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GEOGRAPHIC VARIATION OF THE CURVE-BILLED THRASHER (*TOXOSTOMA CURVIROSTRE*) COMPLEX

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ABSTRACT.—Geographic patterns of variation in morphological characters in the Curve-billed Thrasher (*Toxostoma curvirostre*) have been recognized by the description of seven subspecies. Twelve standard measurements, as well as three colorimetric characters and two color pattern characters, were analyzed to test whether subspecies limits predict patterns of variation. Measurement error was addressed by measuring each character three times and calculating the mean. A total of 821 male study skins were used, representing 29 locations. A variety of analysis revealed two major groups, an eastern and western group, divided by the Sierra Madre Occidental. Those two groups had previously been recognized as the *curvirostre* and *palmeri* groups, respectively. Those groups were also recovered by analysis of mtDNA. The two groups fulfill the requirements for species. The Tiburón Island (*T. c. insularis*) sample was distinct for several characters; however, small sample size precludes formal taxonomic recommendation. Within the two major groups, most characters showed incongruent clinal patterns of variation that did not match subspecies limits. *Received 6 December 2001, accepted 2 February 2003.*

RESUMEN.—Los patrones geográficos de la variación en caracteres morfológicos en *Toxostoma curvirostre* han sido reconocidos a través de la descripción de siete subespecies. Se analizaron 15 caracteres, 12 morfológicos y tres de coloración, además de dos patrones de coloración en el plumaje, esto con el objetivo de probar si las subespecies predecían los patrones de variación. El error de medición fue tratado midiendo tres veces cada caracter y utilizando el promedio. Fueron usados un total de 821 ejemplares, representando 29 unidades geográficas. Diversos análisis revelaron la existencia de dos grupos mayores, uno en el este y otro en el oeste, divididos por la Sierra Madre Occidental. Previamente, estos grupos han sido reconocidos como *curvirostre* y *palmeri*, respectivamente. Estos grupos también fueron obtenidos por otros autores mediante el análisis de ADN mitocondrial, por lo que ambos grupos cubren los requerimientos para ser reconocidos como especies. La población de Isla Tiburón (*T. c. insularis*) fue distinta en diversos caracteres; sin embargo, la muestra tan reducida la excluye de recomendaciones taxonómicas. Dentro de cada uno de los dos grandes grupos, existieron patrones de variación clinal incongruente que no corresponden con los límites geográficos propuestos para cada una de las subespecies.

> Geographic variation is not likely to be due to adaptation of a few characters to a single environmental variable, but is doubtless multidimensional process involving the adaptation of many characters to a variety of interdependent environmental factors whose gradients and ranges probably overlap in a rather complex fashion. (Sokal and Rinkel 1963)

THESE SENTIMENTS EXPRESSED by Sokal and Rinkel lead to a realization that the description of geographic variation is inherently a quantitative exercise, requiring both univariate and multivariate analysis. Such quantitative descriptions of the spatial patterns of variation provide a basis for making inferences about the origin of geographic differences and their taxonomic recognition. It is generally understood that geographic differences might reflect local adaptation, where variation is shaped in reference to locally varying environmental regimes. For example, many studies have shown that regional tendencies in plumage coloration cooccur across species (Zink and Remsen 1986); this observation, summarized as Gloger's rule, suggests a common underlying cause of variation. Two assumptions of most evolutionary studies of geographic variation are that geographic differences represent local adaptation, and that geographic differentiation is a stage in the speciation process (Zink 1989). However, speciation cannot be considered as a simple extension of geographic variation (Cracraft 1983, Zink 1989).

Studies of geographic variation in birds have

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traditionally been focused on taxonomic aspects of variation in morphology and plumage coloration (Haffer and Fitzpatrick 1985). Avian taxonomic studies have tended to include only portions of species' ranges and to emphasize single characters (Zink and Remsen 1986), causing an indiscriminate description of subspecies. Hence, many avian subspecies are artificial rather than historical entities (Ball and Avise 1992). An important objective studying of geographic variation is to facilitate the understanding of what should be considered units of evolution (Zink 1986) and their rank. A great polemic has existed as to what taxonomic category should be considered an evolutionary unit (Mayr 1970; Cracraft 1983; McKitrick and Zink 1988, 1997). Studies of geographic variation contribute to that debate by clarifying the limits of taxa, usually those that are minimally diagnosable.

Identifying morphological and colorimetric patterns of geographic variation among population samples of the Curve-billed Thrasher (*Toxostoma curvirostre*) complex is an objective of this study. A recent analysis of mtDNA (Zink and Blackwell-Rago 2000) identified three major groups of population samples, corresponding to the Sonoran and Chihuahuan deserts and into southern Mexico. Thus, a second objective is to test whether mtDNA groups and current subspecies limits (see below) predict patterns of variation when multiple characters are considered simultaneously.

Distribution of the complex and subspecies.—The *Toxostoma curvirostre* complex is distributed over most of the arid areas of North America, from Arizona, extreme western Oklahoma, western and central Texas, southward including San Esteban and Tiburón islands in Sonora, through the Mexican Plateau to Oaxaca (American Ornithologists' Union 1983). There are casual records from California, Nevada, Utah, Kansas, South Dakota, Nebraska, Iowa, Louisiana, Wisconsin, and Minnesota (Tweit 1996).

Previous interpretations of morphology and coloration led to the recognition of seven subspecies (Fig. 1): (1) *Toxostoma curvirostre palmeri*, from central Southwestern Arizona (west of the Santa Rita Mountains), western Chihuahua to southern Sonora; (2) *T. c. insularum*, an endemic of San Esteban and Tiburón islands in the Gulf of California; (3) *T. c. maculatum*, from southern Sonora to northern Sinaloa and southwestern Chihuahua; (4) *T. c. occidentale*, from the lowlands of south-central Sinaloa, Nayarit, and Southwest Jalisco; (5) *T. c. celsum*, from Oklahoma, New Mexico, western Texas, to Chihuahua, Durango, northwestern Zacatecas, Coahuila, northeastern Jalisco, Aguascalientes, and northwestern Guanajuato; (6) *T. c. curvirostre*, from the Rio Grande in Texas, New Mexico, Nuevo León, Coahuila, Chihuahua, Durango, and Zacatecas (some suggest that this distribution corresponds to *T. c. celsum;* and that *T. c. curvirostre* occurs in Jalisco, Colima, Michoacán, Guerrero, Morelos, Hidalgo, San Luis Potosí, eastern Veracruz, Querétaro, Distrito Federal, and Oaxaca); (7) *T. c. oberholseri*, southeastern Texas and northeastern Mexico, including the states of Nuevo León, Tamaulipas, and San Luis Potosí (Swainson 1827, Coues 1872, Ridgway 1882, Nelson 1900, Law 1928, Van Rossem 1930, Moore 1941, Miller et al. 1957, Bent 1964). Several authors have recognized two groups of subspecies, the first including *T. c. palmeri*, *T. c. maculatum*, *T. c. insularum*, and *T. c. occidentale*, and the second including *T. c. oberholseri*, *T. c. celsum*, and *T. c. curvirostre* (Phillips 1986, Tweit 1996). Zink and Blackwell-Rago (2000) found strong support for those two groups, and somewhat weaker support for a previously unrecognized third group in southern Mexico. Apparently there is no sexual dimorphism within the complex ("sexes alike in all plumages;" Tweit 1996), although males present slightly longer wings and tail (Pyle et al. 1987); however, that does not play a role in the descriptions of the seven subspecies.

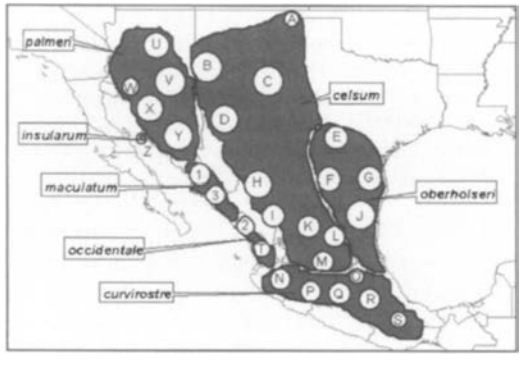

FIG. 1. Distribution of the seven described subspecies and geographical locations of Geographic Units (OGUs). Letters and numbers represent the Geographic Units as indicated in Table 1.

METHODS

Operational geographic units.— In total, 821 specimens of adult males were used. Birds were aged on the basis of the information in labels, for example, ossification and size of gonads, as well as visual confirmation by the plumage. When doubt existed, individuals were excluded. Specimens were grouped in 29 population samples or operational geographical units (OGUs), most of which had proportionally the same area and a minimum of 10 individuals (Table 1). Operational geographical unit boundaries were contained inside the distribution of one of the seven subspecies (Fig. 1), and each subspecies contained at least two OGUs, allowing for testing of the morphological integrity of current subspecies. In addition, multiple OGUs were contained in the two mtDNA defined groups of Zink and Blackwell-Rago (2000).

Characters.—Morphological characters used were length of the central rectrices (TAIL1); length of the outer rectrices (TAIL2); wing chord (WNGLN1); length of the last primary (WNGLN2); bill length (BLLN); bill width (BLLWD); bill depth (BLLDP) (these last three were from the anterior tip of the nares); tarsus length (TRSUS); tarsus width (TARSWD), taken in the middle of the tarsus; middle toe length (MTOE); and hallux length (HALX) (these last two excluded the claw; Baldwin et al. 1931, Zink and Remsen 1986). In addition, bill curvature was measured (CURVE), taking the radius of the height of the upper mandible from the line traced from the base to the tip of the bill. Coloration characters included brightness (Y), hue (X), and chroma (Y2); those were recorded using a Minolta chromometer (model CR-200) and are described in Zink et al. (1997). Two qualitative characters were also used: breast-spot pattern (BRSPT) and tail-spot pattern (TLSPT). Those two characters were scored using intervals with values assigned by spot size and spot color intensity, from 1 to 4 and from 1 to 5, respectively (Fig. 2). Characters used in this study are the same as those used for the previous descriptions of subspecies.

Because measurement error contributes significantly to the total amount of variation (Bailey and Byrnes 1990, Yezerinac et al. 1992), each character was measured three times with the mean of the values

TABLE 1. Operational Geographical units (OGUs) including abbreviation code, number of localities, and specimens.

OGU	Abbreviation code	Number of localities	Number of specimens
*OKL (western Oklahoma)	A	1	4
NM (southeastern New Mexico)	B	11	31
DAV (southeastern Texas)	C	6	14
CHI (western Chihuahua)	D	9	44
LAR (southern Texas and northern Coahuila)	E	7	27
COA (southern Coahuila)	F	10	17
TX (southern Texas)	G	11	88
NDGO (northern Durango)	H	9	14
SDGO (southern Durango)	I	6	14
TAM (southern Tamaulipas)	J	7	19
ZAC (eastern Zacatecas)	K	6	14
SLP (southern San Luis Potosí)	L	11	32
GTO (Guanajuato)	M	7	32
JAL (central Jalisco)	N	12	28
HGO (Hidalgo)	O	8	18
MIC (Michoacán)	P	8	12
MOR (Morelos and Guerrero)	Q	8	22
PUE (southern Puebla and northern Oaxaca)	R	11	13
*OAX (central Oaxaca)	S	2	9
*NAY (Nayarit and northern Jalisco)	T	7	9
PX (central Arizona)	U	18	56
TUC (southern Arizona)	V	24	168
SAL (northeastern Sonora)	W	6	12
*NSON (northern Sonora)	X	6	8
CSON (central Sonora)	Y	9	24
*TIB (Tiburón Island)	Z	1	4
SSON (southern Sonora)	1	10	45
NSIN (northern Sinaloa)	2	14	32
SSIN (southern Sinaloa)	3	9	11

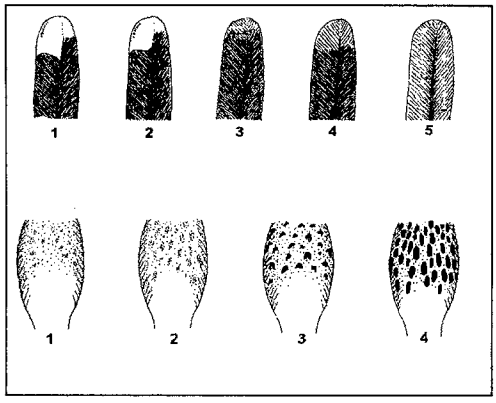

FIG. 2. Scores of the tail and breast spotting patterns. Numbers represent scores for which interval values were assigned based on spot size and spot color intensity.

for each specimen used (Yezerinac et al. 1992). All measurements were taken using an electronic caliper, with an accuracy of 0.01 mm, connected to a portable computer.

Statistical analyses.—The statistical package SAS (SAS Institute 1989) was used. Characters were log-transformed to minimize effects of deviations from normality (Mosimann and James 1979), with the exception of breast- and tail-spot characters. For each population sample, means and standard deviation were computed for each character (not shown).

Three-way analysis of variance (ANOVA, PROC GLM) was used to estimate the contribution to the total variation of OGU, month of the year, and year of collection (only for coloration characters); as well as the respective interactions among OGU versus year of collection and OGU versus month of the year. ANOVA type III was used because the number of samples was not the same for each grouping (OGU, subspecies).

To estimate variation owing to the month of collection (temporal variation), the mean of the values for each month and each character was graphed for the OGU with the largest sample size (Table 1). To show geographic variation in single characters, the mean of each characters value for each OGU was graphed. Only characters with statistically nonsignificant interactions between OGU and month were graphed. A matrix of taxonomic distances (Sokal and Rohlf 1973) was computed for the mean of means for each character for each OGU. Then, a UPGMA cluster analysis (Sneath and Sokal 1973) was constructed using the computer package NTSYS 1.7 (Rohlf 1992). The purpose of that cluster analysis was to determine if subspecies or mtDNA limits predicted hierarchical patterns of morphometric variation.

Principal components analysis (PCA) was performed using the mean of means of the annual values for the morphometric characters of each OGU (qualitative characters were not used) to standardize the contribution of variance for month of collection (temporal variation), thereby considering only geographic variation. Color characters were excluded because variance contributed by year of collection was significant. In later ANOVA, for characters where there was no interaction between OGU and month of collection (CM) or between OGU and year of collection (COLYR), the characters were analyzed directly.

Because two large groups of OGUs were found (east and west), the same analyses were repeated to identify the patterns of geographic variation within each group. For statistical reasons, the number of individuals was reduced to a maximum of 30 per OGU (randomly selected). ANOVA type III was used due to the unequal number of samples per OGU. For each group, Tukey's studentized range test (HSD) was used to reveal maximum homogeneous groupings of OGUs for each character. In addition, patterns of variation in character means as a function of OGU latitude were examined. Principal components analysis (including all individuals) was carried out for each group. The scores of each individual on PC I–III were used as new raw variables in ANOVA and with HSD. Those new variables are uncorrelated and can provide a better description of the overall pattern of geographic variation because they are weighted composites of the original (correlated) variables (Zink 1986).

RESULTS

ANOVA.—Analysis of variance (Table 2) demonstrated that a significant amount of variance is explained by geography (OGU) for all characters ($P < 0.05$). However, for five characters, the OGU by month (CM) interaction was significant ($P < 0.05$). For the color characters, a significant OGU by year (COLYR) interaction existed for chroma ($P < 0.05$).

Temporal variation.—Annual change existed in chroma and TAIL2 (Fig. 3). For chroma, values gradually increased from September, culminating in August when values decreased again. TAIL2 values increased and then decreased from January to August, and then increased steadily through December.

Analysis of population means.—Variation in TLSPT (Fig. 4) is typical of that in other characters and is illustrated here to show the general geographic pattern. Ordering of OGUs was from east to west and from north to south. Two groups were observed, one formed by OGUs located in the east (OKL, NM, DAV, CHI, LAR, COA, TX, NDGO, SDGO, TAM, ZAC, SLP, GTO, JAL, HGO, MIC, MOR, PUE, OAX, and NAY) and

TABLE 2. *F*-values resulting from three-way ANOVA. The contributions of geographic (OGU) and temporal variation (CM) are shown as well as the interaction among these (OGU × CM) for all characters (excepting for the patterns of coloration of the breast and tail), besides the interactions between OGU and year of collection (OGU × COLYR) for the characters of coloration.

Character	Y	X	Y2	TAIL1	TAIL2	WNGLN1	WNGLN2	BLLN
OGU	3.13**	1.86*	2.52**	14.2**	6.91**	7.81**	3.92**	4.17**
CM	2.04*	5.77**	6.2*	2.68*	1.88*	0.6	1.13	5.86**
OGU × CM	1.26	1.06	1.18	1.26*	1.18	1.25*	1.15	0.92
COLYR	1.46*	1.43*	1.85*					
OGU × COLYR	1.35	0.93	1.53*					

Character	BLLWD	BLLDP	CURVE	TRSUS	TARSWD	MTOE	HALX
OGU	3.56**	6.33**	3.35**	3.65**	1.89*	2.48**	3.33**
CM	1.34	3.46**	2.19*	0.55	3.4*	2.58*	1.96*
OGU × CM	1	1.34*	1.19	0.23	1.19	1.28*	1.51*

* = $P < 0.05$; ** = $P < 0.001$

one in the west (PX, TUC, SAL, NSON, CSON, TIB, SSON, NSIN, and SSIN). In the east group, a geographically ordered pattern did not exist; however, in the west group, values tended to decrease from north to south. The OGU TIB stood apart from the clinal pattern in the west group. For other characters (not shown), the same pattern of variation was found.

Cluster analysis.—Cluster analysis (Fig. 5) showed two large groups of samples corresponding to those described in the previous analysis. The phenogram did not reveal a geographic structuring of OGUs, nor did it recover named subspecies, except in the western group in which the cluster containing PX, SAL, and TUC corresponded to the subspecies *T. c. palmeri* (although it did not include other samples assigned to that subspecies). Samples from NAY and SSIN, both representing *T. c. occidentale*, occurred in different clusters. The phenogram recovered the *palmeri* and *curvirostre* groups as diagnosed by mtDNA (Zink and Blackwell-Rago 2000) but did not reveal the small southern mtDNA group.

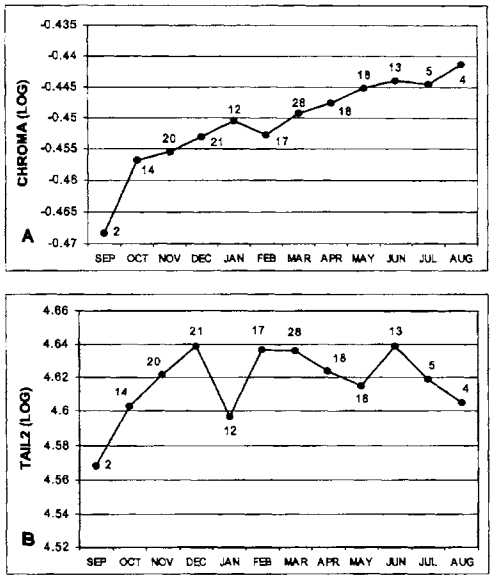

FIG. 3. Mean of the values per month in: (A) chroma (Y2) and (B) length of the outer rectrices (TAIL2) (values log-transformed), for the OGU with the largest sample size (TUC). Number of specimens per month are also indicated.

Principal components analysis.—Variance explained by PC I–III was 82.5%, distributed respectively as 46, 27.8, and 8.8% (Table 3). Characters most contributing to variation along the first principal component were CURVE, TAIL1, TAIL2, BLLDP, and BLLN. Plotting population means on PC I versus PC II revealed two groups, western and eastern (Fig. 6).

ANOVA by group.—All characters exhibited significant geographic variation in each group (west, east; Tables 4 and 5), except for MTOE in the west and TRSWD in the east. In the west

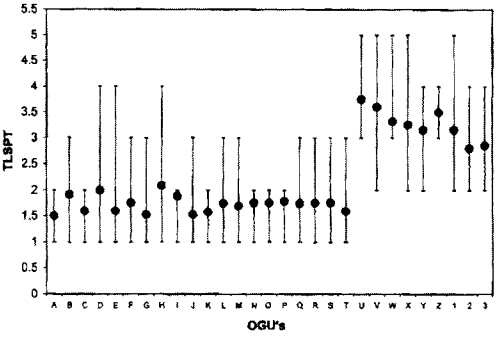

FIG. 4. Analysis of population mean for TLSPT. Range of values for each OGU is indicated.

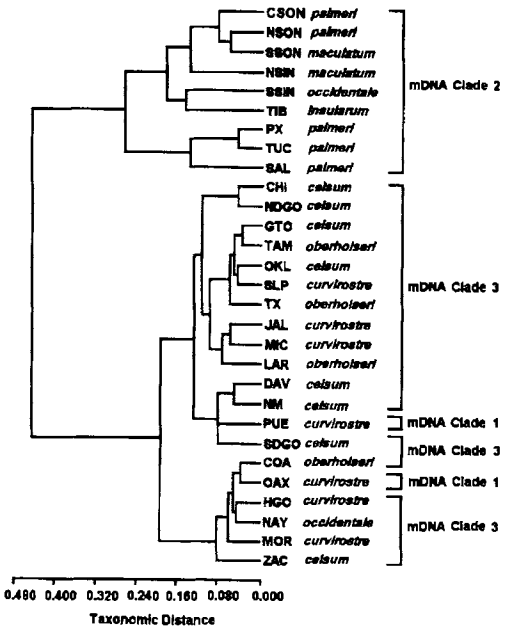

FIG. 5. Cluster analysis. Abbreviations of geographic units correspond to those listed in Table 1, and are followed by the corresponding subspecies. Also shown are mtDNA groupings based on Zink and Blackwell-Rago (2000).

group, variance due to month of collection (CM) was significant ($P < 0.05$) in seven characters; variance due to year of collection for color characters was significant and interaction between OGU and month of collection (CM) were significant ($P < 0.05$) in five of the characters. In the east group, variance due to month of collection (CM) was significant ($P < 0.05$) in eight characters; variance due to year of collection (COLYR) for color characters was significant only in character MY ($P < 0.05$). Interaction between OGU and month of collection (CM) was not significant for any character ($P > 0.05$) except for the character HALX.

The HSD test for all characters (both west and east groups) revealed that the homogeneous groups overlap (not shown). Thus, there were no exclusive groups of samples identified.

Principal components by group.—For the western group (Table 6), variance explained by PC I–III was 66%, distributed respectively as 29, 23, and 14%. Characters contributing most variation to PC I were Y, CURVE, and BLLN.

Analysis of variance for individuals' scores on PC I–V in the western group (Table 7) demonstrated that a significant contribution of variance

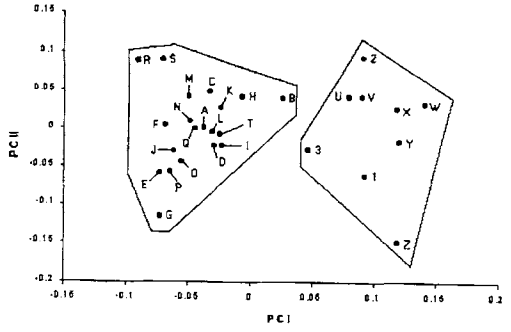

FIG. 6. Results of the PCA. Letters and numbers represent the Geographic Units and correspond to those listed in Table 1.

existed due to geography in the first three components. Three geographically overlapping groups were shown in Figure 7, with the exception of the distinctiveness of the population of Tiburón Island.

For the eastern group (Table 8), the variance explained by PC I–III was 68%, distributed respectively as 34, 21, and 13%. Characters contributing most variation to PC I were Y, CURVE, and BLLN.

Analysis of variance for individuals' scores on PC I–V in the eastern group (Table 9) demonstrated that a significant contribution of variance existed due to the geography in the first four components. There was geographical overlap in the homogeneous groups detected (figure not shown).

DISCUSSION

General analysis of variance.—Variation in each character was due mainly to two sources: the contribution of geography (OGU) and the

TABLE 3. Eigenvectors of the first three principal components. Abbreviations are explained in text.

	PRIN1	PRIN2	PRIN3
TAIL1	0.3739	0.3686	0.2499
TAIL2	0.3526	0.3487	0.1180
WNGLN1	–0.1656	0.3756	0.2228
WNGLN2	–0.1269	0.4119	0.0977
BLLN	0.2642	0.1337	0.4395
BLLWD	–0.1320	0.1747	0.3120
BLLDP	–0.3248	0.3426	0.4518
CURVE	0.6561	0.0966	0.2021
TRSUS	–0.2256	0.2309	0.1499
MTOE	–0.2089	0.3304	0.3148
HALX	–0.0383	0.2230	0.3406
TARSWD	–0.1409	0.2107	0.3022
Variance (%)	46.0	27.8	8.8

TABLE 4. *F*-values from three-way ANOVA for west group. The contributions of geographic (OGU) and temporal variation (CM) are shown as well as the interaction among these (OGU × CM) for all characters (excepting for the patterns of coloration of the breast and tail), besides the interactions between OGU and year of collection (OGU × COLYR) for the characters of coloration.

Character	Y	X	Y2	TAIL1	TAIL2	WNGLN1	WNGLN2	BLLN
OGU	2.14*	2.09	4.30*	5.56**	3.58*	6.71**	4.06*	2.87*
CM	2.32*	4.85**	5.32**	1.96*	1.65	1.44	2.39*	2.44*
OGU × CM	0.79	1.86*	2.36*	1.48*	0.96	1.29	1.02	1.39
OGU × COLYR	2.49*	2.76*	7.86**					
COLYR	1.81*	2.08*	3.09**					

Character	BLLWD	BLLDP	CURVES	TRSUS	TARSWD	MTOE	HALX
OGU	5.05**	6.11**	0.31	5.80**	2.27*	1.78	3.36*
CM	0.99	1.05	1.4	0.72	1.13	2.99*	1.53
OGU × CM	0.77	1.54*	0.99	1.34	1.2	1.39	1.70*

* $P < 0.05$, ** $P < 0.001$

contribution of the temporal variation—that is, to the month (CM) and year of collection (COLYR; Table 2). Significant interactions between OGU and month for TAIL1, WNGLN1, BLLDP, MTOE, and HALX and between OGU and year for Y2, makes interpretation difficult. Nonetheless, it is apparent that geographic variation is significant for all characters.

Temporal variation.—To date, most studies of avian geographic variation have concentrated on character variation among populations. Relatively few studies have considered another potential source of variation, namely annual variation. That is especially important for sedentary birds, because often specimens used were collected throughout the year (studies of geographic variation in migratory species typically only use birds collected during the breeding season). As an example of temporal varia-

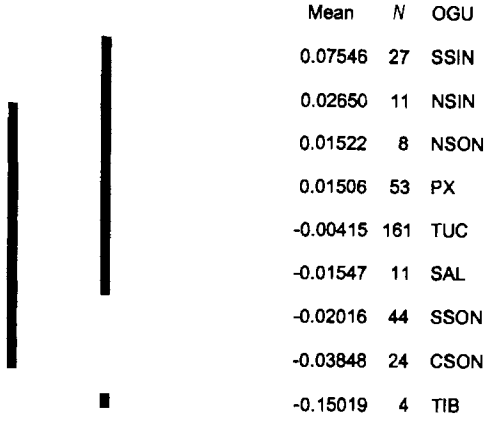

FIG. 7. Tukey's studentized range (HSD) test, for the third principal component for the western group.

TABLE 5. *F*-values from three-way ANOVA for the east group. The contributions of geographic (OGU) and temporal variation (CM) are shown as well as the interaction among these (OGU × CM) for all characters (excepting for the patterns of coloration of the breast and tail), besides the interactions between OGU and year of collection (OGU × COLYR) for the characters of coloration.

Character	Y	X	Y2	TAIL1	TAIL2	WNGLN1	WNGLN2	BLLN
OGU	2.41*	1.71*	2.36*	5.50**	3.12**	7.14**	4.15**	3.50**
CM	1.68	4.51**	4.68**	2.04*	1.78	0.54	0.39	4.34**
OGU × CM	1.17	0.84	0.93	1.18	1.24	1.22	1.13	0.80
OGU × COLYR	0.99	0.84	0.97					
COLYR	1.43*	1.20	1.34					

Character	BLLWD	BLLDP	CURVES	TRSUS	TARSWD	MTOE	HALX
OGU	2.43*	2.94**	1.67*	2.63*	1.60	2.37*	3.03**
CM	1.22	3.75**	2.37*	0.51	4.46**	2.08*	1.80
OGU × CM	1.17	1.25	1.21	1.05	1.13	1.24	1.46*

* $P < 0.05$, ** $P < 0.001$

TABLE 6. Eigenvectors of the three principal components for all characters in the west group. Abbreviations are explained in text.

	Eigenvectors		
Character	PRIN1	PRIN2	PRIN3
Y	–0.7161	0.6381	–0.1962
X	–0.0413	0.0120	0.0110
Y2	–0.0357	0.0146	0.0088
TAIL1	0.0480	0.1261	0.2673
TAIL2	0.0381	0.1557	0.3801
WNGLN1	0.0062	0.1554	0.2591
WNGLN2	–0.0024	0.2343	0.3286
BLLN	0.3068	0.2030	–0.0156
BLLWD	0.1469	0.0507	0.2122
BLLDP	0.1090	0.1242	0.2642
CURVE	0.5834	0.5682	–0.4710
TRSUS	0.0699	0.0801	0.1990
MTOE	0.0709	0.1451	0.2837
HALX	0.0574	0.1377	0.1750
TARSWD	0.0406	0.2119	0.2868
Variance (%)	29	23	14

tion, Figure 3 shows that values of chroma (Y2; graph A) and length of outer rectrices (TAIL2; graphic B) change through the year.

Temporal differences can be explained by two main factors: molt and feather wear. Minimum value for chroma occurs during September and increases gradually through the year. Body molt occurs during July, August, and September. Thus, in September, dorsal feathers are new, and then wear during the year due to exposure to sun, vegetation, and dust. Increasing values for chroma throughout the year need to be studied. For the length of the outer rectrices, temporal differences are not so clearly explained by molt and feather wear because the pattern of change is not gradual. Age-related differences (in different age classes) likely explains the temporal pattern. Thus, it is clear that although there are significant geographic differences in most characters, it is important to control for the effect of the time of year the specimen was collected.

Collection date of specimens contributes to variation in color characters because of postmortem changes. Such variation can be removed with regression of values of the characters and year of collection and subsequently using residuals. However, in this study, although regressions were used, it was not possible to eliminate that variation, and those characters were not considered in some of the analyses.

TABLE 7. ANOVA for individuals' values on PC I–V in the west group.

	PRIN1	PRIN2	PRIN3	PRIN4	PRIN5
Source	*F* value	*F* value	*F* value	*F* value	*F* value
OGU	5.08**	12.63**	6.53**	1.67	2.37*

*$P < 0.05$, **$P < 0.001$

Many previous studies of *T. curvirostre* or other birds (not accounting for quantitative changes in coloration due to specimen age) are likely strongly biased. In conclusion, temporal variation exist throughout the year in birds and must to be considered in further studies of geographic variation.

Geography of variation and identification of units.—A plot (Fig. 4) of mean OGU values for tail spot (TLSPT) shows two large geographical groups, an eastern one including OGUs from the Mexican central plain (including the largest part of the Chihuahuan desert and arid areas of southern Mexico) and a western group including OGUs found mainly in the Sonoran desert. Within the western group, the TIB sample is clearly distinct. Several other characters also show two geographical groups: eastern and western. Although suggestive, analysis of single characters must be followed by analysis that considers all characters simultaneously, so that the main trends in variation can be discovered. Reliance on single characters and failure to account for temporal variation has likely led to the description of too many subspecies, both

TABLE 8. Eigenvectors of the three principal components for all characters in the east group. Abbreviations are explained in text.

Character	PRIN1	PRIN2	PRIN3
Y	–0.7920	0.6049	0.0133
X	0.0061	0.0041	0.0200
Y2	0.0010	0.0096	0.0135
TAIL1	0.0803	0.1207	0.3015
TAIL2	0.0627	0.1406	0.3534
WNGLN1	0.1103	0.1078	0.2974
WNGLN2	0.0794	0.0917	0.3793
BLLN	0.2582	0.2831	–0.0525
BLLWD	0.0678	0.1526	0.1572
BLLDP	0.1794	0.2157	0.1548
CURVE	0.4692	0.6237	–0.4672
TRSUS	0.0678	0.0528	0.1801
MTOE	0.0981	0.1299	0.3742
HALX	0.0581	0.0596	0.2168
TARSWD	0.0517	0.1319	0.2489
Variance (%)	34	21	13

TABLE 9. ANOVA for individuals' scores on PC I–V in the eastern group.

	PRIN1	PRIN2	PRIN3	PRIN4	PRIN5
Source	*F* value	*F* value	*F* value	*F* value	*F* value
OGU	9.65**	3.43**	6.27**	4.98**	1.61*

*$P < 0.05$, **$P < 0.001$

in the Curve-billed Thrasher and in other birds in general (Zink et al. 2000).

Cluster analysis (Fig. 5) reveals two large clusters of OGUs, as suggested by the previous analysis. One cluster (western samples) shows two subgroups including southern and northern populations. That can be interpreted as the existence of two ecogeographical subgroups, probably divided by the Pinacate Desert, one of the hottest and driest habitats in the area located between subgroups. The second (eastern) cluster shows no clear geographical pattern, except for small clusters formed by the populations CHI, NDGO, JAL, MIC, DAV, and NM, which correspond to local geography. The cluster analysis does not support recognition of any named subspecies, although it recovers the two main groups.

Principal component analysis (Fig. 6) also shows the existence of two nonoverlapping groups, differentiated mainly by principal component I. Within each group, no geographically structured pattern of variation exists, except in the eastern group, where highest values on PC II are from southern-most populations (PUE and OAX). Examination of plots of some character means as a function of OGU latitude reveal clinal variation but some others do not. Thus, univariate and multivariate analyses identify two main groups without geographically patterned variation within them.

In the western group alone (Table 4), interactions were still present between the geography and month (OGU × CM $P < 0.05$). A population that does not belong (at least statistically) to that group, such as TIB, could inflate variability. On the other hand, in the east group, all interactions between OGU and month of collection (OGU × CM $P < 0.05$) were eliminated (Table 5), except for MHALX; that can demonstrate that in the east group all the populations tend to be homogeneous (at least statistically). That suggests a further biological difference between the two groups, namely one in annual cycle.

Prinicipal components analyses confirm the existence of geographic variation in both groups. In the western group, the first three components explain 66% of variation (Table 6) and the variation contributed to geography is significant (Table 7). For the eastern group, the first three components explain 68% of variation (Table 8), and the variation contribution (due to geography) is significantly high for the first four components (Table 9). Prinicipal components analyses does not reveal a geographic pattern in either group, except for PC II and PC III in the west group, where TIB differs from the rest of the populations (Figs. 6 and 7). Thus variation within groups does not correspond to environmental conditions that change abruptly. That suggests that environmental gradients affect characters in independent and overlapping ways, preventing existence or maintenance of consistent geographical patterns across characters, as predicted by Sokal and Rinkel (1963). Furthermore, the contribution of genetic and environmental effects is unknown.

Units of evolution and their taxonomic category.—The main problem in defining units of evolution resides in the difference between the recognition of groupings and rank (e.g. species, subspecies) that they should receive. Since Darwin (1859), and in particular in the last 20 years, the view of what constitutes the units of evolution has changed, including methods for reconstruction of evolutionary patterns. Some authors follow the phylogenetic species concept (Cracraft 1983, McKitrick and Zink 1988, Zink 1997), and have concluded that evolutionary units are species that cannot be further subdivided. Under the phylogenetic species concept, subspecies do not exist.

Alternatively, the biological species concept (Mayr 1942) is most commonly accepted in ornithology (American Ornithologists' Union 1998). Under that concept, subspecies are accepted. If evolutionary units are regarded as biological species, then those would lack historical value because subspecies are recognizable taxa. On the other hand, if subspecies are considered as historical or evolutionary units, recognition of historical patterns could be similar to that obtained by using phylogenetic species. However, that would be true only if subspecies were equivalent to phylogenetic species. Unfortunately, that is relatively infrequent because many subspecies are not units of evolution, as this study suggests.

For that reason, one of the main goals of this study was to test whether subspecies limits in

the *Toxostoma curvirostre* complex correspond to historical patterns of variation. Most analyses (Figs. 4–6) demonstrated that the seven described subspecies are almost certainly arbitrary divisions of discordant single character clines (the case of populations from Tiburón Island is discussed below). Genetic studies have also questioned the validity of many avian subspecies (Ball and Avise 1992), and in particular, Zink and Blackwell-Rago (2000) showed that only two or probably three historical units exist in Curve-billed Thrashers—not seven as suggested—if current subspecies are units of evolution.

The correspondence of morphometric and mtDNA analyses (Zink and Blackwell-Rago 2000) suggests that the two main groups (*curvirostre* and *palmeri*) of *Toxostoma curvirostre* should be considered as independent evolutionary units (species) that would receive the names *"Toxostoma curvirostre"* for the eastern group and *"Toxostoma palmeri"* for the western group. Morphological and color characters vary discontinuously between both groups, even in the contact areas between both forms in southeast of Arizona and northern of Jalisco. The Sierra Madre Occidental likely acted as a barrier between groups, and that could be the main factor that caused differentiation.

Tiburón Island.—Tiburón and San Esteban islands, located in the Gulf of California, contain an endemic subspecies *Toxostoma curvirostre insularum* (Van Rossem 1930). This work confirms that the population of Tiburón Island (OGU TIB) is differentiated in some characters from the western group, including TLSPT (Fig. 4). The HSD test for the ANOVA on PC scores (Fig. 7) clearly separates TIB. Attending to the morphology, it does not constitute an ecogeographical group due to discontinuity in variation of many characters. Thus the population of Tiburón Island could be considered as an independent evolutionary unit, at least morphologically, and could be treated as an independent species (*T. insularum*). However, lack of a significant number of specimens (only 4), does not give enough statistical support to justify taxonomic conclusions about that population. Genetic data are needed to test the species status of that population.

CONCLUSION

Analyses of morphological and coloration characters are useful tools for understanding geographic variation in the *Toxostoma curvirostre* complex. Unlike most studies of avian geographic variation, specimens collected throughout the year were used. The reason was that the Curve-billed Thrasher appears sedentary (Tweit 1996). However, I found significant variation in measurements within and among years. Therefore, it is important to control for that variation statistically. Quantitative analysis of color and morphology corroborated the existence of the two subspecies groups, the eastern group corresponding to the Sonoran Desert and the Pacific slope, and the western group found on the Mexican plateau and south, separated from one another by the Sierra Madre Occidental. The agreement of mtDNA patterns (Zink and Blackwell-Rago 2000) and my analyses of qualitative patterns of the coloration (tail-spot pattern and PCA) confirm the existence of two diagnosable entities: *T. curvirostre* (eastern group), which has big and well-defined spots (dark in breast and white in tail); and *T. palmeri* (western group), in which spots are missing or are poorly marked. Although not evident in wild birds, in *T. curvirostre* exhibits well-defined white wingbars, whereas in *T. palmeri* they are hardly distinguishable. That supports Zink and Remsen's (1986) suggestion, that "...discontinuous variation is more of an interspecific phenomenon, whereas geographically variable characters are continuously distributed." The pattern of variation in color and morphology does not match the seven described subspecies, even when using the same characters used in the initial subspecies descriptions. It seems likely, then, that subspecies of the *T. curvirostre* complex were based on analysis of insufficient numbers of characters and specimens. Quantitative and comprehensive analyses will show that many avian subspecies are not evolutionary groups and do not merit formal taxonomic names.

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