennsylvania (PA)	37–45	72–79
Utah (UT)	36–45	104–114
Kansas (KS)	36–43	99–103
Missouri (MO)	34–40	92–95
Kentucky (KY)	34–42	80–89

the lower edge of the mandible, at the anterior end of the nares. In adult kingbirds the inner webs of the longest primaries are cut out, especially in breeding males (Pyle et al. 1987). Therefore, on males, we also measured the *length* and *width of the tip of the longest primary* (*PML PMW*); thus, for males we examined 14 characters.

For the interspecific comparisons required to test our prediction about the relative size

TABLE 2
SAMPLES OF MALE EASTERN KINGBIRDS: NAMES AND COORDINATES

Sample location	Latitude (°N)	Longitude (°W)
British Columbia (BC)	47–53	112–122
Alberta (AB)	49–54	106–114
North Dakota (ND)	47–52	99–104
Manitoba (MB)	48–53	92–98
Northern Ontario (NO)	47–55	80–90
Wyoming (WY)	44–46	103–113
Wisconsin (WI)	44–46	85–93
Southern Ontario (SO)	44–46	80–84
New England (NE)	44–47	70–79
Utah (UT)	40–43	110–112
Nebraska (NK)	40–43	99–106
Illinois (IL)	40–43	88–97
Ohio (OH)	40–43	80–86
Pennsylvania (PA)	40–43	72–79
New Mexico (NM)	36–39	103–106
Texas (TX)	35–39	99–102
Oklahoma (OK)	34–44	91–98
North Carolina (NC)	31–34	77–84

TABLE 3
MEAN MEASUREMENTS (MM) OF 12 VARIABLES FOR FEMALE EASTERN KINGBIRDS[a]

Sample (N)	WL	T10	T5	T4	TSC	OTL	ITL	TRL	CLL	CLN	CLW	CLD
BC (16)	115	6	22	27	27	80	84	18.8	22.1	13.4	7.6	6.2
SK (12)	114	5	22	27	28	81	84	19.3	22.1	13.6	7.8	6.3
MB (41)	114	7	22	28	27	81	83	19.0	22.2	13.6	8.0	6.4
NO (13)	112	6	22	27	25	78	81	18.8	21.2	13.1	7.7	6.5
SO (27)	112	6	21	27	25	79	82	18.7	21.4	13.2	7.7	6.4
PA (19)	112	6	21	27	28	80	82	18.6	21.9	13.3	7.7	6.2
UT (19)	114	6	22	27	29	80	83	19.1	21.8	13.3	7.7	6.2
KS (14)	112	6	21	26	29	80	83	18.9	21.7	13.3	7.6	6.3
MO (16)	112	6	21	26	28	78	81	18.9	22.1	13.5	7.7	6.1
KY (17)	112	6	22	26	25	79	82	18.8	21.4	13.2	7.8	6.3

[a] Sample names are identified in Table 1; variables are identified in the text.

of the species in sympatry and allopatry, we used measurements (also made by MacKenzie) on 561 Western Kingbirds (*T. verticalis*) and 234 Cassin's Kingbirds (*T. vociferans*) (comparable feather measurements on Scissor-tailed Flycatchers [*T. forficatus*] are not available). For this interspecific comparison we used only eight characters: wing length, outer and inner tail feather lengths, tarsus length, total culmen length, culmen length from nares, culmen width and culmen depth. Because skin measurements were not available for Scissor-tailed Flycatchers, Rising measured 27 features on 91 skeletons of males of four species of *Tyrannus*: 31 Cassin's Kingbirds, 25 Western Kingbirds, 21 Eastern Kingbirds, and 14 Scissor-tailed Flycatchers. The characters include those described by Rising (1988), as well as the length of the premaxilla from the skull, the phalanx length, and the length of the synsacrum. Not enough skeletal material for females was available to warrant analyses.

Statistical methods.—We calculated the means and standard deviations for each of the variables (Tables 3 and 4). Univariate evidence of geographic variation and sexual dimorphism among the 10 samples (Fig. 2) was tested with two-way ANOVAs (SAS 1987). One-way ANOVAs followed by a posteriori Student-Newman-Keuls (SNK) (SAS 1987) tests were used to elucidate patterns of geographic variation for each sex.

We used principal components analysis (PCA) (NTSYS/FACTOR, Version 4, Level 6, 1984; Rohlf 1985) on a matrix of correlations among the averages for the 12 characters of males and females from the 10 localities delimited in Table 1. Within sex, we used PCA on correlations of the sample means of the 18 males (14 characters) and 10 females (12 characters) samples to detect broad patterns of geographic variation. For interspecific comparisons, we again used PCA, based on matrices of correlations among means of Eastern, Western, and Cassin's kingbirds, with sexes analyzed separately. To assess evidence of character displacement, we divided the Eastern Kingbirds into three groups, those that are from allopatric populations ("allopatric," Fig. 4), and those that are from areas where they would be sympatric with Western Kingbirds ("sympatric-2"), and those that would be sympatric with both Western Kingbirds and Scissor-tailed Flycatchers ("sympatric-3"). For the skeletal data, we used all 91 (male) individuals, and did a PCA on the matrix of correlations among the 27 variables.

We used Mantel's test (1967) to compare matrices of phenotypic differences (average taxonomic distances based on averages of all 14 or 12 skin measurements) and matrices of

TABLE 4

MEAN MEASUREMENTS (MM) OF 14 VARIABLES FOR MALE EASTERN KINGBIRDS.[a]

Sample (N)	WL	T10	T5	T4	TSC	TPL	TPW	OTL	ITL	TRL	CLL	CLN	CLW	CLD
BC (17)	120	6	25	30	31	8.8	3.1	84.8	87.1	18.9	22.3	13.4	7.7	6.3
AB (19)	119	6	25	31	29	9.5	3.0	85.3	87.1	19.0	22.1	13.5	7.5	6.2
ND (17)	120	6	25	31	31	9.1	3.0	84	88	19.2	22.3	13.7	7.6	6.2
MB (49)	118	7	25	31	28	9.7	3.0	85.0	87.2	18.9	22.3	13.7	7.7	6.2
NO (10)	119	5	25	31	31	8.9	3.1	84.8	87.2	18.8	21.7	13.6	7.5	6.1
WY (11)	120	6	25	31	30	9.3	3.3	84	87	19.6	22.1	13.6	7.7	6.1
WI (19)	116	6	25	30	28	8.3	3.1	82	85	19.1	21.9	13.4	7.5	6.4
SO (20)	116	6	24	29	27	8.4	3.1	81.7	84.4	18.6	22.0	13.3	7.4	6.1
NE (21)	117	6	24	29	32	8.7	3.0	81	86	18.2	21.8	13.4	7.5	6.2
UT (14)	119	6	24	30	31	8.3	3.0	84	87	19.0	22.5	13.8	7.7	6.0
NK (13)	120	6	25	31	33	8.8	3.2	84	86	19.3	22.8	14.0	7.6	6.2
IL (16)	117	6	24	29	31	8.1	3.0	82	84	19.0	22.1	13.5	7.5	6.3
OH (19)	119	6	25	31	29	9.7	3.1	84	87	18.6	22.1	13.6	7.6	6.2
PA (10)	116	6	24	29	32	8.3	3.0	81.6	84.9	18.6	21.6	13.5	7.6	6.3
NM (12)	119	6	24	31	34	9.5	3.0	85	87	16.2	22.1	13.7	7.6	6.1
TX (17)	116	6	24	30	31	8.7	3.0	82	84	16.7	22.2	14.0	7.5	6.2
OK (13)	117	6	24	30	30	8.6	3.0	82	84	16.4	22.5	13.9	7.6	6.1
NC (11)	116	6	24	29	34	8.5	3.0	80	83	17.2	21.3	13.5	7.5	6.2

[a] Sample names are identified in Table 2; variables are identified in the text.

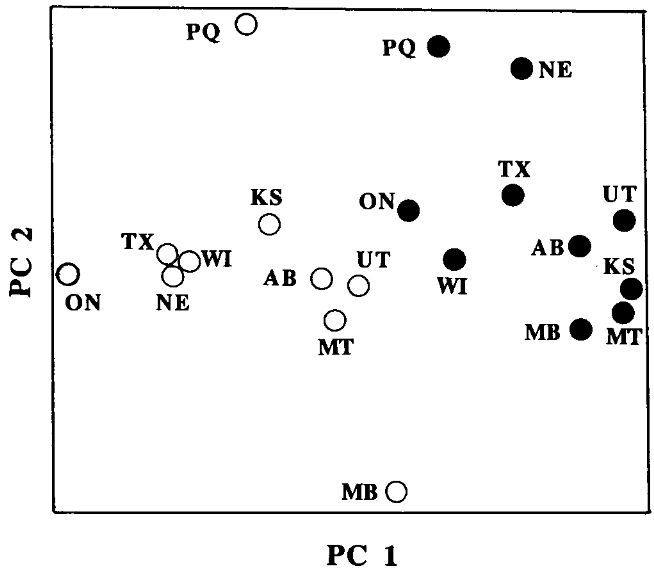

FIG. 3. Two-dimensional plot showing the positions of 10 samples of male (black dots) and female (open dots) Eastern Kingbirds in the space defined by principal component 1 and principal component 2 from a principal components analysis of the correlations among the averages of 12 measurements. The abbreviations used for the samples are: AB = Alberta, KS = Kansas, MB = Manitoba, MT = Montana, NE = New England, ON = Ontario, PQ = Québec, TX = Texas, UT = Utah, and WI = Wisconsin; these samples are all from areas of equal geographic size, and are the ones delimited in Fig. 2.

geographic distances and reciprocals of geographic distances. These tests indicate whether or not patterns of phenotypic variations simply reflect the geographic distances among the localities; the reciprocals emphasize patterns of variation among geographically close localities. NTSYS-PC, version 1.50, program MXCOMPG (Rohlf 1988) was used for Mantel's tests; 1000 random permutations were done for each test.

RESULTS

Sexual dimorphism.—Ten of 12 characters exhibited significant sexual dimorphism ($P < 0.05$ for bill height and $P < 0.001$ for the others) (Table 5). We found no sexual dimorphism in tarsus length or length of wingtip to the 10th primary, but we did find significant dimorphism in all measures of bill size. The interaction between sex and locality was not significant for any of the 12 features, indicating that there is no geographic variation in the magnitude of sexual dimorphism. In PCA among the 10 sample means for both sexes, the first component (PC 1) explains 48.0%, PC 2, 19.2%, and PC 3, 11.0%. The next several components are of nearly equal size, and each explains little of the total variance; thus, these are

TABLE 5
RESULTS OF TWO-WAY ANOVA OF GEOGRAPHICAL VARIATION AND SEXUAL DIMORPHISM AMONG EASTERN KINGBIRDS

Variable	Among samples (df = 9)	Between sexes (df = 1)	Interaction (df = 9)	Larger sex
Wing length	***	***	ns[a]	m > f
Tip to 10th length	**	ns	ns	m = f
Tip to 5th length	***	***	ns	m > f
Tip to 4th length	***	***	ns	m > f
Tip to secondary length	***	***	ns	m > f
Outer tail length	***	***	ns	m > f
Inner tail length	***	***	ns	m > f
Tarsus length	***	ns	ns	m = f
Total culmen length	***	***	ns	m > f
Culmen from nares	***	***	ns	m > f
Culmen width	***	***	ns	f > m
Culmen depth	***	*	ns	f > m

*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; [a] ns = $P > 0.05$.

not discussed here. PC 1 is highly and positively correlated with measures of wing, and especially wing tip length, tail length, and bill length, and negatively correlated with bill height; PC 2 is negatively correlated with measures of bill size, and wing and tarsus length (Table 6). The PC 1 axis separates males from females (Fig. 3), with males having larger PC 1 scores, and hence longer tail feathers, wing-tips, and bills than females. Birds from the Québec sample and New England (especially males) have large values for PC 2, whereas those from Manitoba (especially females) have low values (Fig. 3).

Interspecific differences.—In the among-species PCAs for both males and females, the correlations of all eight variables are high and positive with the first component (Table 7), which represents an approximate measure of overall body size (Rising and Somers 1989). For both sexes, the three samples of Eastern Kingbirds cluster together, and are smaller on the PC 1 axis than the Western Kingbird which is, in turn, smaller than the Cassin's Kingbird (Fig. 4). Also in both sexes PC 2 is positively correlated with tail length and negatively correlated with tarsus and bill lengths (Table 7); thus populations with high values for PC 2 have relatively long legs and bills, and short tails. Western Kingbirds are separated from the others on this axis (Fig. 4). Thus, with regard to these eight study skin measurements, Eastern Kingbirds are smaller than either of the other two, but are similar in PC 2 values to Cassin's Kingbirds. In both sexes, however, the populations that are sympatric with Western Kingbirds

TABLE 6

CORRELATIONS BETWEEN MEASUREMENTS AND THE FIRST THREE PRINCIPAL COMPONENTS FROM A PRINCIPAL COMPONENTS ANALYSIS OF A MATRIX OF CORRELATIONS AMONG THE AVERAGES OF 12 MEASUREMENTS FOR MALE AND FEMALE EASTERN KINGBIRDS

Character	PC 1	PC 2	PC 3
Wing length	0.41[a]	−0.53	0.34
Wing tip to 10th		−0.62	0.55
Wing tip to 5th	0.90		
Wing tip to 4th	0.91		
Wing tip to secondary	0.80		−0.30
Outer tail length	0.92		
Inner tail length	0.89		
Tarsus length	0.34	−0.67	−0.47
Total bill length	0.81	−0.34	−0.35
Culmen length (from nares)	0.79		−0.43
Culmen width (at nares)		−0.81	
Culmen depth (at nares)	−0.48	−0.54	
Eigenvalue	5.8	2.3	1.3
Variance explained	48.0%	19.2%	11.0%

[a] Correlations <0.30 not printed.

("sympatric-2" in Fig. 4) are also the ones that are most like Western Kingbirds on the PC 1 axis, and the differences among the three groups of Eastern Kingbirds on the PC 2 axis seem inconsequential. Thus, we see no evidence for character displacement in these data.

In the PCA of the 27 skeletal variables, of 91 individuals of four species of *Tyrannus,* the first PC explains 45.7% of the total variance, the second 10.8%, and the third 7.4% (Table 8). All of the variables are positively correlated with PC 1, and all of the correlations are greater than 0.4; thus the PC 1 scores are an approximate measure of overall body size (Rising and Somers 1989). PC 2 contrasts measures of bill size with measures of pectoral girdle size (scapula, sternum, etc.) and synsacrum size; thus, individuals with large PC 2 scores have relatively small bills and large pectoral girdles (Table 8). In the plot (Fig. 5) of PC 1 vs PC 2, Eastern Kingbirds and Scissor-tailed Flycatchers overlap considerably on the PC 1 axis (and thus are of similar body size); there is also substantial overlap of these two species with the Western Kingbird; Cassin's Kingbird generally tends to be of larger body size.

On the PC 2 axis there is again considerable overlap among species, especially among Eastern and Western kingbirds and Scissor-tailed Flycatchers. Thus these three *Tyrannus* are very similar in skeletal size, although the Eastern Kingbird tends to be smaller than the others (small PC 1 values) with relatively larger bill and pectoral elements (large PC 2

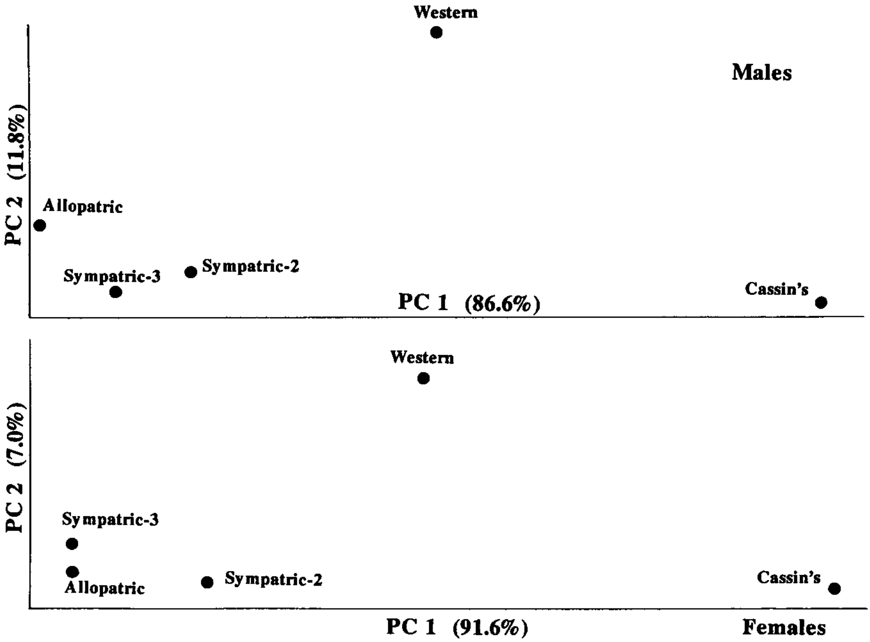

FIG. 4. Two-dimensional plots of the positions of three groups of Eastern Kingbirds (*Tyrannus tyrannus*) and Western and Cassin's kingbirds (*T. verticalis* and *T. vociferans*) in spaces defined by PC 1 and PC 2 of principal components analyses of the correlations among the averages of eight variables. The axes are proportional to the eigenvalues of the components.

TABLE 7

CORRELATIONS BETWEEN MEASUREMENTS AND THE FIRST TWO COMPONENTS FROM PRINCIPAL COMPONENTS ANALYSIS OF MATRICES OF CORRELATIONS AMONG THE MEANS OF EIGHT CHARACTERS FROM THREE SPECIES OF *TYRANNUS*

Character	Males		Females	
	PC 1[a]	PC 2	PC 1	PC 2
Wing length	0.96		0.98	
Outer tail length	0.90	0.42	0.94	0.35
Inner tail length	0.95	0.30	0.99	
Tarsus length	0.83	−0.51	0.95	
Culmen length (total)	0.99		0.99	
Culmen length (from nares)	0.90	−0.42	0.95	
Culmen width (at nares)	0.92	−0.38	0.90	−0.43
Culmen depth (at nares)	0.98		0.96	
Eigenvalue	6.9	0.9	7.3	0.6
Variance explained	86.6%	11.8%	91.6%	7.0%

[a] Correlations <0.30 not printed.

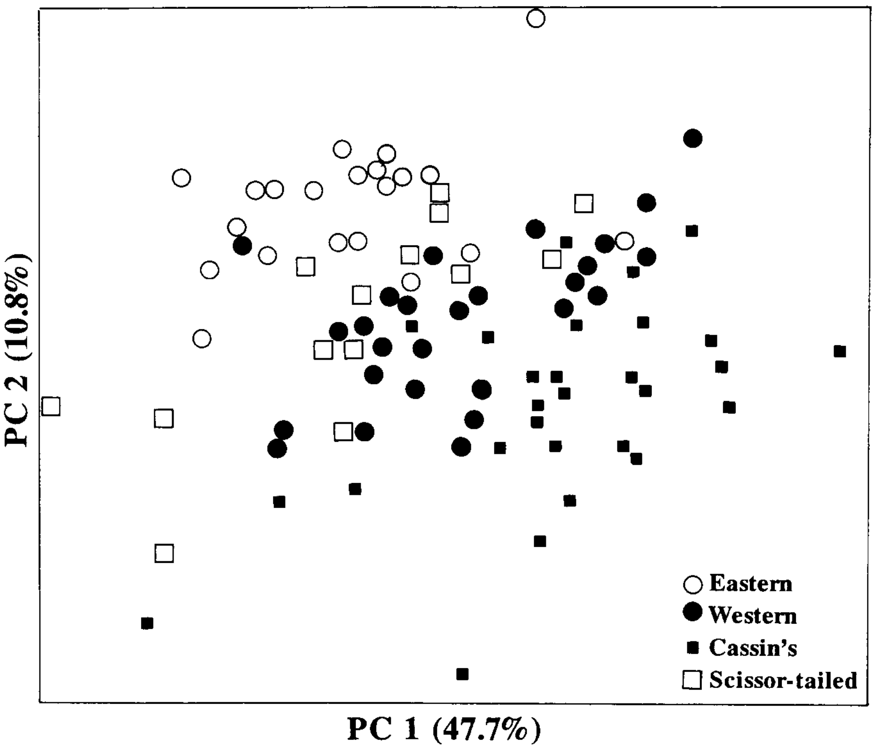

FIG. 5. Two-dimensional plot of the positions of 91 individuals of four taxa of *Tyrannus* from a principal components analysis of the correlations among 27 skeletal characters.

values). Therefore, if character displacement were occurring, we predict that it will be evident in these features in populations of *T. tyrannus* that are sympatric with one or (especially) two other *Tyrannus,* namely *T. verticalis* or both *T. verticalis* and *T. forficatus.*

Geographical trends.—The univariate analyses show that there is little geographic variation in size and there are no clear geographic patterns. In females, seven of the 12 characters measured show statistically significant variation. However, the 10 samples are divided into only two, or at most three (for wing length) statistically homogeneous sets, and there is, in all instances, a great deal of overlap between or among sets. Looking at the characters in concert, there is a tendency for northwestern females (British Columbia, Saskatchewan, and Manitoba) to be larger than eastern ones. Although there is significant geographic variation in 10 of the 14 characters for males, no trends are obvious; there is perhaps a tendency for western birds to be larger than eastern ones. The Mantel's tests revealed

TABLE 8

CORRELATIONS BETWEEN MEASUREMENTS AND THE FIRST THREE COMPONENTS FROM A PRINCIPAL COMPONENTS ANALYSIS OF CORRELATIONS AMONG THE MEANS OF 27 SKELETAL CHARACTERS OF 19 *TYRANNUS* OF FOUR SPECIES

Character	PC 1	PC 2	PC 3
Skull length	0.77[a]		
Premaxilla length (total)	0.73	−0.48	
Skull width	0.87		
Premaxilla length (nares)	0.71	−0.38	
Premaxilla depth	0.56		
Narial width	0.57		0.39
Premaxilla width	0.68		
Interorbital width	0.41		0.41
Mandible length	0.78	−0.48	
Gonys length	0.60	−0.59	
Mandible depth	0.40	−0.48	
Coracoid length	0.81		
Scaupla length	0.73	0.36	
Femur length	0.84		−0.38
Femur width	0.45		
Tibiotarsus length	0.76		−0.45
Tarsometatarsus length	0.79		−0.45
Humerus length	0.84		
Ulna length	0.72		
Carpometacarpus length	0.82		
Phalanx length	0.59		
Hallux length	0.53		−0.50
Sternum length	0.53	0.61	
Sternum depth	0.52	0.33	0.45
Keel length	0.53	0.51	0.33
Synsacrum width	0.73	0.34	
Synsacrum length	0.61	0.52	−0.31
Eigenvalue	12.3	2.9	2.0
Variance explained	45.7%	10.8%	7.4%

[a] Correlations <0.30 not printed.

a positive, but not significant ($P > 0.05$) relationship between phenotypic (ATD) distance and geographic distance and a significant ($P < 0.01$) negative correlation between the ATD and the reciprocal of geographic distance. Thus, although geographic distance does not predict phenotypic distance, samples from adjacent localities are more similar to each other than would be predicted by chance alone.

These geographic trends are best summarized by the multivariate (PCA) analyses. In the PCA for females, all characters except culmen width and

TABLE 9

CORRELATIONS BETWEEN MEASUREMENTS AND THE FIRST THREE PRINCIPAL COMPONENTS FROM A PRINCIPAL COMPONENTS ANALYSIS OF A MATRIX OF CORRELATIONS AMONG THE MEANS OF 12 CHARACTERS OF 10 SAMPLES OF FEMALE EASTERN KINGBIRDS

Character	PC 1	PC 2	PC 3
Wing length	0.96[a]		
Wing tip to 10th		−0.77	0.49
Wing tip to 5th	0.73	−0.61	
Wing tip to 4th	0.62	−0.64	
Wing tip to secondary	0.59	0.59	0.34
Outer tail length	0.91		
Inner tail length	0.89		
Tarsus length	0.66		−0.53
Total bill length	0.80	0.35	
Culmen length (from nares)	0.76	0.40	
Culmen width (at nares)			−0.93
Culmen depth (at nares)		−0.75	−0.30
Eigenvalue	5.5	2.7	1.7
Variance explained	46.1%	22.1%	14.3%

[a] Correlations <0.30 not printed.

bill height are correlated positively with PC 1 (the correlation between wing-tip to 10th, however, is small) (Table 9). Thus females with large PC 1 scores are large, with relatively long and thin bills. PC 2 is highly negatively correlated with the three primary wing-tip characters and bill height, and positively correlated with wing-tip to secondary and measures of bill length. Hence, birds with large values for PC 2 have relatively round wings and long, thin bills.

The females from the northwestern part of the range have the largest PC 1 values, thus generally have longer wing, tails and bills than birds from the east, although the sample from Montana is an exception to this trend (Fig. 6). To the extent that PC 1, from this analysis, could be interpreted as a general measure of body size, these data indicate that female Eastern Kingbirds increase in size from east to west. PC 2, which explains an additional 22.1% of the variance, especially separates the samples from northern Ontario and Manitoba from Montana and Saskatchewan.

The PCA for the males shows a similar, although more complicated pattern. PC 1, which explains 42.3% of the total variance, is highly positively correlated with wing length, three of the wing-tip lengths, both tail lengths, tarsus length, and bill length and width (Table 10). Males with

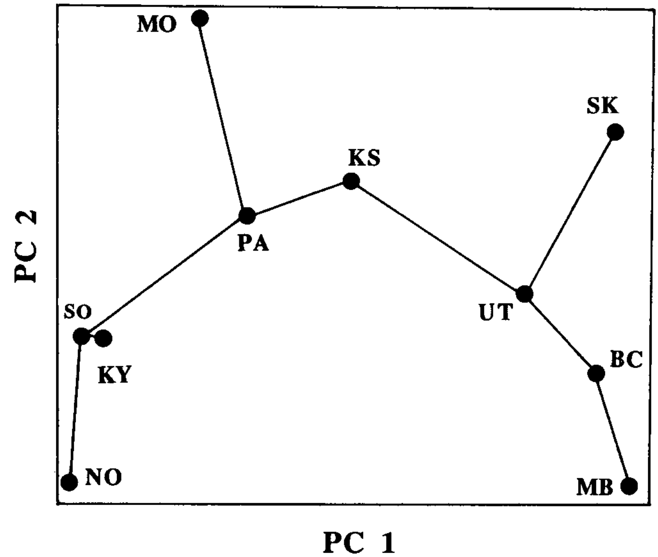

FIG. 6. Two-dimensional plot of the positions of the averages of 10 samples of female Eastern Kingbirds in the space defined by PC 1 and PC 2 from a principal components analysis of the correlations among the means of 12 measurements. PC 1 explains 46.1% of the total variance among the means, and PC 2 explains an additional 22.1%. The locality abbreviations are: BC = British Columbia, KS = Kansas, KY = Kentucky, MB = Manitoba, MO = Missouri, NO = northern Ontario, PA = Pennsylvania, SK = Saskatchewan, SO = southern Ontario, and UT = Utah. Each sample includes birds from states or provinces other than those named.

large values for this component have relatively long and round wings, long tails and tarsae, and large bills, and by these criteria, the males from the west (Manitoba, Wyoming, Nebraska, Alberta, and North Dakota) are the largest. However, birds from Illinois, Ohio, and northern Ontario are nearly as large, whereas birds from North Carolina and Pennsylvania are the smallest, with birds from southern Ontario, British Columbia, and New England being nearly as small (Fig. 7). PC 2, which explains an additional 15.1% of the variation, contrasts wing shape (wing-tip to secondary), bill length and width with tarsus length and bill height, and separates southwestern birds (Utah, Oklahoma, Texas, New Mexico, and Nebraska) from the others (Fig. 7). PC 1 and PC 2, however, together explain just over half of the total variation, and the minimum spanning tree, which summarizes the relationships among the localities in the 14 dimensional space shows some of the distortions in this two dimensional

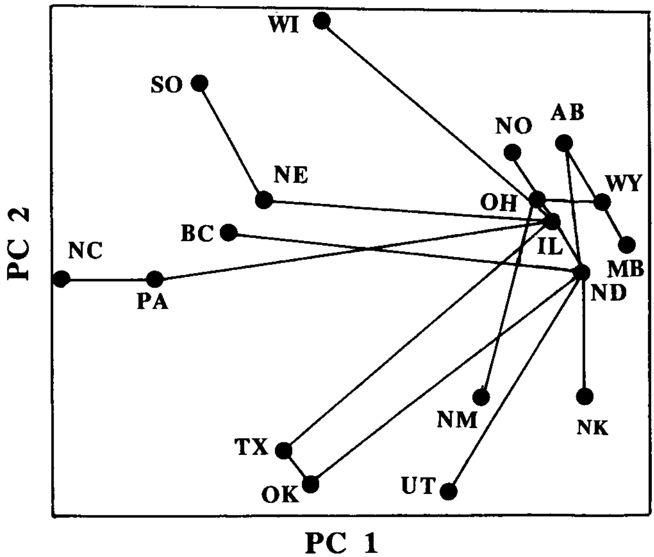

FIG. 7. Two-dimensional plot of the positions of the means of 18 samples of male Eastern Kingbirds in the space defined by PC 1 and PC 2 of a principal components analysis of the correlations among the averages of 14 measurements. PC 1 explains 42.3% of the total variance in the matrix and PC 2 explains an additional 15.1%. The abbreviations for the sample names are: AB = Alberta, BC = British Columbia, IL = Illinois, MB = Manitoba, NC = North Carolina, ND = North Dakota, NE = New England, NK = Nebraska, NM = New Mexico, NO = northern Ontario, OH = Ohio, OK = Oklahoma, PA = Pennsylvania, SO = southern Ontario, TX = Texas, UT = Utah, WI = Wisconsin, and WY = Wyoming.

representation (Fig. 7). For example, British Columbia, which appears to be close to New England and Pennsylvania in the two dimensional space is closer to North Dakota in the 14 dimensional one.

DISCUSSION

Sexual dimorphism.—Although there is no sexual dimorphism in plumage pattern or coloration in Eastern Kingbirds, we find however that there is a significant sexual dimorphism in 10 of 12 measurements. Tarsus length, however, is one of the characters that does not vary with sex. Murphy (1988) likewise found no dimorphism in tarsus length in Eastern Kingbirds from eastern Kansas. If tarsus length is a measure of body size *per se* in kingbirds as suggested elsewhere (Haberman et al. 1991), then there is no sexual dimorphism in size in Eastern Kingbirds. Additionally, although the shape of the outer primaries differs between sexes in *Tyrannus,* there is no dimorphism in distance between the wing tip and the tip

TABLE 10

CORRELATIONS BETWEEN MEASUREMENTS AND THE FIRST THREE PRINCIPAL COMPONENTS FROM A PRINCIPAL COMPONENTS ANALYSIS OF A MATRIX OF CORRELATIONS AMONG THE AVERAGES OF 14 MEASUREMENTS ON 18 SAMPLES OF MALE EASTERN KINGBIRDS

Character	PC 1	PC 2	PC 3
Wing length	0.93[a]		
Wing tip to 10th			−0.92
Wing tip to 5th	0.88		
Wing tip to 4th	0.95		
Wing tip to secondary		−0.51	0.31
Wing tip length	0.75		
Wing tip width	0.39		0.46
Outer tail length	0.94		
Inner tail length	0.92		
Tarsus length	0.42	0.54	
Total bill length	0.60	−0.48	
Culmen length (from nares)		−0.84	
Culmen width (at nares)	0.56	−0.51	
Culmen depth (at nares)		0.44	−0.58
Eigenvalue	5.9	2.1	1.6
Variance explained	42.3%	15.1%	11.7%

[a] Correlations <0.30 not printed.

of the 10th primary in Eastern Kingbirds. Male Eastern Kingbirds have longer wings, wing tips (distance between the tip of the longest primary, and either the 4th or 5th primary or the longest secondary), tails, and bills than females, but females have more robust bills (larger culmen width and depth). The longer wings, wing tips, and tails of male Eastern Kingbirds probably result from the aerial and visual displays that the males perform during courtship and in territorial defense. Females do not patrol and rarely guard the territory (Smith 1966). Longer wing and tail feathers of males relative to the same body size probably facilitate these displays. It is also possible that they reflect sexual differences in migratory behavior, although no such differences have been reported.

Even though we found sexual dimorphism in bill size, possibly indicating that the sexes feed on somewhat different prey, there is no geographic variation in the extent of bill dimorphism in Eastern Kingbirds. Thus there is no indication that the magnitude of such dimorphism is influenced by interspecific competition, as would be predicted by the niche variation hypothesis (Van Valen 1965, Haberman et al. 1991).

Geographic variation in size and shape.—Although there is significant geographic variation in all of the features that we measured on Eastern

Kingbirds, there are few clear geographic trends. As a general rule, the largest individuals are found in the northern Great Plains (and for females in British Columbia as well), whereas the smallest individuals are found in the east. There is, thus, no indication that this species conforms to the trend described by Bergmann's Rule (James 1970, Zink and Remsen 1986, Aldrich and James 1991). As mentioned above, the species is highly migratory, and leaves North America before the inception of cold weather. Thus the significance of size to thermoregulation (commonly postulated to select for relatively large body size in cold regions) is probably relatively unimportant in these kingbirds. The Eastern Kingbird can be added to the list of migratory species that do not support Bergmann's rule (Zink and Remsen 1986). The absence of any geographic trends in size variation also indicates that there is no interspecific character displacement in Eastern Kingbirds, and the PC analysis likewise gives no indication of character displacement (Fig. 4).

The Eastern Kingbird is multivariately most like the Scissor-tailed Flycatcher of the four *Tyrannus* studied, and least like Cassin's Kingbird. Eastern Kingbirds differ from Scissor-tailed Flycatchers and Western Kingbirds primarily by having smaller bills. There is, however, no evidence of character displacement in bill size in Eastern Kingbirds in populations that are sympatric with one or both of these congeners. This suggests that interspecific niche partitioning is not occurring in North American *Tyrannus.*

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