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Correspondence between ecomorphotype and use of arthropod resources by bats of the genus *Myotis*

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Arthropods are the primary dietary constituents of species of the genus *Myotis*. The genus comprises 3 ecomorphotypes of polyphyletic origin, each associated with a different foraging strategy: aerial, trawling, and gleaning, related to the subgenera *Selysius*, *Leuconoe*, and *Myotis*, respectively. We explored the extent to which differences in diet characterized these ecomorphotypes. Based on a broad review of the literature, we classified the diet of species of *Myotis* based on hardness and vagility of consumed prey. A significant negative relationship was found between the percent volume consumption of hard and soft arthropods and between the aerodynamic characteristics of fast- and slow-flying prey. A cluster analysis yielded 3 groups of *Myotis* species based on their diet: 1) those for which hard prey represent more than 80% of the volume of excreta; 2) those for which hard prey represent 45% to 80% of the volume of excreta; and 3) those for which hard prey represent less than 45% of the volume of excreta. These 3 groups are related to bat size and consistent with the recognition of 3 ecomorphotypes. Nonetheless, some species may display flexibility in diet composition depending on food availability. More specifically, larger species that consume hard prey also consume soft prey, whereas smaller bats may be unable to consume hard prey because of biomechanical limitations. Regardless of their phylogenetic lineages, latitudinal distribution, or biogeographic affinity, species of *Myotis* of similar size and morphology consume arthropods with similar characteristics.

Los artrópodos son los principales componentes de la dieta de las especies del género *Myotis*. El género comprende 3 ecomorfotipos de origen polifilético, cada uno asociado con una estrategia de alimentación diferente: aérea, arrastre y recolector, relacionados con los subgéneros *Selysius*, *Leuconoe* y *Myotis*. Exploramos en qué medida las diferencias en la dieta caracterizan estos ecomorfotipos. Con base en una amplia revisión de la literatura, clasificamos la dieta de las especies de *Myotis* en función de la dureza y la vagilidad de las presas consumidas. Se encontró una relación negativa significativa entre el porcentaje de volumen consumido de artrópodos duros y blandos, y entre las características aerodinámicas de las presas de vuelo rápido y lento. Un análisis de conglomerados arrojó 3 grupos de *Myotis* basados en su dieta: 1) aquellos para los cuales las presas duras representan más del 80% del volumen de excretas; 2) aquellos para los cuales las presas duras representan del 45% al 80% del volumen de excretas; y 3) aquellos para los cuales las presas duras representan menos del 45% del volumen de excretas. Estos 3 grupos obtenidos están relacionados con el tamaño del murciélago y con los 3 ecomorfotipos. No obstante, algunas especies pueden mostrar flexibilidad en la composición de la dieta dependiendo de la disponibilidad de alimentos. Específicamente, las especies más grandes consumen presas duras, además también pueden consumir presas blandas, mientras que los murciélagos más pequeños pueden ser incapaces de consumir presas duras debido a limitaciones biomecánicas. Nuestros resultados indican que, independientemente de sus linajes filogenéticos, distribución latitudinal o afinidad biogeográfica, las especies de *Myotis* con tamaño y morfología similares consumen artrópodos con características similares

Key words: arthropodophagy, dietary ecology, ecomorphotype, entomophagy, insectivory, *Myotis*, trophic ecology

On a global scale, *Myotis* is the most diverse and widely distributed genus of bats and is the second most species-rich genus of mammals, comprising over 100 species (Hutson and Mickleburgh 2001; Simmons 2005). In general, species of *Myotis* share morphological characteristics that have remained relatively unchanged from the ancestral bauplan (Horáček et al. 2000; Ruedi and Mayer 2001). Nonetheless, species of *Myotis* differ in morphological traits associated with foraging behaviors that potentially enhance resource partitioning (e.g., Fenton and Bogdanowicz 2002; Gardiner et al. 2011). In particular, characteristics related to echolocation and aerodynamics have been used widely to characterize foraging strategies such as aerial, trawling, or gleaning predators (Schnitzler and Kalko 2001).

The genus has been classified into 7 subgenera (*Selysius*, *Isotus*, *Paramyotis*, *Chysopteron*, *Myotis*, *Leuconoe*, and *Rickettia*) based on phenetic assessments (Tate and Archbold 1941). The subgenera *Myotis*, *Leuconoe*, and *Selysius* are widely recognized and validated based on morphological differentiation, and each represents a different foraging strategy (Findley 1972): aerial (*Selysius*), trawling (*Leuconoe*), and gleaning (*Myotis*). However, molecular studies show that species within groups defined by feeding strategy are not monophyletic groups (Godawa 1998; Ruedi and Mayer 2001; Stadelmann et al. 2004; Ghazali et al. 2016).

Many phenetic characteristics distinguish the 3 ecomorphotypes (Tate and Archbold 1941; Findley 1972; Godawa Stormark 1998; Ghazali et al. 2016). Ecomorphotypes were named just like the subgenera by Ghazali et al. (2016), but without italic letters. The aerial (selysius) ecomorphotype includes bats with short rostra and small jaws, small teeth, poorly developed sagittal crests, short legs, and calcanea that anchor uropatagia to the bottom of legs. These bats are aerial hunters capable of fast and direct flight, and use the uropatagium as a net to catch arthropods during flight. The trawling (leuconoe) ecomorphotype includes small- to medium-sized bats with elongated jaws, but with less conical rostra than in the aerial ecomorphotype, elongated teeth with a lesser reduction of the lower premolars, less-developed sectoral molars, elongated legs, a short tail, and small wings. These bats are specialized hunters that use their feet to catch prey over water bodies. The gleaning (myotis) ecomorphotype includes bats with large skulls and elongated rostra, developed sagittal crests, small incisors and premolars, elongated sectorial teeth, long ears directed to the front of the rostrum, wide wings, and long legs but small feet. The constituent species fly slowly and are adept at maneuvering, facilitating the capture of prey from surfaces. In general, species are assigned to each group based on morphological inference about prevailing foraging behavior. However, bats can display plasticity in foraging depending on food availability (Kunz 1974; Belwood and Fenton 1976; Anthony and Kunz 1977; Faure and Barclay 1994; Schnitzler and Kalko 2001; Ratcliffe and Dawson 2003; Denzinger et al. 2016).

In general, species of *Myotis* feed primarily on arthropods, except for a few taxa that occasionally consume fish (Ghazali et al. 2016). Those species in the gleaning ecomorphotype consume hard prey, whereas species in the aerial and trawling ecomorphotypes feed on softer prey (Ghazali et al. 2016). In North American *Myotis*, food preference is for slow and soft-to-medium-hard prey. This pattern is even more predominant in South American species (Segura-Trujillo et al. 2016). The hardness of consumed arthropods is related to bat size (Aguirre et al. 2003; Freeman and Lemen 2007; Segura-Trujillo et al. 2016). This association is inferred from the relationship between bite strength and bat size or mass (Nogueira et al. 2009; Freeman and Lemen 2010).

Ecological differentiation among ecomorphological groups is primarily related to foraging habit (Fenton and Bogdanowicz 2002). However, arthropodophagous bat species also differentiate foods according to prey characteristics, such as hardness of the exoskeleton and flight capacity of prey, but not with regard to the taxonomic affiliation of prey (Freeman and Lemen 2007; Segura-Trujillo et al. 2016). Each ecomorphological group of the genus *Myotis* comprises species that have converged morphologically and share distinctive foraging strategies. We propose that species sharing similar morphological traits and belonging to the same ecomorphological group, regardless of evolutionary lineage or ecogeographic affiliation, should forage on prey with similar characteristics. Our hypothesis is that characteristics of prey should differ among the 3 ecomorphotypes, and be related to body size and ecomorphological affiliation of species.

Materials and Methods

Data collection.—An extensive review of the literature was conducted using Google Scholar, ISI Web of Knowledge, Proquest, JSTOR, and Elsevier search engines and electronic databases. The search used the words "*Myotis*" combined with "diet," "resource partitioning," "insectivory," or "trophic resource." For quantitative analyses, studies were selected if the information on diet fulfilled 3 criteria. First, information was expressed in terms of percent volume of each taxon of consumed prey based on the morphology of exoskeleton fragments in excreta or gut contents of bats (Whitaker 1988). Second, taxonomic determination of diet included familial designation of arthropods (to achieve a precise and accurate classification of prey). Third, the identity of the bat species that was associated with feces was clear; for example, we did not use information from samples taken from mixed species or abandoned roost sites. We excluded data regarding consumption of ectoparasites known to infect bats (e.g., dust mites, Order Mesostigmata), as this phenomenon is likely associated with grooming rather than food acquisition. Search results were summarized in a database that detailed the taxonomic composition of the diet for each species of *Myotis*. In addition, arthropod taxa were classified based on flight characteristics (non-flying [apterans], slow-flying, and fast-flying) and hardness (soft, medium-hard, and hard—Segura-Trujillo et al. 2016).

Statistical analyses.—Quantitative analyses were performed with program Statistica 7 (Statsoft Inc. 2004) for data collected for 22 species of *Myotis*. Two principal component analyses (PCA) were performed using the maximum likelihood method for factor extraction with a varimax rotation. The first PCA was executed on the taxonomic composition of the diet (percent of diet for each prey taxon) and the second PCA was executed based on characteristics representing prey flight and hardness of prey. Principal components (PCs) with eigenvalues greater than 1 were considered to be significant representations of interspecific variation in dietary characteristics of species of *Myotis*. The contribution of a characteristic to interspecific variation was considered to be significant when its loading was ≥ 0.7 (James and McCulloch 1990; Jackson 1993). Monotonic associations between characteristics of the prey based on percent volume of excreta (i.e., hard-bodied versus soft-bodied, hard-bodied versus moderately hard-bodied, fast-flying versus slow-flying, non-flying versus slow-flying) in species of *Myotis* were assessed by Spearman rank correlation analyses (Sokal and Rohlf 2011) separately for each foraging habit of bats (gleaning, aerial, and trawling).

Latitudinal gradients in ordinal richness or class richness of arthropods in the diets of *Myotis* were determined via least-squares regression analyses (Sokal and Rohlf 2011). In addition, cluster analysis (unweighted pair-group average method of the Euclidean distances) was performed to identify groups of species with similar dietary composition based on prey characteristics. The strength and direction of monotonic associations between prey characteristics related to flight (percent volume of non-flying, slow-flying, or fast-flying arthropods in excreta) and hardness (percent volume of soft-, medium-hard-, or hard-bodied arthropods in excreta) and morphological characteristics (i.e., mass, total length, ear length, forearm length, tail length, body length, and skull length) were quantified via Spearman rank correlation analyses (Sokal and Rohlf 2011). All data were obtained from scientific publications (see Table 2; Supplementary Data SD1).

To avoid confusion associated with homonyms for generic (e.g., *Myotis*) and subgeneric (e.g., *Myotis*) classifications (Tate and Archbold 1941; Findley 1972) and for ecomorphotypic classifications (Ghazali et al. 2016) of species, we refer to each ecomorphotype according to its distinctive foraging habit (Table 1): gleaning, trawling, and aerial.

Results

Eighteen publications describing the diet of *Myotis* provided data to the level of family for most orders of arthropods. Nonetheless, these studies generally did not identify dietary items to a taxonomic level lower than order for Araneae, Ephemeroptera, Isoptera, Lepidoptera, Plecoptera, Trichoptera, and Dermaptera, or lower than class for Chilopoda, Dictyoptera, and Odonata. In addition, information was gathered from 57 reports describing the taxonomic composition of excreta for 22 species of *Myotis*, 17 from America, 3 from Europe, 1 from Asia, and 1 from Africa (Table 2). The number of bat specimens considered in each report was quite variable (i.e., 1 to 1,502 specimens), and in some instances, the number of bats was not provided because excreta were collected as composite samples from a roost. By volume, excreta contained mostly arthropods identified to at least ordinal level (mean 99.55%; *SD* = 3.09%), although some were identified to at least familial level (mean 24.57%; *SD* = 18.81%). Only a small quantity of excreta, by volume, contained unidentifiable dietary constituents (mean 0.44%; *SD* = 0.53%). Diptera, Lepidoptera, and Coleoptera were arthropod orders constituting the highest percent volume of excreta (Fig. 1). Prey taxa with the lowest representation in volume of excreta were Isoptera, Orthoptera, Neuroptera, Ephemeroptera, Plecoptera, and Siphonaptera.

Table 1.—Classification and equivalence of the subgenera described by Tate and Archbold (1941), the subgenera and groups described by Findley (1972), the ecomorphotypes detailed by Ghazali et al. (2016), and the trophic designations from this study. An asterisk (*) indicates that a particular taxon was not evaluated in this study.

Tate and Archbold (1941)	Findley (1972)			Ghazali et al. (2016)	This study
Subgenus	Subgenus	Group	Foraging habit	Ecomorphotype	Trophic group
Myotis	*Myotis*	*Bechsteini*	Gleaning	myotis	I
Chrysopteron		*Formosus*			*
		Emarginatus			II
Isotus		*Natteri*			*
Paramyotis		*Bechsteini*			*
		Evotis			III
Selysius	*Selysius*	*Mystacinus*	Aerial	selysius	*
		Leibi			III
		Sodalis			
		Muricola			*
		Altarium			*
Leuconoe	*Leuconoe*	*Adversus*	Trawling	leuconoe	*
		Montivagus			II
		Peytoni			II
		Grisescens			II
		Capaccini			*
		Macrotarsus			*
		Austoriparius			II
Rickettia		*Ricketti*			*

Table 2.—List of studies reporting information on the prey composition of excreta for species of *Myotis*. *n* = number of specimens from which excreta were obtained. Ecomorphotype (foraging habit) of each species based on classification of Ghazali et al. (2016). An asterisk (*) indicates samples from roosts for which the number of individual bats is not known.

Species	Ecomorphotype	Reference	*n*	Latitude
America				
M. albecens	Trawling	Whitaker and Findley (1980)	1	10°
M. austoriparius	Trawling	Feldhamer et al. (2009)	10	38°
M. californicus	Aerial	Lacki et al. (2007)	45	47°
		Whitaker et al. (1977)	31	47°
M. evotis	Gleaning	Lacki et al. (2007)	39	47°
		Whitaker (1977)	13	47°
M. grisescens	Trawling	Lacki et al. (1995)	47	38°
		Lacki et al. (1995)	30	38°
		Lacki et al. (1995)	14	38°
M. keaysi	Aerial	Whitaker and Findley (1980)	5	10°
M. leibii	Aerial	Moosman et al. (2007)	19	43°
M. lucifugus	Trawling	Feldhamer et al. (2009)	8	38°
		Whitaker (2004)	51	39°
		Whitaker et al. (1977)	67	47°
M. nigricans	Aerial	Whitaker and Findley (1980)	1	10°
		Bracamonte (2013)	7	−24°
M. occultus	Trawling	Valdez and Bogan (2009)	50	38°
		Valdez and Bogan (2009)	50	34°
		Valdez and Bogan (2009)	18	24°
M. oxyotis	Trawling	Whitaker and Findley (1980)	1	10°
M. riparius	Trawling	Whitaker and Findley (1980)	10	10°
M. septentrionalis	Gleaning	Feldhamer et al. (2009)	116	38°
		Whitaker (2004)	107	39°
M. sodalis	Aerial	Feldhamer et al. (2009)	12	38°
		Whitaker (2004)	15	39°
		Tuttle et al. (2006)	*	41°
		Kurta and Whitaker (1998)	233	43°
		Kurta and Whitaker (1998)	101	43°
		Kurta and Whitaker (1998)	48	43°
M. velifer	Trawling	Kunz (1974)	11	37°
		Kunz (1974)	15	37°
		Marquardt and Choate (2009)	*	37°
		Marquardt and Choate (2009)	*	37°
		Marquardt and Choate (2009)	*	37°
		Marquardt and Choate (2009)	*	37°
M. volans	Trawling	Lacki et al. (2007)	68	47°
		Whitaker et al. (1977)	25	47°
M. yumanensis	Trawling	Easterla and Whitaker (1972)	14	29°
		Whitaker (1972)	14	39°
		Whitaker et al. (1977)	25	47°
Europe				
M. alcathoe	Aerial	Lucan et al. (2009)	184	49°
		Lucan et al. (2009)	1,502	49°
		Lucan et al. (2009)	106	50°
M. blythii	Gleaning	Arlettaz et al. (1997)	29	40°
		Arlettaz et al. (1997)	29	40°
		Arlettaz et al. (1997)	50	46°
		Arlettaz et al. (1997)	119	46°
M. myotis	Gleaning	Arlettaz et al. (1997)	23	35°
		Arlettaz et al. (1997)	2	35°
		Arlettaz et al. (1997)	8	40°
		Arlettaz et al. (1997)	13	42°
		Arlettaz et al. (1997)	19	47°
		Arlettaz et al. (1997)	70	46°
		Arlettaz et al. (1997)	82	46°
Asia				
M. chinensis	Gleaning	Ma et al. (2008)	63	40°
Africa				
M. goudoti	Gleaning	Rakotoarivelo et al. (2007)	24	18°

The first 4 PCs accounted for 49.4% of interspecific dietary variation among the 22 species of *Myotis* based on classification of prey into 11 taxonomic categories of arthropods (Table 3). PC 1 reflected percent volume of Lepidoptera (factor loading, −0.84) and of Coleoptera (factor loading, 0.75); PC 2 reflected percent volume of Diptera (factor loading, −0.96); PC 3 reflected percent volume of Orthoptera (factor loading, −0.98); and PC 4 reflected percent volume of Trichoptera (factor loading, 0.76). The first 3 PCs accounted for 78.9% of interspecific dietary variation among the 22 species of *Myotis* based on 6 prey characteristics related to hardness and flight capacity (Table 3). PC 1 reflected prey flight speed (factor loading for "slow," 0.87; factor loading for "fast," −0.98); PC 2 reflected consumption of hard-bodied prey (factor loading for "hard," 0.71; factor loading for "soft," −0.99); and PC 3 reflected consumption of medium-hard prey (factor loading of −0.90).

Taxonomic richness of arthropod prey in the diet of *Myotis* increased with increasing latitude (Fig. 2). Higher percent volumes of hard prey were associated with lower percent volumes of soft prey ($r = -0.63$; $P < 0.01$; Fig. 3A). In contrast, association between percent volume of hard and medium-hard prey in the diet of *Myotis* was positive ($r = 0.72$; $P < 0.01$), and the association between fast-flying and slow-flying prey in

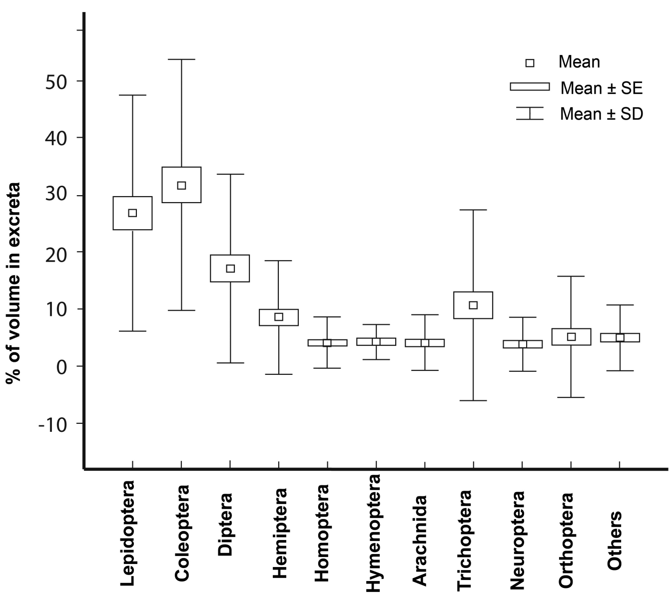

Fig. 1.—Descriptive statistics (mean, *SD*, and *SE*) of the % volume of each arthropod taxon in excreta of *Myotis*.

Table 3.—Results from principal component analysis based on the taxonomic composition of the diet or the prey characteristics in the diet of species of *Myotis*. PC = principal component.

	Eigenvalue	Percent variance explained	Cumulative variance explained
Taxonomic composition			
PC 1	1.33	12.12	12.12
PC 2	1.67	15.26	27.38
PC 3	1.27	11.54	38.93
PC 4	1.14	10.45	49.38
Prey characteristic			
PC 1	1.93	32.17	32.17
PC 2	1.64	27.49	59.67
PC 3	1.15	19.32	78.99

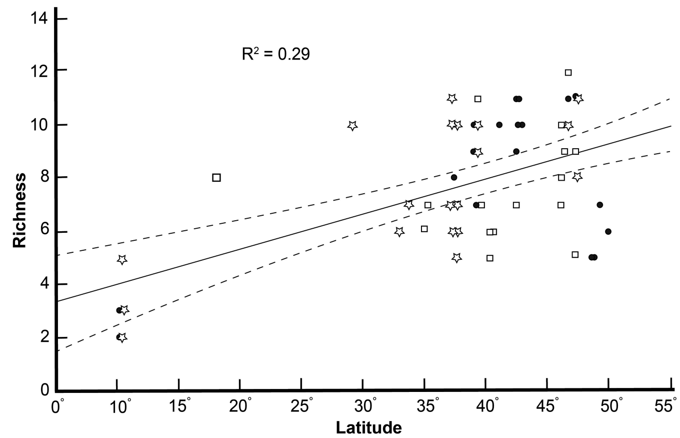

Fig. 2.—Relationship between the richness of arthropod taxa consumed by bats of the genus *Myotis* and latitude. Symbols indicate foraging habit of bats species: squares are gleaning, stars are aerial, and dots are trawling. Solid line represents best-fit least-squares relationship ($Y = 2.68 + 0.13X$, where Y = richness and X = latitude); dashed lines represent 95% *CI*s.

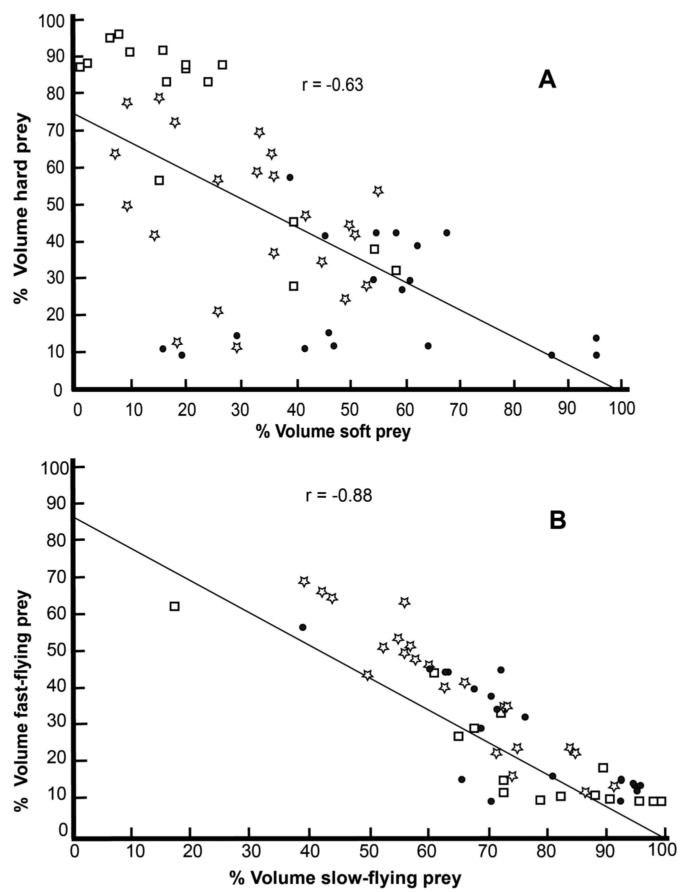

Fig. 3.—Association between the percent consumption of hard and soft arthropod prey for species of *Myotis*. Symbols indicate foraging habit of bats species: squares are gleaning, stars are aerial, and dots are trawling. Spearman rank correlation is represented by *r*. A) Association between the percent consumption of hard and soft arthropod prey. B) Association between the percent consumption of fast-flying prey and slow-flying prey.

the diet of *Myotis* was positive (r = 0.88; P < 0.01; Fig. 3B). Association between percent volume of non-flying prey (apterans) and percent volume of fast-flying prey was positive (r = 0.39; P = 0.003). However, correlation analyses for each group of species belonging to each of the 3 ecomorphotypes yielded different levels of significance. For example, only the gleaning ecomorphotype showed a statistically significant negative association between percent volume of hard and soft prey (r = −0.85; P < 0.01), whereas trawling types showed a negative correlation between these variables (r = −0.35; $P \geq 0.05$) and the aerial ecomorphotype showed a marginally significant negative value (r = 0.45; P = 0.07). The trawling, gleaning, and aerial types all showed a significant negative correlation between the percent volume of hard and moderately hard prey (r = −0.66; $P \leq 0.001$, r = −0.68; P < 0.01, and r = −0.63; P < 0.001). A significant negative association between the percent volume of slow- and fast-flying prey was obtained for each of the 3 ecomorphotypes (trawling r = −0.93, P = 0.001; gleaning r = −0.89, P = 0.001; aerial r = −0.75, P = 0.0014). The gleaning ecomorphotype was unique in yielding a significant positive association between percent consumption of non-flying and slow-flying prey (r = 0.5; P < 0.05).

Cluster analysis revealed 3 groups of *Myotis* based on dietary considerations (Fig. 4). Group I included the Eurasian gleaning species (*M. myotis*, *M. chinensis*, *M. blythi*), in which more than 80% of the volume of excreta represents hard prey. It included the largest bats, with a total length > 100 mm and forearm length > 48 mm. Group II included trawling species plus 1 African gleaning species (*M. gouduti*). The percent volume of hard prey consumed ranged between 45% and 80%. This group included medium-sized bats (body length between 48 and 100 mm; forearm length between 42 and 38 mm). Group III corresponded to the aerial ecomorphotype plus 2 North American gleaning species (*M. evotis* and *M. septentrionalis*) and 5 trawling species (*M. albescens*, *M. yumanensis*, *M. austoriparius*, *M. lucifugus*, and *M. velifer*); *M. velifer* is represented by only 6 specimens, 1 clustering with the aerial group and the others with the trawling group. Group III represented bats that have the lowest percent consumption of hard prey (< 45% by volume). This included smaller bats with body and forearm lengths < 48 mm and < 38 mm, respectively.

In general, the associations between the mean of each external measure and of the skull with mean percent volume of hardness or aerodynamic characteristics of the consumed prey were significant (Table 4). Percent volume of slow-flying, fast-flying, and medium-hardness prey was not associated significantly with morphological measures (Table 4).

Discussion

Use of arthropods as a food resource differed among the 3 ecomorphotypes of *Myotis* that originally were described as subgenera (Tate and Archbold 1941; Findley 1972). In a recent study, Ghazali et al. (2016) reported that these 3 subgenera can be differentiated into a group that feeds on hard prey, including the gleaning ecomorphotype (*Myotis*), and the group consuming soft prey, comprising the trawling (*Leuconoe*) and aerial (*Selysius*) ecomorphotypes. We quantified greater dietary differentiation among the 3 ecomorphotypes.

The subgenus *Myotis* (sensu Tate and Archbold 1941) and the group *Bechsteini* of the subgenus *Myotis* (sensu Findley

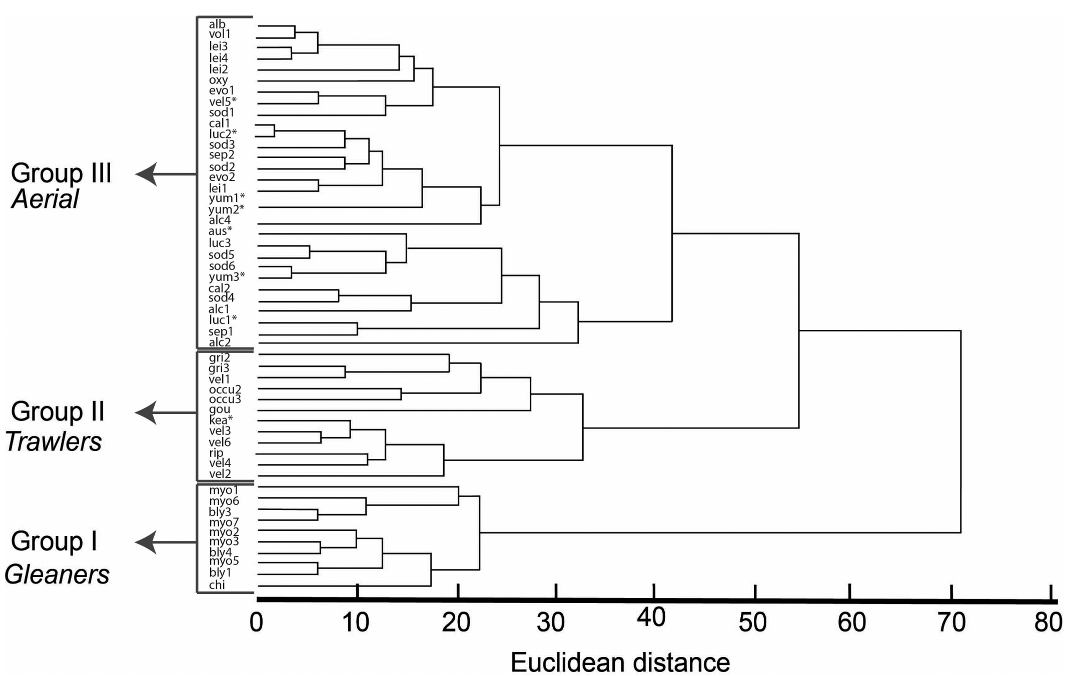

Fig. 4.—Relationship of species of *Myotis* (species names are abbreviated with the first 3 letters of the specific epithet, with numbers representing associated references in Table 2) based on arthropod prey characteristics (flight speed and hardness). Clustering algorithm was based on the unweighted pair-group method of arithmetic means using Euclidean distances.

Table 4.—Associations (Spearman rank correlation coefficients) between the means of prey type consumed (column headings) and morphological characteristics (row headings) of species of *Myotis*.

	Apterans (non-flying)	Slow-flying	Fast-flying	Soft	Medium-hard	Hard
Weight	0.676	−0.144	−0.055	−0.589	−0.305	0.644
Ear length	0.552	0.110	−0.279	−0.603	−0.364	0.712
Forearm length	0.532	0.120	−0.284	−0.557	−0.363	0.703
Tail length	0.723	−0.331	0.121	−0.380	−0.274	0.456
Total length	0.681	−0.258	0.064	−0.502	−0.325	0.589
Body length	0.612	−0.182	0.011	−0.587	−0.355	0.680
Skull length	0.636	−0.144	−0.024	−0.628	−0.307	0.689

1972) are consistent with the gleaning ecomorphotype (Group I) that mainly feeds on hard prey (more than 80% of the volume consumed), mostly apterans or slow-flying taxa. This group includes large bat species (total length > 100 mm) distributed in Eurasia (*M. blythi*, *M. chinensis*, and *M. myotis*). Our results differ from those of Ghazali et al. (2016) in that the diet of the other species in the gleaning ecomorphotype is characterized by a preference for arthropods with different hardness and aerodynamic characteristics (fast-flying, slow-flying, and non-flying).

Bat species for which hard arthropods represent 45–80% of the diet by volume (Group II) consume more fast-flying arthropods than does the gleaning ecomorphotype. This group includes medium-sized bat species with body lengths of 48–100 mm. It consists of the species of the trawling ecomorphotype, in addition to the African gleaning species *M. goudoti*. This is consistent with the idea that *M. goudoti* belongs to the subgenus *Chrysopteron*, which is morphologically different from the subgenus *Myotis* (Tate and Archbold 1941). Bat species that consume low percentages of hard prey (< 45%) and a moderate consumption of slow-flying arthropods include small bats (total length < 47 mm) in Group III. Group III mostly comprises aerial species, in addition to the gleaning species of the Americas that correspond to the *Evotis* group (sensu Findley 1972). Gleaning species of the Americas were not included in the work of Tate and Archbold (1941). However, Tate and Archbold (1941) did consider the gleaning *Myotis* species of the Americas to belong to a subgenus that was different from the European *Myotis* subgenus.

Myotis albescens, *M. yumanensis*, *M. austoriparius*, *M. lucifugus*, and *M. velifer*, which belong to the gleaning ecomorphotype (Ghazali et al. 2016), have a greater affinity with aerial species in terms of diet composition. The diet of *M. velifer* is grouped with that of the aerial habit in 1 study (Barclay and Brigham 1991) but with the trawling group in 5 other studies (Tate and Archbold 1941; Findley 1972; Fenton and Bogdanowicz 2002; Ghazali et al. 2016; Segura-Trujillo et al. 2016). These results suggest intraspecific foraging flexibility (Ratcliffe and Dawson 2003) or plasticity in feeding habits (Schnitzler and Kalko 2001).

Bat size is associated with biting strength (Nogueira et al. 2009; Freeman and Lemen 2010). For example, species in Group I, which are larger and feed on hard arthropods, also can feed on softer insects when the typically hard prey are scarce. In contrast, bats in Group III, associated with the consumption of soft prey, lack the biting strength needed to consume hard prey. Large-sized bats have the capacity to prey on hard and soft prey, but the small-sized bats do not have the strength to consume hard prey, so they are constrained to feed on softer prey. Wide variation in the composition of the diet has been documented for *M. lucifugus*, *M. yumanensis*, and *M. velifer* (e.g., Kunz 1974; Belwood and Fenton 1976; Anthony and Kunz 1977), species that Ghazali et al. (2016) classified as trawling species. Indeed, the consumption of aquatic insects by these bats is opportunistic, and trawling behavior is not always displayed when hunting; instead, composition of the diet is highly related to food availability (Belwood and Fenton 1976; Anthony and Kunz 1977). Some report that *M. lucifugus* displayed gleaning habits (Ratcliffe and Dawson 2003), but this is contrary to the classification of Ghazali et al. (2016). North American species of *M. evotis* and *M. septentrionalis* traditionally are considered to be gleaning bats (Findley 1972; Ghazali et al. 2016). However, our work revealed that both species have a greater affinity with aerial species. Our results are consistent with previous reports describing that these 2 species have facultative aerial and gleaning habits of hunting (Faure and Barclay 1994; Ratcliffe and Dawson 2003).

The analysis of external morphological traits identified 3 main foraging habits within the genus *Myotis* (Schnitzler and Kalko 2001; Fenton and Bogdanowicz 2002) with many of the traits that characterize the ecomorphotypes being cranial (Tate and Archbold 1941; Fenton and Bogdanowicz 2002) or related to morphological size (Findley 1972). These differences may be associated with trophic specialization (Fenton and Bogdanowicz 2002; Aguirre et al. 2003; Freeman and Lemen 2007; Segura-Trujillo et al. 2016). We posit that species of the genus *Myotis* have undergone convergent evolution throughout their distributional range, leading to the independent evolution of the 3 ecomorphotypes that are associated with optimization for a particular type of arthropod prey. This convergence has been documented for gleaning, trawling, and aerial ecomorphotypes on 3 continents (America, Europe, and Africa), but patterns likely are global. Importantly, our work is limited by data availability. We only analyzed about 22% of *Myotis* species of the world. Moreover, species differ greatly in the availability of dietary data (Table 2). Consequently, more dietary information is needed on species of *Myotis* to confirm the generality of our conclusions. In particular, dietary information for more species from throughout their latitudinal extents is necessary for improving our understanding of the generality of associations between ecomorphotypes and dietary characteristics.

Myotis has evolved 3 different morphotypes associated with gleaning, trawling, and aerial habits, which in turn are associated with differential use of arthropods as food resources. This possibly facilitates the coexistence of several species of congeners in the same environment. These 3 groups had previously been considered as subgenera (Tate and Archbold 1941; Findley 1972), even though each was a polyphyletic taxon (Ruedi and Mayer 2001; Hoofer 2003; Kawai et al. 2003; Bickham et al. 2004; Ghazali et al. 2016). Moreover, some species display flexibility in the diet that may arise because of variation in food availability (i.e., opportunistic feeding).

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Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Publications consulted for morphological measurements (i.e., mass, total length, ear length, forearm length, tail length, body length, and skull length) of species of *Myotis.*

Literature Cited

Aguirre, L., A. F. Herrel, R. Van Damme, and E. Matthysen. 2003. The implications of food hardness for diet in bats. Functional Ecology 17:201–212.

Anthony, E. L., and T. H. Kunz. 1977. Feeding strategies of the little brown bat, *Myotis lucifugus*, in southern New Hampshire. Ecology 58:775–786.

Arlettaz, R., N. Perrin, and J. Hausser. 1997. Trophic resource partitioning and competition between the two sibling bat species *Myotis myotis* and *Myotis blythii*. Journal of Animal Ecology 66:897–911.

Barclay, R. M., and R. M. Brigham. 1991. Prey detection, dietary niche breadth, and body size in bats: why are aerial insectivorous bats so small? The American Naturalist 137:693–703.

Belwood, J. J., and M. B. Fenton. 1976. Variation in the diet of *Myotis lucifugus* (Chiroptera: Vespertilionidae). Canadian Journal of Zoology 54:1674–1678.

Bickham, J. W., J. C. Patton, D. A. Schlitter, I. L. Rautenbach, and R. L. Honeycutt. 2004. Molecular phylogenetics, karyotypic diversity, and partition of the genus *Myotis* (Chiroptera: Vespertilionidae). Molecular Phylogenetics and Evolution 33:333–338.

Bracamonte, J. C. 2013. Hábitos alimenticios de un ensamble de murciélagos insectívoros de bosque montano en las yungas argentinas. Chiroptera Neotropical 19:1157–1162.

Denzinger, A., E. K. Kalko, M. Tschapka, A. D. Grinnell, and H. U. Schnitzler. 2016. Guild structure and niche differentiation in echolocating bats. Pp. 141–166 in Bat bioacoustics (M. B. Fenton, A. D. Grinnell, A. Popper, and R. R. Fay, eds.). Springer, New York.

Easterla, D. A., and J. O. Whitaker. 1972. Food habits of some bats from Big Bend National Park, Texas. Journal of Mammalogy 53:887–890.

Faure, P. A., and R. M. Barclay. 1994. Substrate-gleaning versus aerial-hawking: plasticity in the foraging and echolocation behaviour of the long-eared bat, *Myotis evotis*. Journal of Comparative Physiology, A. Sensory, Neural, and Behavioral Physiology 174:651–660.

Feldhamer, G. A., T. C. Carter, and J. Whitaker, Jr. 2009. Prey consumed by eight species of insectivorous bats from southern Illinois. The American Midland Naturalist 162:43–51.

Fenton, M. B., and W. Bogdanowicz. 2002. Relationships between external morphology and foraging behaviour: bats in the genus *Myotis*. Canadian Journal of Zoology 80:1004–1013.

Findley, J. S. 1972. Phenetic relationships among bats of the genus *Myotis*. Systematic Biology 21:31–52.

Freeman, P. W., and C. A. Lemen. 2007. Using scissors to quantify hardness of insects: do bats select for size or hardness? Journal of Zoology 271:469–476.

Freeman, P. W., and C. A. Lemen. 2010. Simple predictors of bite force in bats: the good, the better and the better still. Journal of Zoology 282:284–290.

Gardiner, J. D., G. Dimitriadis, J. R. Codd, and R. L. Nudds. 2011. A potential role for bat tail membranes in flight control. PLoS One 6:e18214.

Ghazali, M., R. Moratelli, and I. Dzeverin. 2016. Ecomorph evolution in *Myotis* (Vespertilionidae, Chiroptera). Journal of Mammalian Evolution 24:475–484.

Godawa Stormark, J. 1998. Phenetic analysis of Old World *Myotis* (Chiroptera: Vespertilionidae) based on dental characters. Acta Theriologica 43:1–11.

Hoofer, S. R., and R. A. van Den Bussche. 2003. Molecular phylogenetics of the chiropteran family Vespertilionidae. Acta Chiropterologica 5:1–63.

Horáček, I., V. Hanák, and J. Gaisler. 2000. Bats of the Palearctic Region: a taxonomic and biogeographic review. Pp. 11–157 in (B. W. Woloszyn, ed.), Proceedings of the VIIIth European Bat Research Symposium, Krakow, Poland.

Hutson, A. M., and S. P. Mickleburgh. 2001. Microchiropteran bats: global status survey and conservation action plan. IUCN, Gland, Switzerland and Cambridge, United Kingdom.

Jackson, D. A. 1993. Stopping rules in principal components analysis: a comparison of heuristical and statistical approaches. Ecology 74:2204–2214.

James, F. C., and C. E. McCulloch. 1990. Multivariate analysis in ecology and systematics: panacea or Pandora's box? Annual Review of Ecology and Systematics 21:129–166.

Kawai, K., et al. 2003. The status of the Japanese and East Asian bats of the genus *Myotis* (Vespertilionidae) based on mitochondrial sequences. Molecular Phylogenetics and Evolution 28:297–307.

Kunz, T. H. 1974. Feeding ecology of a temperate insectivorous bat (*Myotis velifer*). Ecology 55:693–711.

Kurta, A., and J. O. Whitaker, Jr. 1998. Diet of the endangered Indiana bat (*Myotis sodalis*) on the northern edge of its range. The American Midland Naturalist 140:280–286.

Lacki, M. J., L. S. Burford, and J. O. Whitaker, Jr. 1995. Food habits of gray bats in Kentucky. Journal of Mammalogy 76:1256–1259.

Lacki, M. J., J. S. Johnson, L. E. Dodd, and D. Baker. 2007. Prey consumption of insectivorous bats in coniferous forests of north-central Idaho. Northwest Science 81:199–205.

Lucan, R. K., et al. 2009. Alcathoe bat (*Myotis alcathoe*) in the Czech Republic: distributional status, roosting and feeding ecology. Acta Chiropterologica 11:61–69.

Ma, J., B. Liang, S. Zhang, and W. Metzner. 2008. Dietary composition and echolocation call design of three sympatric insectivorous bat species from China. Ecological Research 23:113.

Marquardt, S. R., and J. R. Choate. 2009. Influence of thermal environment on food habits of female cave *Myotis* (*Myotis velifer*). The Southwestern Naturalist 54:166–175.

Moosman, P. R., H. H. Tomas, and J. P. Veilleux. 2007. Food habits of eastern small-footed bats (*Myotis leibii*) in New Hampshire. The American Midland Naturalist 158:354–360.

Nogueira, M. R., A. L. Peracchi, and L. R. Monteiro. 2009. Morphological correlates of bite force and diet in the skull and mandible of phyllostomid bats. Functional Ecology 23:715–723.

Rakotoarivelo, A. A., N. Ranaivoson, O. R. Ramilijaona, A. F. Kofoky, P. A. Racey, and R. K. Jenkins. 2007. Seasonal food habits of five sympatric forest microchiropterans in western Madagascar. Journal of Mammalogy 88:959–966.

Ratcliffe, J. M., and J. W. Dawson. 2003. Behavioural flexibility: the little brown bat, *Myotis lucifugus*, and the northern long-eared bat, *M. septentrionalis*, both glean and hawk prey. Animal Behaviour 66:847–856.

Ruedi, M., and F. Mayer. 2001. Molecular systematics of bats of the genus *Myotis* (Vespertilionidae) suggests deterministic ecomorphological convergences. Molecular Phylogenetics and Evolution 21:436–448.

Schnitzler, H. U., and E. K. V. Kalko. 2001. Echolocation by insect-eating bats. Bioscience 51:557–569.

Segura-Trujillo, C. A., W. Z. Lidicker, and S. T. Álvarez-Castañeda. 2016. New perspectives on trophic guilds of arthropodivorous bats in North and Central America. Journal of Mammalogy 92:644–654.

Simmons, N. B. 2005. Order Chiroptera. Pp. 312–529 in Mammal species of the world: a taxonomic and geographic reference (D. E. Wilson, D. M. Reeder, eds.). Johns Hopkins University Press, Baltimore.

Sokal, R. R., and F. J. Rohlf. 2011. Biometry: the principles and practice of statistics in biological research. 4th ed. W. H. Freeman, New York.

Stadelmann, B., D. S. Jacobs, C. Schoeman, and M. Ruedi. 2004. Phylogeny of African *Myotis* bats (Chiroptera, Vespertilionidae) inferred from cytochrome b sequences. Acta Chiropterologica 6:177–192.

StatSoft Inc. 2004. Statistica, data analysis software system, version 7. Oklahoma.

Tate, G. H. H., and R. Archbold. 1941. A review of the genus *Myotis* (Chiroptera) of Eurasia: with special reference to species occurring in the East Indies. Bulletin of the American Museum of Natural History 78:537–565.

Tuttle, N. M., D. P. Benson, and D. W. Sparks. 2006. Diet of the *Myotis sodalis* (Indiana bat) at an urban/rural interface. Northeastern Naturalist 13:435–442.

Valdez, E. W., and M. A. Bogan. 2009. Does variation in cranial morphology of *Myotis occultus* (Chiroptera: Vespertilionidae) reflect a greater reliance on certain prey types? Acta Chiropterologica 11:443–450.

Whitaker, J. O., Jr. 1972. Food habits of bats from Indiana. Canadian Journal of Zoology 50:877–883.

Whitaker, J. O., Jr. 1988. Food habits analysis of insectivorous bats. Pp. 171–189 in Ecological and behavioral methods for the study of bats (T. H. Kunz, ed.). Smithsonian Institution Press, Washington, D.C.

Whitaker, J. O., Jr. 2004. Prey selection in a temperate zone insectivorous bat community. Journal of Mammalogy 85:460–469.

Whitaker, J. O., Jr., and J. S. Findley. 1980. Foods eaten by some bats from Costa Rica and Panama. Journal of Mammalogy 61:540–544.

Whitaker, J. O., Jr., C. Maser, and L. E. Keller. 1977. Food habits of bats of western Oregon. Northwestern Science 5:46–55.

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