

## MORPHOLOGICAL DIFFERENCES AMONG WESTERN LONG-EARED MYOTIS (*MYOTIS EVOTIS*) POPULATIONS IN DIFFERENT ENVIRONMENTS

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We compared the external morphology of western long-eared myotis (*Myotis evotis*) living in mountain (cool, wet) and prairie (warm, dry) environments in southern Alberta to test whether flight permits genetic exchange between populations thereby limiting divergence in morphological traits. We measured size of the body (forearm length and mass), ears, and wings for males and females. Ears and wings were significantly larger for bats in the mountains, suggesting that there is limited gene flow between populations despite their geographic proximity, and adaptation to differences in aridity or foraging habitat. However, body size was similar between environments, suggesting that either *M. evotis* possesses an ecologically flexible body type or that differences in extremity size are the result of environmentally induced phenotypic plasticity. Within environments, females were larger than males for all morphometrics. However, the degree of dimorphism was similar for mountain and prairie populations, indicating that dimorphism is not the result of different thermoregulatory needs in these populations.

Key words: Chiroptera, geographic variation, morphology, *Myotis*, reproduction, sexual dimorphism, thermoregulation, western long-eared myotis

Across the range of a species, populations in one environment may experience different selective pressures than populations elsewhere, leading to differences in morphological traits. Differentiation is facilitated by obstructions to gene flow between populations, such as geographic distance, physical barriers (e.g., water), or isolating mechanisms (e.g., nonrandom mating), and is most likely shaped by ecological factors (e.g., climate, food availability, etc.). In the absence of barriers, high genetic exchange between populations may constrain their ability to adapt to local conditions (Slatkin 1987). In these situations, individuals may possess traits that allow them to be ecologically flexible, or exploit a wide range of environmental conditions, without conspicuous differences among populations (Futuyma and Moreno 1988; Levins 1968).

Many bat species occupy wide geographic ranges and inhabit various environments. As flying animals, the potential for gene exchange between populations is high, suggesting that morphological differentiation among bat populations may be rare. Despite this, geographic variation in morphological features has been reported for a number of temperate-zone insectivorous bat species. Geographic distance and climate differences appear to explain much of the morphological variation across the ranges

of *Eptesicus fuscus* (Burnett 1983a) and *Myotis daubentoni* (Bogdanowicz 1990), 2 of the most widely distributed bats in North America and Europe, respectively. The body size of these species is positively correlated with latitude and negatively correlated with environmental temperature, presumably due to isolation-by-distance and the thermoregulatory advantage of decreased surface area-to-volume ratios in cooler climates. Similar patterns have been reported for *Pipistrellus hesperus* (Findley and Traut 1970), *Myotis fortidens*, and *M. lucifugus* (Findley and Jones 1967) in the southwestern United States and Mexico. However, few studies have compared bat populations on small geographic scales (but see Stebbings 1973). Genetic exchange may be greater between bat populations living in nearby environments, and this may limit morphological divergence even if selection pressures differ between environments.

Within an environment, different reproductive investment by female and male bats may result in dimorphism. In most species of temperate-zone insectivorous bats, females are solely responsible for rearing young (Racey and Speakman 1987). To minimize costs of reproduction, selection may favor larger bodies in females. Larger body size can confer various reproductive advantages, including the ability to produce larger offspring, provide more milk, and carry heavier loads (Myers 1978; Ralls 1976).

The degree of sexual dimorphism might vary among bat populations because of different thermoregulatory needs in different environments. For example, low ambient temperatures

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and high precipitation can increase the time females spend in torpor, thereby delaying parturition (Grindal et al. 1992; Lewis 1993; Racey et al. 1987), shortening the growing season (Kunz et al. 1988), and decreasing overwinter survival (Ransome 1989). In such an environment, larger body size may be especially beneficial to females, allowing them to remain homeothermic longer (Williams and Findley 1979).

The goals of our study were to determine whether morphological differences occur between populations of insectivorous bats living in climatically distinct but geographically proximal environments, whether sexual dimorphism occurs, and whether the degree of sexual dimorphism differs among environments because of different thermoregulatory requirements. We predicted that, if high dispersal ability facilitates gene flow between populations, no difference in the external morphology of bats would exist between environments, and the degree of sexual dimorphism would be consistent. On the other hand, if populations are sufficiently genetically separated, we predicted that morphology would differ between populations living in hot, dry environments and those in cool, wet ones, and that dimorphism would differ. We tested these predictions by comparing within and among populations of western long-eared myotis (*Myotis evotis*) in mountain versus prairie landscapes of Alberta, Canada.

## MATERIALS AND METHODS

*Myotis evotis* occupies much of western North America and inhabits a variety of environments. Populations occur from sea level to 2,830 m in habitats ranging from semiarid shrublands and shortgrass prairie to subalpine forests (Manning and Jones 1989). Two subspecies are currently recognized: *M. e. pacificus* mainly occurs along the coast, whereas *M. e. evotis* is found primarily in the interior of western North America, including all of southern Alberta (Manning and Jones 1989). *M. evotis* can glean insects from foliage (Faure and Barclay 1994) and most likely occupies a distinct foraging niche in our study areas, although little brown bats (*M. lucifugus*) are able to glean under some conditions (Ratcliffe and Dawson 2003). Throughout its range, *M. evotis* roosts in crevices and cavities of snags, stumps, boulders, and rock outcrops, as well as in caves, mines, and man-made structures (Chruszcz and Barclay 2002; Holloway 1998; Manning and Jones 1989; Rancourt et al. 2005; Vonhof and Barclay 1997; Waldien et al. 2000). Adults typically roost alone or in small groups (2–14 individuals) of mothers and young (Chruszcz and Barclay 2002; Holloway 1998; Rancourt et al. 2005; Vonhof and Barclay 1997; Waldien et al. 2000). Females bear a single young during summer, and are solely involved in rearing it before the onset of hibernation.

From May to August 2001 and 2002, we examined the morphology of *M. evotis* in the mountains and prairies of southern Alberta. In the mountains, we captured bats in the Kananaskis Valley (51°00'N, 115°5'W) and Sheep River Valley (50°39'N, 114°39'W). Both sites are located in the foothills of the Rocky Mountains and consist of a river surrounded by modest peaks (elevation 1,350–2,500 m). Extensive lodgepole pine (*Pinus contorta*) and mixed aspen–pine (primarily quaking aspen [*Populus tremuloides*]) forests cover the valley bottoms and mountain ridges, whereas cliffs, talus slopes, and boulder fields occupy the steeper regions. In the prairies, about 400 km to the east, we captured bats along the South Saskatchewan River Valley (50°38'N, 110°11'W, 600–720 m), near Bindloss, along the Red Deer River Valley (50°46'N, 111°29'W, 621–727 m) in Dinosaur Provincial Park,

and along the Milk River Valley (49°7'N, 110°55'W, 863–935 m), 30 km west of Onefour. Each site is situated in badlands–grassland habitat consisting of numerous drainage coulees eroded from sandstone cliffs. The terrain is devoid of trees, except for cottonwood (*Populus* spp.) stands near the river's edge. The minimum, maximum, and mean daily temperatures of all prairie sites are on average 4–7°C warmer than those of the mountain sites during summer, and have 33–50% less precipitation ([http://www.climate.weatheroffice.ec.gc.ca/climate\\_normals/index\\_e.html](http://www.climate.weatheroffice.ec.gc.ca/climate_normals/index_e.html); Solick 2004).

We captured bats in mist nets and harp traps placed in various locations, and determined species, age, sex, and reproductive condition. To avoid collecting data on the same individual twice, we marked bats with colored, numbered plastic split-rings (A. C. Hughes Ltd., Middlesex, United Kingdom). Juveniles (young-of-the-year) were distinguished from adults based on the degree of epiphysal fusion at the finger joints (Anthony 1988). Juveniles were not used in our analyses. We determined the reproductive condition of adult females (i.e., pregnant, lactating, postlactating, or nonreproductive—Racey 1988). Females in late pregnancy had an obviously distended abdomen and palpable embryo. Lactation was indicated by expression of milk or by the presence of bare patches around noticeably swollen teats. Regrowth of fur around the teats indicated postlactation, and females lacking any of these characteristics were considered to be nonreproductive. The procedures used in this study were reviewed and approved by the University of Calgary Animal Care Committee and met the guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998).

To determine whether reproduction by bats in the mountains was delayed compared to bats in the prairies, we performed 1-tailed *t*-tests comparing the dates that lactating bats and volant young were 1st captured in each habitat. We used Julian date of 1st capture based on our own data, as well as capture records of researchers who had worked in the study areas during previous years (B. Chruszcz, P. Faure, and G. Holloway, in litt.). We did not compare the dates that pregnant bats were 1st captured because of the unreliability of detecting early pregnancy.

We used forearm length and body mass as indicators of body size. We measured length of the right forearm (to the nearest 0.01 mm) using calipers, and combined our data with those of previous studies in the study areas (B. Chruszcz, P. Faure, and G. Holloway, in litt.). We analyzed forearm length using analysis of variance (ANOVA) with environment (mountains or prairies), sex, and study site (nested within environment) as categorical factors. We nested study site within environment to account for differences among study sites within the 2 environments. In this and subsequent morphological analyses, we included the interaction between environment and sex to compare the degree of dimorphism between environments.

Bats were held for at least 30 min after capture before being weighed to the nearest 0.01 g on a Sartorius PT600 electronic balance ( $\pm 0.1$  g; Sartorius AG, Goettingen, Germany). We excluded the mass of pregnant females from our analyses. We compared only the 2001 data from the Kananaskis Valley and Bindloss study sites because this was the only season during which trapping was concurrent in both environments throughout the entire summer, thus permitting a comparison of mass gain over time. We analyzed mass using analysis of covariance (ANCOVA) with location (Kananaskis and Bindloss) and sex as categorical factors, and forearm length and Julian date as covariates.

We measured length of the ear from base to tip by placing a ruler within the inner fold of the right ear. To determine ear width, we flattened the right ear using a hinged, clear plastic ruler and measured the widest point. To reduce error, we used the average of

TABLE 1.—Characteristics for female and male *Myotis evotis* in the mountains and prairies of Alberta.

Variable	Mountains				Prairies			
	Females		Males		Females		Males	
	<i>n</i>	$\bar{X} \pm SE$	<i>n</i>	$\bar{X} \pm SE$	<i>n</i>	$\bar{X} \pm SE$	<i>n</i>	$\bar{X} \pm SE$
Forearm length (cm)	87	38.20 ± 0.13	159	37.50 ± 0.09	91	38.11 ± 0.14	112	37.24 ± 0.15
Mass (g)	32	6.82 ± 0.11	37	6.25 ± 0.10	16	6.92 ± 0.14	25	6.27 ± 0.13
Ear area (mm <sup>2</sup> )	24	189.62 ± 3.47	24	180.11 ± 2.95	13	176.45 ± 3.98	21	171.98 ± 3.16
Ear shape	24	1.59 ± 0.04	24	1.57 ± 0.03	13	1.64 ± 0.05	21	1.64 ± 0.04
Wing area (cm <sup>2</sup> )	32	112.32 ± 1.38	53	107.77 ± 1.85	13	103.97 ± 1.82	25	103.30 ± 1.35
Wing loading (N/m <sup>2</sup> )	28	5.96 ± 0.11	53	5.73 ± 0.08	13	6.32 ± 0.17	25	6.04 ± 0.14
Wingspan (cm)	32	24.13 ± 0.24	53	23.56 ± 0.18	13	23.47 ± 0.37	25	23.27 ± 0.27
Aspect ratio	32	5.18 ± 0.08	53	5.12 ± 0.06	13	5.23 ± 0.13	25	5.21 ± 0.09

3 measurements. We estimated surface area of the ear by multiplying ear length and width. We divided ear length by ear width to determine shape of the ear. Values >1 correspond to a long, narrow ear, whereas values <1 correspond to a short, broad ear. Because of the difficulty of standardizing ear-width measurements, we only analyzed the measurements taken by one of us (DIS). We analyzed ear area and shape using ANCOVAs with environment, sex, and study site (nested within environment) as categorical factors, and forearm length as a covariate to account for variation in body size.

We determined wing dimensions (area, span, aspect ratio, and loading) from hand tracings and digital photographs of bat wings. For both methods, bats were held with the tail and wing membranes outspread, and the wing slightly forward of the body (e.g., Saunders and Barclay 1992). We photographed bats using a tripod-mounted Sony Mavica FD-87 digital camera (Sony Corporation, New York, New York), and included a ruler within the frame to indicate scale. We scanned wing tracings and imported digital images into a computer. Images were analyzed using BatWing.exe 1.0 (Harley and Miller-Butterworth 2000). Following Norberg and Rayner (1987), we calculated wing area as the combined area of both wings, the entire tail membrane, and the body area between the wings, excluding the head. One-half the wingspan was measured from the midpoint between the shoulders to the point where the shoulder and wing met, along a straight line to the base of the thumb, and ending at a point perpendicular to the tip of the wing. That distance was doubled to obtain total wingspan.

We calculated wing loading and aspect ratio as in Norberg and Rayner (1987). A low wing loading represents a bat with a large wing area relative to body mass, which confers greater maneuverability than does a wing with high loading. Aspect ratio describes wing shape, with a high aspect ratio indicating a relatively long, narrow wing. We analyzed wing area, wingspan, and aspect ratio using general linear models with environment, sex, and study site (nested within environment) as categorical factors. Forearm length was included as a covariate. We analyzed wing loading using a general linear model with the same factors and covariate as above, but also considered Julian date as a covariate. We excluded wing loadings of pregnant females from this analysis.

We used subsets of bats in the analyses because some morphological measures were not obtained for all individuals (e.g., ear area and wing area), and some data were not suitable for particular tests (e.g., pregnant females were excluded from mass and wing loading analyses). ANOVAs, ANCOVAs, and general linear models were performed using SAS 8.0 (SAS Institute Inc., Cary, North Carolina) and *t*-tests were performed using SYSTAT 10.2 (SPSS Inc., Chicago, Illinois) and software. We used a type I error rate of  $\alpha = 0.05$  and present least square means  $\pm SE$  throughout.

## RESULTS

We captured 218 *M. evotis* in the mountains (male : female, 68:75 in Kananaskis, 64:11 in Sheep River) and 121 in the prairies (52:25 in Bindloss, 16:10 in Dinosaur, 8:10 in Onefour) during the study period. For our analyses of reproduction and forearm length, we included 45 males and 30 females from previous work in the Kananaskis Valley (P. Faure, in litt.), and 54 males and 50 females from previous studies in the Bindloss study area (B. Chruszcz and G. Holloway, in litt.). *M. evotis* was the most abundant bat captured in the mountains and was 2nd only to the western small-footed myotis (*Myotis ciliolabrum*) in the prairie.

Sixty-eight percent ( $n = 41$ ) of females captured on or after capture of the 1st lactating female in the prairies were reproductive, whereas 55% ( $n = 58$ ) of females were reproductive in the mountains. This difference was not significant ( $\chi^2 = 1.23$ ,  $df = 1$ ,  $P > 0.05$ ). The date on which lactating females were 1st captured occurred significantly earlier ( $t = 3.94$ ,  $df = 8$ ,  $P < 0.01$ ) in the prairies ( $n = 6$  years) than in the mountains ( $n = 4$  years). The mean date was 10 July (range = 5–14 July) in the prairies and 20 July (range = 14–23 July) in the mountains, a difference of  $10.1 \pm 0.36$  days. Similarly, volant young were 1st captured  $11.3 \pm 0.80$  days earlier in the prairies ( $\bar{X} = 27$  July; range = 21 July–6 August;  $n = 3$  years) than in the mountains ( $\bar{X} = 7$  August; range = 29 July–22 August;  $n = 4$  years), but this difference was not statistically significant ( $t = 1.47$ ,  $df = 5$ ,  $P > 0.05$ ).

The ANOVA describing forearm length explained a significant proportion of the variation ( $R^2 = 0.14$ ,  $F = 11.63$ ,  $df = 6$ , 446,  $P < 0.001$ ). Forearm length did not differ significantly between environments ( $F = 1.37$ ,  $df = 1$ , 442,  $P > 0.05$ ), although *M. evotis* in the mountains had slightly longer forearms (Table 1). Sex explained a significant amount of variation in forearm length ( $F = 51.39$ ,  $df = 1$ , 442,  $P < 0.001$ ), with females having longer forearms than males in both environments. The degree of dimorphism in forearm length was similar between environments (environment  $\times$  sex interaction;  $F = 0.55$ ,  $df = 1$ , 442,  $P > 0.05$ ). Forearm lengths did not differ among study sites within environments ( $F = 1.47$ ,  $df = 3$ , 442,  $P > 0.05$ ).

Mass varied significantly ( $R^2 = 0.48$ ,  $F = 19.38$ ,  $df = 5$ , 109,  $P < 0.001$ ) among *M. evotis* in the Kananaskis and Bindloss study sites during summer of 2001. Mass increased significantly

**TABLE 2.**—Results of analysis of covariance models comparing ear measurements of *Myotis evotis* between environments (mountains versus prairies), sexes, and study sites (nested within environment). Forearm length was included as a covariate. Asterisks indicate probability levels: \*  $P < 0.05$ ; \*\*  $P < 0.01$ .

	Ear area (mm <sup>2</sup> )		Ear length (mm)		Ear shape		Ear width (mm)	
	df.	F	df.	F	df.	F	df.	F
Model	6, 81	3.78**	6, 81	2.61**	6, 81	1.12	6, 81	1.44
Environment	1, 81	9.30**	1, 81	0.57				
Sex	1, 81	4.16*	1, 81	2.46				
Environment × sex	1, 81	0.49	1, 81	0.54				
Study site (environment)	2, 81	3.28*	2, 81	4.18**				
Forearm length	1, 81	0.09	1, 81	0.22				

during the summer ( $F = 63.00$ ,  $df. = 1, 109$ ,  $P < 0.001$ ), and individuals in the Bindloss area were significantly heavier ( $F = 4.33$ ,  $df. = 1, 109$ ,  $P < 0.05$ ) than bats in the Kananaskis Valley at similar dates throughout much of the summer. However, individuals of *M. evotis* in the Bindloss area were active after hibernation at an earlier date (based on capture data) than individuals in the Kananaskis Valley and thus were able to start feeding and gaining mass sooner. To account for this delay, we subtracted 10 days (the mean difference in date of lactation between environments; see above) from the date of capture for bats in the Kananaskis Valley. When we included these standardized dates in the model, mass no longer differed significantly between locations ( $F = 0.20$ ,  $df. = 1, 109$ ,  $P > 0.05$ ). At both locations, females maintained heavier mass than males ( $F = 23.91$ ,  $df. = 1, 109$ ,  $P < 0.001$ ), and this dimorphism was similar between locations (environment × sex interaction;  $F = 0.15$ ,  $df. = 1, 109$ ,  $P > 0.05$ ). Forearm length did not influence mass significantly ( $F = 2.82$ ,  $df. = 1, 109$ ,  $P > 0.05$ ).

Most ear and wing variables exhibited significant variation (Tables 2 and 3). Ear surface area was significantly larger for *M. evotis* in the mountains than for bats in the prairies, and was significantly larger for females than for males in both environments (Table 1). The degree of sexual dimorphism in ear area was similar in both environments (environment × sex interaction). The model describing ear shape was not significant,

although individuals of *M. evotis* in the mountains had slightly shorter and broader ears than those in the prairies.

Wing area was significantly larger for *M. evotis* in the mountains (Tables 1 and 3). Forearm length also explained significant variation in wing area, although this relationship differed between males and females (Table 3; Fig. 1A). Wing area increased significantly with forearm length for males (partial regression coefficient,  $b \pm SE = 1.04 \pm 0.01$ ,  $t = 5.67$ ,  $df. = 1, 122$ ,  $P < 0.001$ ), whereas females possessed a relatively large wing area irrespective of forearm length ( $b \pm SE = 1.01 \pm 0.01$ ,  $t = 1.10$ ,  $df. = 1, 122$ ,  $P > 0.05$ ). Wing area also differed significantly among study sites. Wing loading was significantly lower for *M. evotis* in the mountains than for those in the prairies (Tables 1 and 3). Julian date explained significant variation in wing loading, although this relationship differed between males and females (Table 3; Fig. 1B). Wing loading increased significantly during summer for males ( $b \pm SE = 4.14 \pm 0.01$ ,  $t = 3.94$ ,  $df. = 1, 116$ ,  $P < 0.001$ ), but not for females ( $b \pm SE = 1.01 \pm 0.01$ ,  $t = 1.65$ ,  $df. = 1, 116$ ,  $P > 0.05$ ). Wingspan and aspect ratio did not vary significantly by environment or sex, but did increase significantly with forearm length (Table 3). Aspect ratio also differed significantly among study sites (Table 3). The degree of dimorphism for all wing variables was similar between environments (environment × sex interaction; Table 3).

**DISCUSSION**

*Between environments.*—We found morphological differences between *M. evotis* in the mountains and prairies of Alberta. This suggests that these populations are sufficiently isolated to have allowed the evolution of differences in morphology, and that gene flow is limited despite the relatively small geographic scale and the ability of bats to fly long distances. Previous studies that found geographic variation within species of bats dealt with much larger distances (e.g., Bogdanowicz 1990; Burnett 1983a). Indeed, Barclay (1991) suggested that the absence of female little brown bats (*M. lucifugus*) in our mountain study sites might be explained by their movement out into the prairies during the breeding season. We do not know the dispersal distances of *M. evotis*, but recent evidence suggests that individuals in the prairies may mate and hibernate there (C. Lausen, pers. comm.).

**TABLE 3.**—Analysis of general linear models comparing wing measurements of *Myotis evotis* between environment (mountains versus prairies), sexes, and study sites (nested within environment). Forearm length and date were included as covariates. Asterisks indicate probability levels: \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

	Wing area (cm <sup>3</sup> )		Wing loading (N/m <sup>2</sup> )		Wingspan (cm)		Aspect ratio	
	df.	F	df.	F	df.	F	df.	F
Model	7, 122	12.69***	8, 116	8.55***	6, 122	9.37***	6, 122	7.00***
Environment	1, 122	19.51***	1, 116	6.47*	1, 122	2.99	1, 122	0.56
Sex	1, 122	6.48*	1, 116	5.16*	1, 122	2.04	1, 122	0.19
Environment × sex	1, 122	1.69	1, 116	0.03	1, 122	0.53	1, 122	0.02
Study site (environment)	2, 122	6.26**	2, 116	9.32***	2, 122	1.92	2, 122	13.27***
Forearm length	1, 122	18.45***	1, 116	0.04	1, 122	26.03***	1, 122	7.00**
Forearm length × sex	1, 122	6.21*						
Date			1, 116	16.82***				
Date × sex			1, 116	4.27*				

Genetic exchange with populations in the mountains may thus be more limited than expected, allowing evolution of local morphological adaptations.

There are several reasons why different ear and wing morphologies of *M. evotis* might be favored in the 2 habitats we studied. In some organisms, extremity size is smaller in colder environments, presumably related to thermoregulatory advantages ("Allen's rule"—Allen 1877; Johnston and Selander 1971; Lindsay 1987; Wathen et al. 1971). However, our results were opposite to this expectation in that mountain individuals had larger ears and wings. Extremity size in *M. evotis* instead may be related to water conservation needs. *M. evotis* in the warm, dry prairies spends more than 17 h per day inside roosts, without access to food or water (Chruszcz and Barclay 2002). Rates of evaporative water loss are high for bats (Webb et al. 1995), and small extremities may help conserve water in an arid environment (Peters 1983). However, as with minimizing heat loss, furred wings probably minimize water loss more effectively than decreasing the size of the flight membrane. *M. evotis* is not known to fold the ears, so this remains a potential source of water loss.

Differences in extremity size between environments could also be related to foraging habitat. Although *M. evotis* is able to hawk insects from the air (Faure and Barclay 1994), individuals in the forested mountains may rely more heavily on gleaning insects from foliage than do bats in open prairies. *M. evotis* locates nonairborne targets using low-frequency auditory cues (e.g., the fluttering of moth wings), rather than high-frequency echolocation signals (Faure et al. 1990). In bats, larger ears amplify and improve directionality of detection of low-frequency sounds compared to smaller ears (Coles et al. 1989; Guppy and Coles 1988; Obrist et al. 1993; Simmons 1982). Therefore, *M. evotis* in the mountains may increase detection distance and improve localization of insect prey against foliage by having larger ears.

Larger wings contribute to the lower wing loading of *M. evotis* in the mountains, making these bats more maneuverable when pursuing insects through dense vegetation, and reducing the costs of hovering when gleaning (Norberg and Rayner 1987). In contrast, the smaller ears and wings observed in prairie *M. evotis* may reflect a greater abundance of flying prey or a need to forage more extensively on aerial insects because of fewer gleaning substrates in this habitat. Indeed, *M. evotis* in the mountains consume more Lepidoptera (insects likely to be gleaned; 60%,  $n = 31$ —Barclay 1991) than individuals in the prairies (48%,  $n = 65$ —Holloway 1998).

Without standardizing for the seasonal delay between environments, *M. evotis* in the prairies also differed in mass compared to individuals in the mountains. However, parturition occurred on average 10 days later in the mountains. In other studies, such delays are attributed to increased use of torpor in response to low ambient temperatures (Lewis 1993) and high precipitation (Grindal et al. 1992), conditions that are common at our mountain sites. However, *M. evotis* in the mountains spend less time in torpor than do individuals in the prairies (Solick 2004). Instead, low temperatures during late spring may postpone arousal from hibernation at higher elevations, resulting in a later start to gestation (Racey 1982).

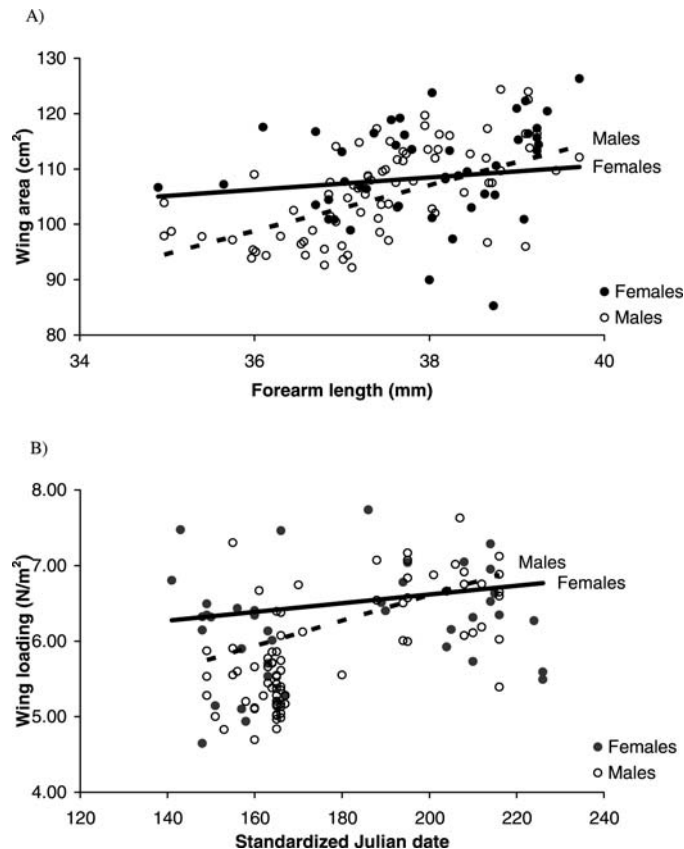


FIG. 1.—The effect of A) sex and forearm length on wing area and B) sex and date on wing loading, for female and male *Myotis evotis* in Alberta. We standardized Julian date in B to account for the seasonal delay in the mountains.

Once we accounted for the seasonal delay in the mountains, there was no difference in body mass between *M. evotis* in the mountains compared to the prairies of Alberta. Although mass may be a relatively insensitive measure of body size because of daily and seasonal fluctuations, we also found no difference in our other measure of body size, forearm length. This is despite differences in other morphological traits (ears and wings) and potentially important differences in selection on body size in the 2 environments. Studies on other species of bats have found larger body sizes in cooler environments (e.g., Bogdanowicz 1990; Burnett 1983a), and this is common in many endotherms ("Bergmann's rule"—Bergmann 1847; Meiri and Dayan 2003).

The lack of difference in body size between *M. evotis* in the mountains and prairies may be explained in at least 2 ways. First, gene flow may be restricted between populations in the 2 environments, as differences in ears and wings suggest, but body size is not a target of strong differential selection between the areas. Perhaps *M. evotis* possesses a body type that is well suited to a range of environmental conditions, or individuals make behavioral or physiological adjustments to local conditions.

A 2nd explanation for our finding of differences in some morphological traits but not others is that gene flow does occur between environments, and the differences in extremity size reflect environmentally induced phenotypic variation or phenotypic plasticity (Stearns 1989). Plasticity in fixed traits, such as ears and

wings, may occur in response to environmental factors experienced during development (Levins 1968). For example, plasticity of ear and tail length has been demonstrated by rearing laboratory mice (*Mus musculus*) in hot or cold environments (Barnett and Mount 1967); longer extremities are observed for mice in the hot environment, presumably related to heat dumping (Peters 1983).

*Within environments.*—In both environments, female *M. evotis* had larger bodies than did males, supporting our hypothesis that greater reproductive investment by females would result in sex-based morphological differences. Indeed, females are larger than males in many temperate-zone insectivorous bats, and this has been attributed to various elements of the “big mother” hypothesis (Ralls 1976), such as reduced costs of remaining euthermic (Williams and Findley 1979), increased load-bearing ability (Myers 1978), and production of larger offspring (Fujita 1986). For example, larger bat mothers may be able to remain euthermic for longer periods than smaller individuals, thereby reducing the costs of delayed reproduction associated with entering torpor (Williams and Findley 1979). Following Burnett (1983b), we interpret this hypothesis to predict greater dimorphism in body size among *M. evotis* living in the cool, wet mountains. However, we found similar dimorphism in forearm length and mass between the 2 environments, suggesting that similar selection affects female-biased dimorphism in body size, and that these pressures are not related to different thermoregulatory needs between environments.

The larger body size of females in dimorphic bat species may act to reduce the costs of the additional load carried during pregnancy (20–30% of body mass), and larger wings may improve flight performance (Myers 1978). From this hypothesis, Myers (1978) predicted that wing size would be larger for female bats if body size were equal between sexes. In our study, the relationship between wing area and body size (i.e., forearm length) differed for female and male *M. evotis*. Wing area was independent of body size for females, whereas wing area and body size were positively correlated in males. Consequently, small-bodied females had relatively large wings compared to males of similar size, but this dimorphism disappeared among larger individuals. Because of this interaction, we are unable to test Myers’s (1978) prediction.

It is unclear why the wing size of female *M. evotis* in Alberta is independent of body size. One explanation is that selection may favor larger offspring at high latitudes (Fujita 1986), which may in turn influence the wing size of females. Large offspring at birth would be more likely to reach the same size as their lower-altitude counterparts before hibernation, thus improving their likelihood of overwinter survival (Ransome 1989). If a minimum neonate mass is required for survival, then the offspring of small females would be proportionately larger than those of larger females, imposing greater flight demands. Selection may therefore favor females with a minimum wing size to maximize flight performance during pregnancy.

Ultimately, given the number of possible advantages for large size in females, it is unlikely that any one factor is entirely responsible for sexual dimorphism in *M. evotis*. In addition to the benefits discussed above, larger females can provide more milk (Ralls 1976), store more fat (Weber and Findley 1970),

and eat a wider variety of prey (Wilson 1975) than smaller females, but the relative importance of each of these factors to dimorphism is difficult to assess. Female-biased dimorphism also is not universal among other mammals, other bats, or even among *M. evotis* (e.g., males are larger than females in New Mexico—Williams and Findley 1979). For *M. evotis* in Alberta, a combination of maternal benefits probably contributes to dimorphism in body size within environments. These benefits presumably outweigh any selective advantages that males gain from large body size. However, reducing the cost of remaining euthermic does not appear to be a factor contributing to dimorphism of *M. evotis* in Alberta.

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