

CHARACTER DISPLACEMENT AND ECOMORPHOLOGICAL ANALYSIS OF TWO LONG-EARED *MYOTIS* (*M. AURICULUS* AND *M. EVOTIS*)

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Ecomorphological analysis was used to evaluate ecological relationships between 2 species of bats, *Myotis auriculus* and *M. evotis*. We imaged jaws and skulls of 242 specimens from 20 localities within the range of both taxa, emphasizing their southwestern regional area of sympatry. Using traditional morphometric and geometric morphometric methods, values for characters taken from dentaries of both species were analyzed in detail. Both methods detected character displacement and allowed us to detect differences in jaw size and shape within both species. The morphological difference in jaw shape is more emphasized within sympatric populations of *M. evotis* than in *M. auriculus*. This may indicate that competitive selection acts more on *M. evotis*. At sympatric localities, *M. evotis* displayed a shift to a more specialized trophic state with a trophic architecture (more highly placed articular process and robust molars) likely better at capturing beetles, whereas *M. auriculus* may have a greater advantage for capturing soft-bodied prey such as moths. On the other hand, the articular process is located lower relative to the toothrow of the dentary in *M. auriculus*. Also the shape of the jaw in this species suggests a weaker bite, more shearing force, and wider gape. All shape differences in jaw morphology are emphasized in sympatry, confirming active competitive interactions between these 2 species.

Key words: biogeographic cline, character displacement, competitive exclusion, geometric morphometrics, interspecific competition, trophic structure

Ecological morphology, or study of relationships between morphology and ecology, has often been used to examine interspecific interactions that cannot otherwise be observed or that might be difficult to study experimentally. Use of morphological character patterns to infer processes of selection can provide useful insight into ecological questions such as assembly of communities. For instance, historical range shifts or interruption in gene flow could result in some mismatch of morphological characters, but consistent differences in morphology among groups at sites might indicate process-level changes. Patterns from more plastic, polygenic character suites (e.g., behaviors or vocalizations) that are not as easily quantified as morphological characters also can aid in resolving questions regarding species interactions (Gannon and Lawlor 1989).

Based on the competitive exclusion principle (Gause 1934; Grinnell 1917), no 2 species can occupy the same ecological niche at the same time and same locality. An interesting

phenomenon arises when 2 species with similar ecological needs come into contact at the edge of their distribution. In this contact zone, competition should force each species to occupy different ecological niches. The morphological manifestation of this competition was termed “character displacement,” where species with similar ecological needs are morphologically more different in the contact zone (Brown and Wilson 1956). As a result of scientific debate, several conditions were proposed to test character displacement versus alternative hypotheses (Arthur 1982; Grant 1972). Moreover, Robinson and Wilson (1994) stated that in analytical tests of character displacement, localities of sympatry and allopatry should be ecologically similar so that character change in sympatry would result from presence of competitors rather than environmental structure. In reality, testing whether all conditions are met for character displacement is not always feasible. Since the foundational papers in the 1960s and early 1970s, documenting morphological character displacement became a central theme in demonstrating selection under strong competition between ecologically similar species (Hutchinson 1959). Studies of character displacement among closely related species are important in that they can show changes that occur during or shortly after speciation, how ecological factors influence adaptive radiations at the microscale, and how interspecific

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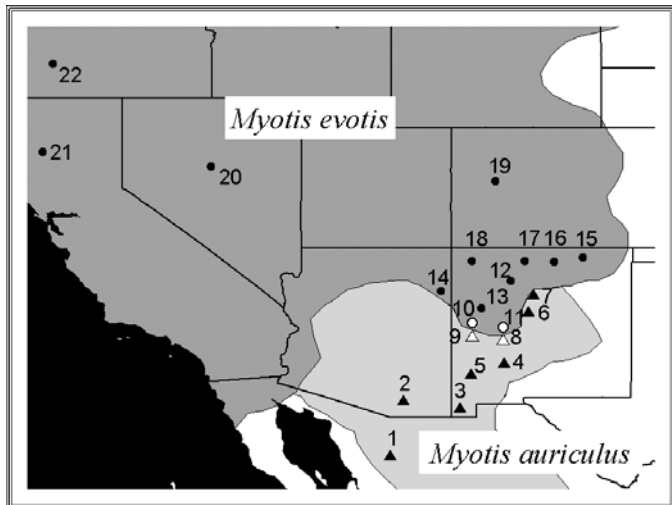


FIG. 1.—Ranges and sampling localities in the western United States for *Myotis auriculus* (triangles) and *M. evotis* (circles) examined in this study. Sites, numbered 1–22, are listed in Appendix I. All sites are marked with closed symbols, except for sites 8 and 9 (open triangles, *M. auriculus*) and 10 and 11 (open circles, *M. evotis*), which are syntopic (Gannon 1998).

interactions influence the geographic distributions of species and assembly of communities (Grant 1994).

In the last decade discussions of character displacement have emphasized that morphological variables associated with prey capture are likely to demonstrate differences (Brown and Wilson 1956; Dayan and Simberloff 1998; Kieser 1995; Robinson and Wilson 1994; Schluter 1994). In an experimental model of character displacement, Schluter (1994) described density-dependent effects of interspecific competition and natural selection for divergent morphologies in sticklebacks (*Gasterosteus*). Dayan and Simberloff (1994; see also Dayan et al. 1992; Kieser 1995) found support for prey-size partitioning reflected in several morphological characteristics of 3 guilds of carnivores: mustelids, felids, and canids.

Although several papers demonstrated resource partitioning among sympatric bats (Arlettaz 1999; Kingston et al. 2000), morphological character displacement among these species of bats has received little attention (Arlettaz 1995). Perhaps resources, such as food, are not limited (Fenton 1985) and thus bats are less affected by interspecific competition than are other mammalian groups (Schum 1984). However, within *Myotis* there is evidence that at least some species compete for food resources (Arlettaz 1995; Husar 1976). Character displacement presumably reflects selection for trophic traits that reduce competition between sympatric populations of different species for food resources. The primary trophic structures of vertebrates on which natural selection should act are the jaws (Kieser 1995; Ruedas et al. 1994). In this paper we examine morphological differences between *Myotis evotis* and *M. auriculus* found in syntopy and allopatry to discern if any morphological differences observed between species occurs in the trophic apparatus of these bats.

The long-eared bats *M. auriculus* and *M. evotis* have been shown to share localities and resources at the same time and

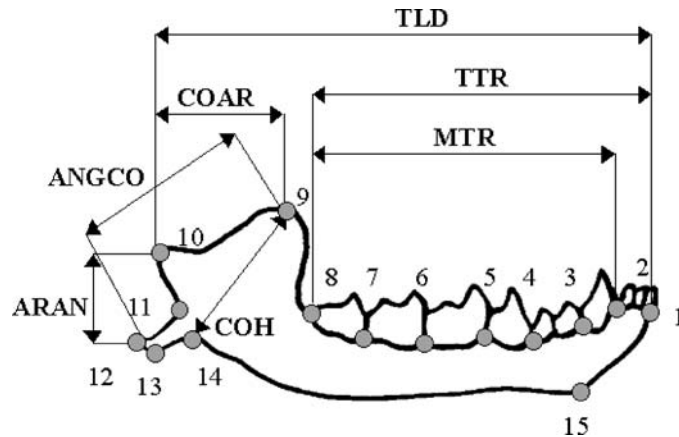


FIG. 2.—Right dentary, stylized, from *Myotis*, depicting landmarks (1–15) and distances measured. Variables are defined in the text.

in the same place (Black 1974; Gannon 1998). Husar (1976) found behavioral character shifts when the 2 species occurred sympatrically; *M. auriculus* fed in greater frequency on moths and *M. evotis* on beetles. In allopatry, both species fed on moths and beetles in equal proportion. No ecomorphological analyses have been conducted on these species, and several investigators (Fenton 1985; Warner 1985) have questioned the claims of Husar (1976) and urged further work on these species (Findley and Wilson 1982). Here, we examine museum specimens using 2 methods, traditional morphometrics and geometric morphometrics, to test a hypothesis of character displacement between *M. auriculus* and *M. evotis*.

MATERIALS AND METHODS

We examined 242 specimens of long-eared *Myotis* (121 *M. auriculus* and 121 *M. evotis*) from localities throughout their geographic range, including 2 localities where these species have frequently been found to coexist in syntopy (Appendix I; Fig. 1). Only adult specimens were selected for the study. Age was judged based on the following criteria: presence of adult pelage (not short and gray), epiphyses of phalanges and metacarpals fused with diaphyses, and full ossification of skull. Also, only specimens with intact jaws were measured. All specimens used in analyses were from the Division of Mammals, Museum of Southwestern Biology (MSB), University of New Mexico. The recorded data included MSB catalog number, species identification, state, county, and sex. Parameters measured were modeled after those used in previous studies of mandibular morphology (Findley and Wilson 1982; Freeman 1981, 1988; Manning 1993; Reduker 1983).

We photographed the buccal view of the right mandible with an analog video camera (Panasonic WV-BL 600, Full Compass, Middleton, Wisconsin). To standardize measurements, each picture was calibrated against a 10.00-mm object. Pictures were digitized at 300 dpi and saved as tagged image file format files on a computer. We used thin-plate spline digitizing analysis software (tpsDIG—Rohlf 2001) to set 15 landmarks on the image of each jaw (Fig. 2).

Traditional morphometric methods.—To analyze jaw shape following the traditional morphometric methods, we calculated distance between characteristic points. We took 7 measurements (Fig. 2): height of coronoid process (COH), from superiormost tip of coronoid process to edge of deepest ventral depression on ramus; distance from

angular process to coronoid (ANGCO), from ventral edge of angular process to anterosuperior edge of coronoid process; distance from articular (condylar) process to angular process (ARAN), from anterior edge of articular condyle to ventral border of angular process; distance from coronoid process to articular process (COAR), from superior-most tip of coronoid process to midpoint of articular process; total length of dentary (TLD), from midpoint of angular condyle to anteriormost edge of dentary; length of mandibular tooththrow (MTR), greatest distance from posteriormost surface of 3rd lower molar to anteriormost edge of lower canine; and total tooththrow length (TTR), greatest distance from posteriormost edge of 3rd lower molar to anteriormost edge of 1st incisor. In addition, jaw closure ratio (JCR) was calculated by dividing height of coronoid process by total length of dentary (COH/TLD). This ratio allows a comparison of the height of the coronoid process with dentary length to infer jaw closure speed and force. For example, a medium jaw length (approximately 12 mm) and high coronoid process (>3.5 mm) would provide a high jaw closure ratio (>0.3) indicating potential for a swift, forceful bite.

We analyzed jaw measurements by univariate *t*-test and multivariate Hotelling's *T*-test using Statistica statistical analysis software (StatSoft Inc. 1998). Males and females of both species were compared at 1 locality to detect sexual dimorphism (Socorro County, New Mexico; *M. evotis* *n* = 34 females, *n* = 38 males; *M. auriculus* *n* = 14 females, *n* = 19 males). Because Hotelling's *T*-test did not reject a null hypothesis of sexual dimorphism, additional pairwise tests were made between both species (allopatric *M. auriculus* versus allopatric *M. evotis*; sympatric *M. auriculus* versus sympatric *M. evotis*) and within species (allopatric versus sympatric *M. auriculus*; allopatric versus sympatric *M. evotis*). Finally, we used discriminant function analysis to reduce number of variables and visualize differences between 4 groups (1 = allopatric *M. auriculus*, 2 = sympatric *M. auriculus*, 3 = allopatric *M. evotis*, and 4 = sympatric *M. evotis*). Squared Mahalanobis distances among centroids of the 4 groups were calculated to detect character displacement between species at sympatric localities.

Geometric morphometric methods.—Geometric morphometric methods were applied to validate traditional morphometric results and to gain further insight into jaw shape differences between species. The tpsSMALL program (Rohlf 1998) was used to calculate a pairwise Procrustes distance matrix and centroid metric. Shape variables (weight matrix) were calculated using tpsRELW program (Rohlf 1997).

In a similar fashion as was done with jaw measurements, males and females from each species were statistically compared for size and shape differences. Because there were significant differences in size and shape of jaws, the original data set was separated by sexes and further statistical tests were performed separately. Pairwise Procrustes distances were then calculated between pairs of animals from 4 groups (group 1 and 2: allopatric and sympatric *M. auriculus*; group 3 and 4: allopatric and sympatric *M. evotis*). With these 4 groups, there are 10 different combinations of pairing up individuals. From the 10 combinations, we were interested in Procrustes distances between individuals in 6 scenarios: pairwise Procrustes distances were calculated for: 1 = 2 allopatric *M. auriculus*, 2 = 2 sympatric *M. auriculus*, 3 = 2 allopatric *M. evotis*, 4 = 2 sympatric *M. evotis*, 5 = 1 sympatric *M. auriculus* and 1 *M. evotis*, and 6 = 1 allopatric *M. auriculus* and 1 *M. evotis*. The average of Procrustes values describing shape differences among individuals were then statistically compared between these 6 groups using *t*-tests. In this way each individual is compared to all others by pairwise sampling until all specimens are examined.

Average centroid size for both species and sex were tabulated by sympatric and allopatric populations. Jaws of allopatric populations of

TABLE 1.—Average jaw measurements between allopatric and sympatric samples of *Myotis evotis* and *M. auriculus*. Sample sizes: *M. evotis*, allopatric, *n* = 45, sympatric, *n* = 76; *M. auriculus*, allopatric, *n* = 83, sympatric, *n* = 38. Measurement codes are defined in text. Significant values are in bold.

Measurement	Allopatric \bar{X} (mm)	Sympatric \bar{X} (mm)	<i>P</i>
<i>M. evotis</i>			
COH	3.40	3.57	0.000
ANGCO	4.08	4.21	0.000
ARAN	1.73	1.76	0.284
COAR	3.01	3.07	0.039
TLD	11.60	11.91	0.000
MTR	6.79	7.02	0.000
TTR	7.70	7.95	0.000
JCR	0.29	0.30	0.007
<i>M. auriculus</i>			
COH	3.46	3.49	0.339
ANGCO	4.14	4.18	0.156
ARAN	1.60	1.52	0.002
COAR	3.07	3.15	0.021
TLD	11.69	11.70	0.862
MTR	6.86	6.90	0.194
TTR	7.83	7.86	0.400
JCR	0.30	0.30	0.405

M. auriculus were designated as reference shape and 3 other groups (sympatric *M. auriculus*, allopatric *M. evotis*, and sympatric *M. evotis*) were visually compared to the reference group using thin-plate splines.

RESULTS

Traditional morphometrics.—Multivariate analyses did not detect differences in skull measurements between males and females for specimens collected at Socorro County sites (*M. evotis* *n* = 34 females, 38 males; *M. auriculus* *n* = 14 females, 19 males). Although *t*-tests detected significant differences between sexes for certain variables (*M. evotis* variables MTR and TTR, *P* < 0.05; *M. auriculus* variables ANGCO, COAR, TLD, MTR, and TTR, *P* < 0.05), a multivariate Hotelling's *T*-test did not reject the null hypothesis that there are significant differences between males and females at this locality (*M. evotis* *P* < 0.15; *M. auriculus* *P* < 0.109). Based on univariate *t*-test, we found a general tendency of females to be larger than males.

Jaw measurements were significantly different for both species compared either for allopatric or for sympatric populations (Tables 1 and 2). For both *M. evotis* and *M. auriculus*, multivariate Hotelling's *T*-tests showed significant differences in jaw measurements between allopatric (*P* < 0.01) and sympatric populations (*P* < 0.01). Sympatric populations were significantly different for both species in several jaw measurements (COH, ARAN, COAR, TLD, MTR, and TTR, *P* < 0.05) and 2 variables were not significantly different (ANGCO and JCR, *P* > 0.05). Allopatric populations were significantly different for fewer variables (COH, ARAN, COAR, and TTR, *P* < 0.05) and 4 variables were not significantly different (ANGCO, TLD, MTR, and JCR, *P* > 0.05; Tables 1 and 2).

TABLE 2.—Average jaw measurements between sympatric samples of *Myotis auriculus* ($n = 38$) and *M. evotis* ($n = 76$), and between allopatric samples of *Myotis auriculus* ($n = 83$) and *M. evotis* ($n = 45$) are presented. Measurement codes are defined in text. Significant values are in bold.

Measurement	<i>M. auriculus</i> \bar{X} (mm)	<i>M. evotis</i> \bar{X} (mm)	<i>P</i>
Sympatric			
COH	3.49	3.57	0.016
ANGCO	4.17	4.21	0.323
ARAN	1.52	1.76	0.000
COAR	3.15	3.07	0.026
TLD	11.70	11.91	0.001
MTR	6.90	7.02	0.003
TTR	7.86	7.95	0.034
JCR	0.30	0.30	0.614
Allopatric			
COH	3.46	3.40	0.02
ANGCO	4.14	4.08	0.064
ARAN	1.60	1.73	0.000
COAR	3.07	3.00	0.022
TLD	11.69	11.60	0.098
MTR	6.86	6.79	0.079
TTR	7.83	7.70	0.000
JCR	0.29	0.29	0.155

Allopatric *M. evotis* were different from sympatric populations (Hotelling's *T*-test, $P < 0.01$) as were allopatric and sympatric populations of *M. auriculus* (Hotelling's *T*-test, $P < 0.01$). Moreover, jaw measurements of sympatric and allopatric *M. evotis* were significantly different for all variables except ARAN ($P > 0.05$; Table 1), whereas sympatric and allopatric populations of *M. auriculus* were significantly different for the 2 variables ARAN and COAR ($P < 0.05$; Table 1). From jaw measurements, sympatric populations of *M. auriculus* appear to be the same size as their allopatric conspecifics. On the other hand, sympatric *M. evotis*, which represent the southernmost populations of the species, are larger than specimens in allopatric northern populations. This pattern is opposite what would be expected from just a latitudinal size gradient or what has been shown in another bat species (Bogdanowicz 1990). This indicates that competitive pressure in sympatry may be stronger on *M. evotis* than *M. auriculus*. Jaw closure ratio was significantly different only when allopatric and sympatric populations of *M. evotis* were compared (allopatric $JCR_{aver} = 0.293$, sympatric $JCR_{aver} = 0.300$, $P < 0.01$).

Discriminant function analysis showed significant differences between all 4 groups (sympatric *M. evotis* and *M. auriculus*, allopatric *M. evotis* and *M. auriculus*), but separation between these groups is not complete based on jaw measurements (Wilks' lambda = 0.41, $P < 0.0001$; Fig. 3). The squared Mahalanobis distance was largest between the centroid of sympatric populations of *M. evotis* and *M. auriculus* (5.53) and less between allopatric populations of the 2 species (3.11), supporting existence of character displacement between both species in sympatry (Tables 3 and 4). When we compared allopatric and sympatric populations of the same species, Mahalanobis distances were smaller for *M. auriculus* (0.92) and larger for *M. evotis* (2.41; Table 3). These numbers also

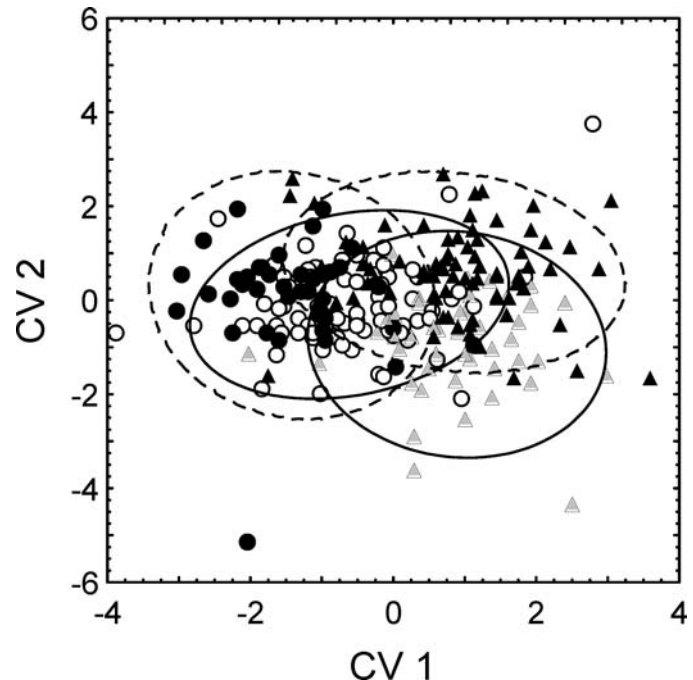


FIG. 3.—Scatterplot of canonical scores (root 1 and root 2) from discriminant function analysis for measurements of *Myotis evotis* and *M. auriculus*. Although points cluster fairly tightly, 4 groups are discerned. Solid lines indicate values for both species in allopatry, dashed lines are for sympatric samples. Open circles indicate allopatric samples of *M. auriculus*, black circle indicate sympatric *M. auriculus*, black triangle is sympatric *M. evotis*, and gray triangle is allopatric *M. evotis*.

show that most of the morphological changes are allocated to sympatric populations of *M. evotis*.

Geometric morphometrics.—No significant differences were found between males and females at locality 8 for *M. auriculus* ($P > 0.05$; Fig. 1), and results of a Hotelling *T*-test were significant in size and shape dimensions between male and female *M. evotis* at locality 11 ($P < 0.001$; Fig. 1). More detailed comparisons revealed that female *M. evotis* are in average larger than males (Table 4). Because there is an allometric relationship between size and shape of skull, size differences between the sexes also is reflected in shape differences in jaw morphology.

For both males and females, average Procrustes distances were significantly larger when *M. auriculus* and *M. evotis* were compared in sympatric populations than between allopatric populations (*t*-test, $P < 0.005$; Fig. 4). Variations in pairwise Procrustes distances were smaller when 2 individuals of the same species were compared than in instances when 2 individuals of opposite species were compared. The only exception to this pattern was observed among sympatric male *M. evotis*, which showed a very high level of within-population morphological variation as compared with other groups (Fig. 4).

Thin-plate spline comparison of jaw shapes showed similar trends for both males and females (Fig. 5). Compared to average jaw shape of allopatric *M. auriculus*, sympatric *M. auriculus* displayed differences in relative position of the

TABLE 3.—Squared Mahalanobis distances between allopatric *Myotis auriculus*, sympatric *M. auriculus*, allopatric *M. evotis*, and sympatric *M. evotis*.

	Squared Mahalanobis distances			
	Allopatric <i>M. auriculus</i>	Sympatric <i>M. auriculus</i>	Allopatric <i>M. evotis</i>	Sympatric <i>M. evotis</i>
Allopatric <i>M. auriculus</i>	0.00	0.92	3.11	2.71
Sympatric <i>M. auriculus</i>	0.92	0.00	6.55	5.53
Allopatric <i>M. evotis</i>	3.11	6.55	0.00	2.41
Sympatric <i>M. evotis</i>	2.71	5.53	2.41	0.00

articular process. In sympatry, the articular process of the jaw is positioned lower and closer to the plane of the toothrow than in the case of allopatric *M. auriculus*. The jaw of *M. evotis* differs from the pattern found for *M. auriculus*, where the articular process is much higher relative to the plane of the toothrow (Fig. 5). For *M. evotis*, the coronoid process is lower, molars are wider, and premolars are narrower than for *M. auriculus* (Fig. 5). These differences in jaw shape between the species are more distinct in sympatry.

Finally, although both morphological analyses detected character displacement between the 2 species, traditional morphometric analyses were less sensitive and did not detect sexual differences within the 2 species. Furthermore, geometric morphometric methods also discerned differences in jaw shape, where the molars of *M. evotis* are more robust and allow this species to feed on hard-bodied types of prey. However, both analytic methods determined that *M. evotis* tends to be larger, and this size difference is more emphasized in the region of sympatry. The shape differences in the jaw between the species can be attributed to differences in the relative position of the articular process. In the case of *M. evotis*, the articular process is positioned higher up (larger measurements between the angular and articular processes and shorter distances between the coronoid and articular processes) and this provides more crushing force during mastication. Also, the articular process is positioned lower in relation to the plane of the teeth in *M. auriculus*, providing this species with a weaker crushing force but more shearing force during bites.

DISCUSSION

The genus *Myotis* is highly diverse (84 species listed by Koopman [1993, 1994]) and has several pairs of closely related species that are sympatric (e.g., *M. myotis* and *M. blythii* [Arlettaz 1995; Koopman 1993, 1994], and *M. auriculus* and *M. evotis* [Black 1974]) that provide an opportunity for examining a character displacement hypothesis. In western North America, there are 11 species of *Myotis* whose ranges overlap (Hall 1981). Of these, 5 are grouped as long-eared *Myotis* and 6 as short-eared *Myotis*. Presumably, long-eared *Myotis* have a foraging style different from that of short-eared *Myotis* because acoustic prey detection abilities are related to ear length (Aldridge and Rautenbach 1987; Findley 1993; Gannon et al. 2001). Of short-eared and long-eared bats, 1 pair of each is truly syntopic.

TABLE 4.—Average centroid size (larger values indicate greater jaw size) for allopatric and sympatric *Myotis auriculus* and *M. evotis*, respectively, calculated from 15 dentary landmarks (Fig. 2).

	Centroid size							
	Female				Male			
	<i>M. auriculus</i>		<i>M. evotis</i>		<i>M. auriculus</i>		<i>M. evotis</i>	
	\bar{X}	<i>n</i>	\bar{X}	<i>n</i>	\bar{X}	<i>n</i>	\bar{X}	<i>n</i>
Allopatric	16.66	43	16.21	14	16.49	40	16.61	31
Sympatric	16.82	18	17.09	35	16.44	20	16.90	42

Myotis evotis is represented by 6 subspecies (Manning 1993) that range from the Mogollón Rim (Arizona and New Mexico) of the southwestern United States northward into British Columbia, Canada. *M. auriculus* is represented by 2 subspecies (Hall 1981) that extend from the Mogollón Rim southward into southern Mexico and perhaps as far south as Guatemala (Hoffmann et al. 1987). The geographic ranges of both species are known to be sympatric along a shallow margin from central New Mexico to Arizona (Hall 1981). Actual syntopy has been documented from only a few localities in Arizona and New Mexico (Gannon 1998).

Although these 2 bats are similar in size and shape, there are subtle phenotypic differences, for example, *M. evotis* has black ears and wing membranes, whereas those of *M. auriculus* are light brown. Reduker et al. (1983) found that all long-eared *Myotis* belong to a monophyletic clade and showed that, despite considerable morphological overlap, they are genetically distinct. In addition it was found that morphological similarity among long-eared *Myotis* is a result of shared primitive characters and similar ecological niches (Manning 1993).

Ecologically, both *M. auriculus* and *M. evotis* inhabit coniferous forest of western North America and forage as gleaners (Findley 1993) and hover-gleaners (Norberg 1994). Fenton and Morris (1976) regarded *M. evotis* as an insectivore that was temporally opportunistic. Examination of stomachs of *M. evotis* revealed that insects from 7 different orders of arthropods are consumed, with beetles (Coleoptera) and moths (Lepidoptera) being most abundant (Whitaker et al. 1977). At a single site in central New Mexico, Black (1974) characterized the insectivorous bat community as composed of either moth strategists or beetle strategists. This dichotomy was modified by Warner (1985), who suggested that beetle-eaters were specialists and the moth-eaters were generalists. Freeman (1979) and Reduker (1983) predicted that species of *Myotis* specialized to feed on harder-bodied beetles would have a greater ability to produce forceful jaw closure than if they were generalists or moth specialists. Jaw attributes, therefore, are predicted to vary with feeding ecology.

Both traditional and geometric morphometrics supported the conclusion that there is morphological character displacement between sympatric populations of *M. auriculus* and *M. evotis*. Landmark-based comparisons of jaws showed that shape of jaws is more different when 2 individuals of 2 species are compared from sympatric than from allopatric populations. In addition, both traditional and geometric morphometric methods

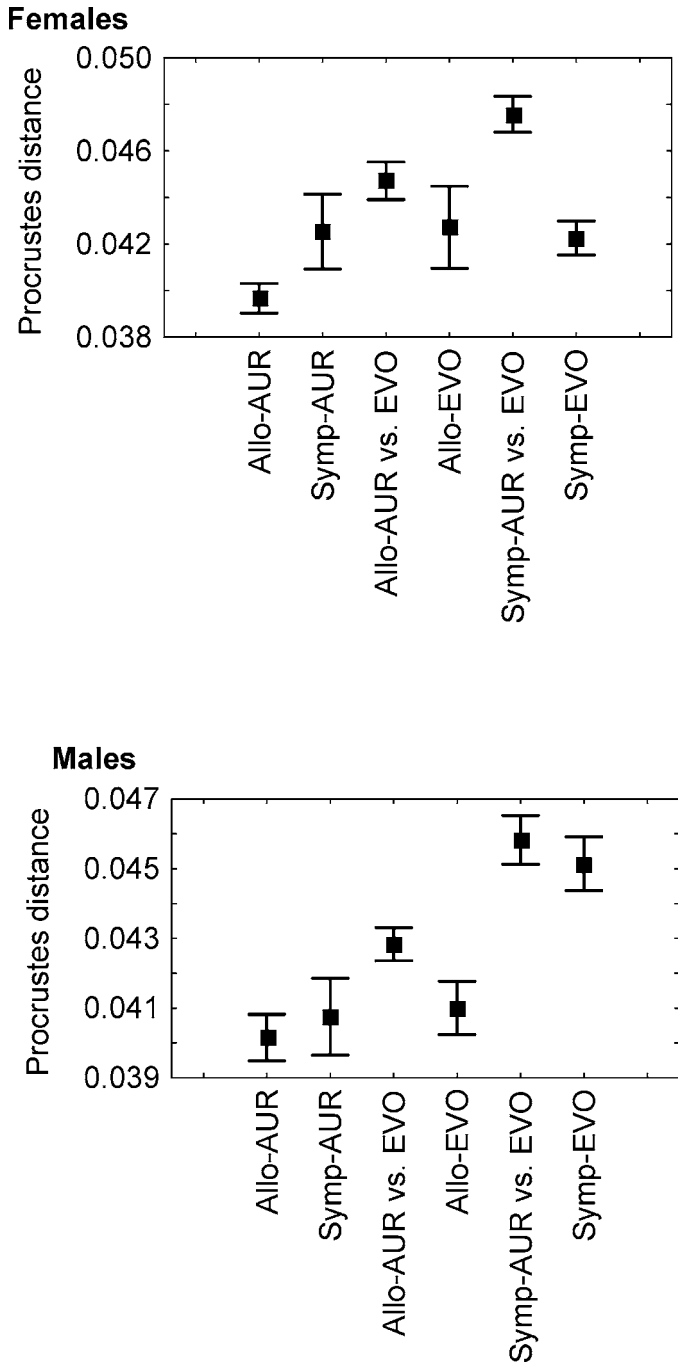


FIG. 4.—Pairwise Procrustes distances generated from jaw landmarks for female (top) and male (bottom) for combinations of sympatric and allopatric samples of *Myotis evotis* and *M. auriculus*. Mean (square) \pm 95% confidence intervals are depicted.

supported that sympatric *M. evotis* is more specialized to feed on hard-bodied prey such as coleopterans than is *M. auriculus*. Conversely, there are differences in detail regarding the way both morphometric methods characterize ecomorphological differences between sympatric and allopatric populations of *M. auriculus* and *M. evotis*.

It is likely that allopatry preceded sympatry, especially if the morphological and ecological relationship between these species is so close that both were derived directly from

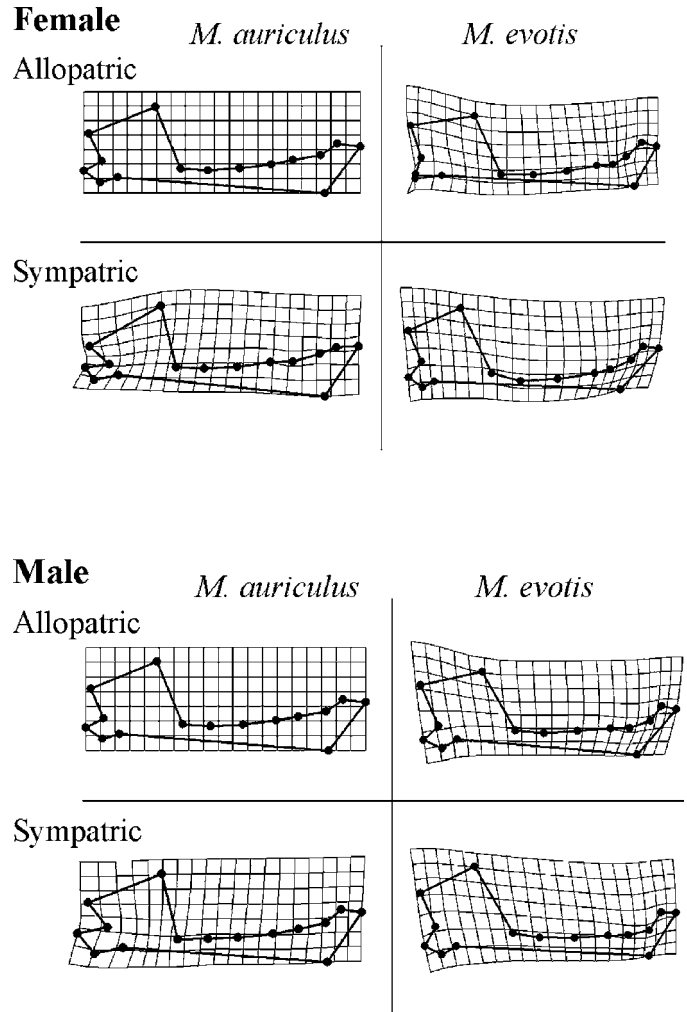


FIG. 5.—Thin-plate spline representations of jaw shape differences among allopatric and sympatric *Myotis evotis* and *M. auriculus* (female, top; male, bottom). The strength of the thin-plate spline method is in effective presentation of visual differences among subtle features. Here we show relative position of the articular process that is much higher relative to the plane of the toothrow in *M. evotis* than in sympatric *M. auriculus*. This display clearly shows functional differences in feeding ecology between the 2 species when they occur together. Allopatric *M. auriculus* was designated as the reference for thin-plate spline.

a common ancestor in recent times (Husar 1976; Mayr 1963). Although syntopy may be rare, a significant strip of overlap occurs between *M. evotis* and *M. auriculus* (Gannon 1998). Manning (1993) claimed that *M. evotis* preferred higher-elevation coniferous areas and *M. auriculus* preferred a middle-elevation coniferous habitat. Although *M. evotis* and *M. auriculus* can be found in very different habitats, generally they both are most common in coniferous forest. In syntopy, there obviously are no habitat differences. Therefore, influences of habitat or other environmental factors would be constant and morphological differences would be due to processes of interactions between both species.

We also found that most instances of the observed character displacement in sympatry can be allocated to the northern

species, *M. evotis*. This indicates that selective pressure may act more strongly on this species than on *M. auriculus*. A similar observation was made on 2 sympatric species of *Neomys* (RÁCZ and Demeter 1998), in which case most of the character displacement was observed among sympatric specimens of the northern species, *Neomys fodiens*, whereas the southern species, *N. anomalus*, was less affected by competition. MacArthur (1972) hypothesized that the southern boundary of a species is limited by competition, whereas at higher latitudes abiotic factors are at play. In the case of the 2 species that we report on, morphological changes are prominent in the more northern species (*M. evotis*) and can be attributed to competition.

Although the 2 morphometric methods used in our study arrived at the same general conclusions, there were areas where 1 or the other method was better suited to answer certain questions. A main distinction between these methods of evaluating differences in morphology is how each visualizes features in jaw morphology between species. Traditional morphometric methods use measurements made by hand, using calipers, such that differences that are found are ascribed only to those particular measurements. Conversely, geometric analysis of shapes extracts size variable (centroid size) and compares shapes that are standardized by size (where centroid size is 1—Rohlf 1990). This technique causes individual measurements to be lost and differences in jaw shape between species are depicted by thin-plate spline diagrams. Thin-plate spline representations of jaws help to identify shape, but not size differences. In this regard, caliper-based measurements emphasize differences in length of jaw and height of coronoid process. As a result of scaling to a centroid size of 1 by the Procrustes method, visual comparison of jaw shapes between species does not emphasize differences in characters such as jaw length or coronoid height. Rather, thin-plate spline representation of differences in jaw morphology emphasizes the relative position of the articular process in relation to the plane defined by the molars. In our study the articular process was found to be positioned higher in *M. evotis* than in *M. auriculus*. Functionally and ecologically this results in *M. evotis* having a narrower gape but greater crushing potential by increased shearing force during mastication. Also, molars of *M. evotis* are more robust than those of *M. auriculus*, indicating that the former is feeding on harder-bodied prey.

Quantitative analyses of jaw morphology support predictions derived from Husar's (1976) study of diet between both species in sympatry. We suggest that competitive interactions between these 2 species in sympatry may be reduced by a larger increase in height of the coronoid process and smaller increase in the length of dentary in *M. evotis* relative to values in allopatry. These changes, in conjunction with the calculated jaw closure ratios, suggest that *M. evotis* has a greater mechanical advantage in capturing or chewing hard-bodied prey such as beetles, and that *M. auriculus* has a wider gape that facilitates capturing fluttering insects such as moths. This evidence also supports the hypothesis that trophic structures (jaws and teeth) in bats reflect essential elements of a species' ecological role (Findley and Wilson 1982).

A question that often occurs when monitoring bats acoustically and in noting the "feeding buzz" emitted by foraging bats is, if a bat encounters prey will it ignore it? Fenton and Morris (1976) regarded *M. evotis* as an insectivorous bat that was temporally opportunistic, but Black (1974) characterized the insectivorous bat community as composed of either moth- or beetle-strategists. This dichotomy was modified by Warner (1985), who suggested that beetle-eaters were specialists and moth-eaters were generalists. In areas of sympatry where numerous species are actively foraging, insect numbers must be limiting. At Nogal Canyon, Socorro County, New Mexico—a well-studied locality of sympatry—as many as 15 species of bats may be foraging together or drinking water from the tank at that site. The number of bats (both in number of individuals and in number of species) is great at this locality because that tank is the only source of water for some distance. Moreover, the site is located at an ecotone between desert grassland, piñon-juniper, and coniferous forest, and is surrounded by an abundance of potential roosting habitat (sheer cliff, rocks and crevices, trees, and caves). It may be very likely that with so many different foraging styles, *M. evotis* and *M. auriculus* do carefully chose the type of prey that they pursue. Species interactions are occurring at a fine scale between species such that direct competition is avoided at localities of syntopy. Biomechanical changes in the relative advantages of jaws allow for selective and successful foraging for different prey types by both species where they occur together.

Resource partitioning within a 12-species assemblage of rhinolophoid bats was suggested by Heller and von Helversen (1989) based on apportionment of the bats' ultrasonic frequencies. One of us (WLG) has observed minimum frequencies of *M. auriculus* to be lower (32.5 kHz) than those of *M. evotis* (35 kHz). This acoustic pattern would be consistent with preying upon larger, slower-flying moths and smaller, faster-flying beetles, respectively.

The relative change in mechanical structure of the jaw between these species is suggestive of the influence that competition has at localities that we examined. The relative importance of the articular process, which contributes to the application of bite force, may be the structure most influenced by these species interactions. This can be interpreted as an advantage when feeding on beetle prey to penetrate a hard carapace or a wider gape that is better for capturing a larger, fluttering target such as a moth. Other species pairs under similar conditions (i.e., similar size, taxonomically distinct sister taxa, and similar foraging mode) such as the European *Myotis myotis* and *M. blythii* also may exhibit this relationship.

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8. *United States: New Mexico, Socorro County (n = 33)*.—MSB-2933, MSB-2934, MSB-2936, MSB-2937, MSB-9412, MSB-9413, MSB-10963, MSB-10964, MSB-10965, MSB-10966, MSB-13775, MSB-13776, MSB-13786, MSB-13789, MSB-13791, MSB-13792, MSB-13793, MSB-13794, MSB-13795, MSB-13796, MSB-13800, MSB-14411, MSB-24981, MSB-25196, MSB-25198, MSB-40864, MSB-40865, MSB-40867, MSB-42473, MSB-53783, MSB-53784, MSB-61102, MSB-61143.
9. *United States: New Mexico, Catron County (n = 5)*.—MSB-9638, MSB-10448, MSB-11280, MSB-12912, MSB-17287.
10. *United States: New Mexico, Catron County (n = 4)*.—MSB-10447, MSB-11291, MSB-11634, MSB-14828.
11. *United States: New Mexico, Socorro County (n = 72)*.—MSB-2918, MSB-2919, MSB-2920, MSB-2921, MSB-2922, MSB-2923, MSB-5098, MSB-5100, MSB-5102, MSB-5103, MSB-5104, MSB-5105, MSB-10913, MSB-10914, MSB-10915, MSB-10916, MSB-11176, MSB-11177, MSB-11178, MSB-11179, MSB-11322, MSB-11323, MSB-11324, MSB-11326, MSB-11328, MSB-12748, MSB-13320, MSB-13321, MSB-13322, MSB-13323, MSB-13324, MSB-13325, MSB-13326, MSB-13756, MSB-13757, MSB-13758, MSB-13787, MSB-13797, MSB-14230, MSB-14231, MSB-14232, MSB-14233, MSB-14234, MSB-14235, MSB-14236, MSB-14376, MSB-14800, MSB-21803, MSB-25195, MSB-37284, MSB-37285, MSB-37427, MSB-40853, MSB-40855, MSB-41604, MSB-41605, MSB-41606, MSB-41607, MSB-41608, MSB-41609, MSB-48002, MSB-48003, MSB-48004, MSB-48005, MSB-53786, MSB-53787, MSB-53788, MSB-57423, MSB-57425, MSB-57426, MSB-57427, MSB-57428.
12. *United States: New Mexico, Cibola County (n = 9)*.—MSB-9910, MSB-9984, MSB-10386, MSB-10395, MSB-10526, MSB-10527, MSB-10528, MSB-10551, MSB-10552.
13. *United States: New Mexico, Sandoval County (n = 16)*.—MSB-6647, MSB-6648, MSB-6649, MSB-6650, MSB-6651, MSB-6652, MSB-6654, MSB-6655, MSB-6656, MSB-14503, MSB-19792, MSB-21452, MSB-21453, MSB-23158, MSB-23159, MSB-54676.
14. *United States: Arizona, Apache County (n = 1)*.—MSB-6981.
15. *United States: New Mexico, Colfax County (n = 3)*.—MSB-27790, MSB-27815, MSB-27816.
16. *United States: New Mexico, Taos County (n = 2)*.—MSB-17885, MSB-18883.
17. *United States: New Mexico, Rio Arriba County (n = 2)*.—MSB-15653, MSB-6805.
18. *United States: New Mexico, San Juan County (n = 3)*.—MSB-60749, MSB-60750, MSB-60751.
19. *United States: Colorado, Archuleta County (n = 2)*.—MSB-10230, MSB-10235.
20. *United States: Nevada, Clark County (n = 1)*.—MSB-61638.
21. *United States: California, Humboldt County (n = 1)*.—MSB-40673.
22. *United States: Oregon, Benton County (n = 5)*.—MSB-40804, MSB-40805, MSB-40806, MSB-40807, MSB-40808.

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APPENDIX I

Specimens examined for this study. All material was examined at the Museum of Southwestern Biology (MSB), University of New Mexico, Albuquerque, New Mexico. Sample size is indicated by *n*. Numbers 1–22 are specimen localities mapped in Fig. 1.

1. *Mexico (n = 2)*.—MSB-19596, MSB-19597.
2. *United States: Arizona, Cochise County (n = 2)*.—MSB-20088, MSB-20089.
3. *United States: New Mexico, Hidalgo County (n = 45)*.—MSB-17296, MSB-17297, MSB-17299, MSB-17300, MSB-17301, MSB-17302, MSB-17319, MSB-17320, MSB-17321, MSB-17922, MSB-19192, MSB-19193, MSB-19194, MSB-19215, MSB-19235, MSB-19236, MSB-19237, MSB-19263, MSB-19264, MSB-19265, MSB-19267, MSB-19268, MSB-19269, MSB-19278, MSB-19284, MSB-19285, MSB-19286, MSB-19748, MSB-19749, MSB-19750, MSB-19759, MSB-19760, MSB-19761, MSB-19762, MSB-19764, MSB-45882, MSB-45883, MSB-45884, MSB-45885, MSB-45887, MSB-45888, MSB-45889, MSB-45890, MSB-45891, MSB-45893.
4. *United States: New Mexico, Sierra County (n = 2)*.—MSB-24991, MSB-24992.
5. *United States: New Mexico, Grant County (n = 2)*.—MSB-24997, MSB-56534.
6. *United States: New Mexico, Sandoval County (n = 5)*.—MSB-26837, MSB-26838, MSB-26839, MSB-26840, MSB-26841.