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PREY SELECTION BY BATS IN FORESTS OF WESTERN OREGON

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We investigated food habits and relationships between food resource abundance and activity of bats. We identified prey remains in guano collected from 337 individuals in the Oregon Coast Range. Guano analyses indicated that 2 species, long-legged myotis (*Myotis volans*) and Townsend's big-eared bat (*Corynorhinus townsendii*), consumed predominantly Lepidoptera; 4 species, California myotis (*M. californicus*), little brown myotis (*M. lucifugus*), Yuma myotis (*M. yumanensis*), and silver-haired bat (*Lasionycteris noctivagans*), consumed predominantly smaller insects likely of aquatic origin (Diptera and Trichoptera); and the remaining 4 species, long-eared myotis (*M. evotis*), fringed myotis (*M. thysanodes*), big brown bat (*Eptesicus fuscus*), and hoary bat (*Lasiurus cinereus*), consumed predominantly larger invertebrates of terrestrial origin (Lepidoptera, Coleoptera, Hemiptera, and Araneae). We hypothesized that bat activity in riparian areas would be correlated with abundance of preferred insect prey and used an information-theoretic approach to determine whether variability in bat activity was more strongly associated with captures of all insects, of taxa most frequently occurring in the diet, or of particular size classes of insects. We found strong associations between activity of small *Myotis* species and number of captures of small insects, but activities of larger *Myotis* species and of non-*Myotis* species were not associated with numbers of insects of any category.

Key words: activity, bats, diet, insects, prey, resource selection, riparian, western Oregon

Distribution and abundance of prey strongly influence distributions of predators (Harwood et al. 2003; Kareiva and Odell 1987; Lima 2002; Sabo and Power 2002). Variability in prey density in conjunction with the energetic expense of locating and capturing prey often results in congregations of predators in areas with high concentrations of prey (Curio 1976; Fauchald et al. 2000; Houghton et al. 2006). Highly mobile predators are able to track fluctuations in prey densities over space and time, and tend to spend longer periods of time in areas where food was recently consumed (Bernstein et al. 1991; Kareiva and Odell 1987).

Mobility is a key characteristic underlying ability to track variation in distribution of food resources (Bernstein et al. 1991; Kotliar and Wiens 1990). Consequently, volant predators ought to be able to track changes in distributions of prey closely and to concentrate their activity in areas with high densities of preferred prey. Accordingly, correlations between bat activity and insect abundance are often reported (Anthony et al. 1981; Avery 1985; de Jong and Ahlen 1991; Hayes 1997; Kusch et al. 2004; O'Donnell 2000; Racey and Swift 1985). However, the strength of this association varies, and in some cases, this pattern is not evident or occurs under a limited range of conditions (Ekman and de Jong 1996; Grindal and Brigham 1999; Lunde and Harestad 1986; Meyer et al. 2004; Rautenbach et al. 1996; Verboom and Spoelstra 1999). Variation in findings may be due in part to variability in metrics used to describe insect abundance, lack of precision in indices of insect abundance, and inclusion of taxa of insects not consumed by a particular species of bat in assessments of prey.

A more complete understanding of the relationship between bat activity and abundance of insects requires information about associations between foraging ecology of individual species of bats and characteristics of the insects they select as prey. Although most studies of prey selection by bats emphasize the

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taxa of insects consumed, size may be a more important determinant of bat prey selection (Aldridge and Rautenbach 1987; Anthony and Kunz 1977; Barclay 1985; Belwood and Fullard 1984). Because insect size and taxon are often partially confounded, determining their relative importance in prey selection by bats is difficult. We know of no study that has formally compared relative strengths of associations between bat activity and prey taxon and prey size under field conditions. Our specific objectives were to determine the taxonomic composition of the diets of bats in the Oregon Coast Range, and to determine the relative strength of associations between bat activity and abundances of all insects, of insects of commonly consumed taxa, and of insects of particular size classes.

MATERIALS AND METHODS

Study area.—We conducted our study throughout the Oregon Coast Range, a region extending approximately 300 km from north to south. The terrain is steep and rugged, with a dense network of streams throughout. Elevation ranges from sea level to 1,250 m. The area is characterized by a maritime climate with wet, mild winters and cool, dry summers (Franklin and Dyrness 1973). Dominant riparian vegetation includes Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), red alder (*Alnus rubra*), big-leaf maple (*Acer macrophyllum*), western redcedar (*Thuja plicata*), vine maple (*Acer circinatum*), hazelnut (*Corylus cornuta*), salmonberry (*Rubus spectabilis*), and swordfern (*Polystichum munitum*).

Diets of bats.—In 2002, we used mist nets to capture bats over randomly selected 2nd- and 3rd-order streams (as determined by 1:24,000 scale topographic quadrangle maps). Because of extremely low capture success ($\bar{X} = 1.1 \pm 0.23$ bats captured per 10-h night of mistnetting effort), in 2003 and 2004 we used H-nets (Waldien and Hayes 1999) and hoop nets to actively net bats while they visited the undersides of bridges to night-roost.

After capture, we held each bat in a clean cloth bag for ~1 h and identified each captured bat to species, sex, and age. Because of the high degree of morphological similarity, we collected wing biopsies from captured Yuma myotis (*Myotis yumanensis*) and little brown myotis (*M. lucifugus*) to confirm species identification based on genetic markers (Scott 2005). We collected the guano that accumulated in each capture bag and stored these in a labeled plastic vial at −10°C. Capture and handling procedures followed guidelines approved by the American Society of Mammalogists (Gannon et al. 2007) and were approved by the Institutional Animal Care and Use Committee of Oregon State University.

In the laboratory, we teased apart guano in a petri dish containing 95% ethyl alcohol. All pellets collected from an individual bat were treated as 1 sample. We identified invertebrate parts in pellets to order using a dissecting microscope, comparing invertebrate fragments in guano pellets to reference mounts made of invertebrates collected nearby. We visually estimated the percentage of each sample composed of each invertebrate order (percent volume), and then calculated the mean percent volume for each order for all individuals of a given species of bat. We also calculated the frequency of occurrence of each order for each species of bat. All samples were processed by a single observer (HKO) so that inter-observer biases were avoided.

We used cluster analysis to sort species of bats into groups according to similarities in diet. We applied an arcsine square-root transformation to the percent volume of each food item consumed by each species and computed a matrix of Euclidean distances for these data. We then conducted a cluster analysis using Ward's minimum variance method to produce a dendrogram reflecting the degree of similarity in food resource use among species. All calculations were done using SAS (version 9.1; SAS Institute Inc., Cary, North Carolina).

Bat activity and insect captures.—We monitored bat and insect activity in 26 randomly selected 2nd- and 3rd-order streams; 12 stream reaches located in the southern Oregon Coast Range in 2003, 12 stream reaches in the northern Oregon Coast Range in 2004, and 2 stream reaches during both years to assess interannual variation in insect abundance and bat activity. Each night we measured activity of bats and assessed abundance of insects along 1 stream reach dominated by hardwood trees and 1 dominated by conifers within either the same watershed where bats were captured under bridges, or an adjacent watershed if an adequate number of bridges were not available. All stream reaches were 3–7 m bank-full width and >0.5 m deep. Each stream reach was sampled from sunset until sunrise once during every 2-week period between mid-June and early September, for a total of 5 all-night visits per stream reach per year.

We captured nocturnal flying insects using Universal Black Light Traps (Bioquip Inc., Rancho Dominguez, California) with 12-W fluorescent black-light tubes, powered with 12-V batteries. Although not all species of insects are equally attracted to blacklight traps, we believe these traps were the best available option for achieving our objectives, because they sample nocturnal, flying insects, and are suitable for making relative comparisons of insect abundance among sites. A "no-pest strip" (Hotshot, Newport Beach, California) was placed in the bottom of each trap as a killing agent. We placed traps 0.5 m off the ground within 2 m of the stream edge in a location selected to maximize visibility from all directions. We began trapping within 30 min of sunset and continued until 0–30 min after sunrise when insects were removed from traps, placed in labeled plastic boxes, and stored at −10°C until analysis. In the laboratory, we sorted insects to order and measured insect body lengths from the anterior of the head to the posterior of the last abdominal segment (antennae and cerci excluded) to the nearest millimeter using a dissecting microscope. We used the number of individuals captured per stream reach per night as an index of abundance.

We assessed activity of bats by recording echolocation calls using calibrated (Larson and Hayes 2000) Anabat II echolocation detectors with Anabat zero crossings analysis interface modules (Titley Inc., Balina, Australia). We activated detectors within 30 min of sunset and stopped them 0–30 min after sunrise. We placed detectors within 2 m of the stream edge, 0.5 m above the surface of the stream, oriented at a 30° angle,

Table 1.—Relationships between abundance of insects and activity of bats predicted by a priori hypotheses and the linear model associated with each.

Hypothesis	Predicted relationship	Model structure
Insect size	Positive effect of abundance of small insects	$y = \beta_0 + \beta_1$(no. captures of insects of body length 0–2 mm)
	Positive effect of abundance of medium insects	$y = \beta_0 + \beta_1$(no. captures of insects of body length 3–6 mm)
	Positive effect of abundance of large insects	$y = \beta_0 + \beta_1$(no. captures of insects of body length $\geq$ 7 mm)
Insect taxon	Positive effect of abundance of Coleoptera	$y = \beta_0 + \beta_1$(no. captures of Coleoptera)
	Positive effect of abundance of Diptera	$y = \beta_0 + \beta_1$(no. captures of Diptera)
	Positive effect of abundance of Hemiptera	$y = \beta_0 + \beta_1$(no. captures of Hemiptera)
	Positive effect of abundance of Lepidoptera	$y = \beta_0 + \beta_1$(no. captures of Lepidoptera)
	Positive effect of abundance of Trichoptera	$y = \beta_0 + \beta_1$(no. captures of Trichoptera)
All insects	Positive effect of abundance of all insects	$y = \beta_0 + \beta_1$(no. captures of all insects)

with the microphone aligned parallel to the main axis of the stream and pointing upstream, and used the same location and orientation for each visit. We always placed blacklight traps within 2 m of detectors so that any biases resulting from influences of insect attraction to traps on bat activity would be consistent among sites.

We used recordings to obtain an index of bat activity rather than to quantify abundance of bats (Hayes 2000). We used Analook (version 4.9j; Titley Inc., Balina, Australia) to view recorded bat echolocation call sequences, and quantified activity by determining the number of minutes per stream reach per night during which echolocation calls were recorded. Ten species are known to occur in the region: Townsend's big eared bat (*Corynorhinus townsendii*), big brown bat (*Eptesicus fuscus*), hoary bat (*Lasiurus cinereus*), silver-haired bat (*Lasionycteris noctivagans*), California myotis (*Myotis californicus*), long-eared myotis (*M. evotis*), little brown myotis (*M. lucifugus*), fringed myotis (*M. thysanodes*), long-legged myotis (*M. volans*), and Yuma myotis (*M. yumanensis*—Verts and Carraway 1998). We could not categorize all echolocation calls to species because of similarities in calls among some species. As a result, we partitioned calls into 1 of 6 phonic groups, with each phonic group composed of species with similar call characteristics: *M. lucifugus*/*M. volans* (MYLU/MYVO); *M. californicus*/*M. yumanensis* (MYCA/MYYU); *M. evotis*/*M. thysanodes* (MYEV/MYTH); *C. townsendii* (COTO); *E. fuscus*/*Lasionycteris noctivagans*/*Lasiurus cinereus* (EPFU/LANO/LACI); or unidentifiable (Ober 2007). A single observer (HKO) processed all echolocation data using a dichotomous key to assign calls to phonic groups.

To determine the potential effect of interannual variation on our analyses, we compared mean numbers of insects captured per night between years for the 2 stream reaches monitored during both years of the study using *t*-tests. We found no statistically significant interannual differences in the number of captures of each of the 6 most-abundant orders of insects at either of the stream reaches ($P \gg 0.05$). We used similar analyses to compare the mean number of minutes during which bat echolocation calls occurred per night between years for each site. We found no statistically significant interannual differences in overall bat activity in either stream reach monitored both years ($P \gg 0.05$). Hence, we assumed that the effect of year was negligible and pooled data across years for subsequent analyses.

We developed a set of working hypotheses reflecting our 2 fundamental hypotheses regarding prey selection by bats. We reasoned that if a given group of bats select prey items primarily on the basis of taxon, then those bats would congregate in areas with high abundances of insects from preferred taxa, and as a consequence bat activity would increase with abundance of insects of preferred taxa. Alternatively, if bats select prey primarily on the basis of body size of the prey, then bats would congregate in areas with high abundances of insects within the preferred size class, and bat activity would increase with abundance of insects in the preferred size class. Finally, if bats respond to prey abundance but do not discriminate on the basis of either size or taxon of prey, bats would congregate in areas with high overall abundance of insects and activity would increase with total abundance of insects. We developed regression models reflecting these hypotheses (Table 1). For each phonic group except *C. townsendii*, we assessed 8 models: 3 models reflecting the numbers of captures of each of the 3 orders of insects consumed in greatest quantities by these bats (as determined via the guano analyses), 3 models reflecting numbers of captures of insects of different sizes (small, 0–2 mm; medium, 3–6 mm; and large, ≥7 mm), 1 model for number of captures of all insects, and a null model (intercept only). The only taxon-specific model we assessed for *C. townsendii* reflected number of captures of Lepidoptera, because of the high degree of dietary specialization of this species.

We used the number of minutes that contained echolocation calls per stream reach per night, averaged over 5 sampling nights, as an index of bat activity at each site (Miller 2001). We used the number of insects captured per stream reach per night, averaged over 5 sampling nights, as an index of insect abundance at each site. We ln-transformed explanatory and response variables to meet assumptions of statistical models, and we checked but did not find severe outliers or evidence of nonlinear relationships. We did not include quadratic equations because there was no evidence of such trends evident from graphs of residuals, there was no biological basis for expecting such relationships, and the number of candidate models would be large relative to our sample sizes if we included models with and without quadratic terms.

We ranked models according to their likelihood, given the data using Akaike's information criterion corrected for small sample sizes (AIC_c—Burnham and Anderson 2002). We evaluated difference between the AIC_c score of each model

TABLE 2.—Mean percent volume of food items identified in fecal pellets of each species of bat in the Oregon Coast Range, summers 2002–2004. Sample sizes (no. samples per species) are given in parentheses.[a]

	COTO (4)	EPFU (67)	LACI (2)	LANO (4)	MYCA (15)	MYEV (23)	MYLU (26)	MYTH (20)	MYVO (106)	MYYU (70)
Acari	0	0	0	0	0	0	1	0	0	1
Araneae	4	0	3	0	2	20	6	24	6	10
Coleoptera	1	37	5	8	8	12	5	14	1	1
Diptera	0	2	0	24	30	5	33	9	5	31
Ephemeroptera	0	0	0	0	0	0	0	0	0	<1
Hemiptera	0	13	18	16	5	14	4	5	3	6
Homoptera	0	1	25	0	1	0	2	19	1	2
Hymenoptera	0	2	3	4	5	1	1	1	0	1
Isoptera	0	9	3	1	5	5	5	1	10	12
Lepidoptera	95	29	40	24	30	35	15	21	72	11
Neuroptera	0	4	3	14	7	3	4	2	1	2
Orthoptera	0	0	0	0	0	1	0	4	0	0
Plecoptera	0	0	0	0	0	0	<1	0	0	<1
Psocoptera	0	0	0	0	1	0	0	0	0	0
Trichoptera	0	3	3	10	7	3	25	2	0	22

[a] COTO = *Corynorhinus townsendii*; EPFU = *Eptesicus fuscus*; LACI = *Lasionycteris noctivagans*; LANO = *Lasiurus cinereus*; MYCA = *Myotis californicus*; MYEV = *Myotis evotis*; MYLU = *Myotis lucifugus*; MYTH = *Myotis thysanodes*; MYVO = *Myotis volans*; MYYU = *Myotis yumanensis*.

and the lowest AIC$_c$ score of all models for that phonic group (ΔAIC$_c$), and considered all models with $\Delta\text{AIC}_c \leq 2.0$ to have substantial empirical support. We used Akaike weights (w_i) to evaluate the relative likelihood of each model, and evidence ratios (w_1/w_2) as the relative evidence in favor of 1 model over another. All analyses were conducted in SAS (version 9.1) using PROC REG.

RESULTS

Diets of bats.—We analyzed 337 samples of guano from 10 species of bats (Tables 2 and 3) and identified 15 orders of invertebrates. Lepidoptera was the order most frequently found; this order was present in all of the samples for 6 species of bats, and >75% of the samples of each of the other 4 species. Diptera occurred 2nd most frequently in guano samples. Coleoptera, Isoptera, Trichoptera, Araneae, Hemiptera, Neuroptera, Homoptera, and Hymenoptera each occurred in >25% of samples of at least 2 species of bats (Table 3). Orthoptera occurred in 30% of samples of *M. thysanodes*, in 17% of samples of *M. evotis*, and in none of the samples of each of the other species of bat. Acari, Psocoptera, Plecoptera, and Ephemeroptera occurred in <20% of the samples for all species of bat. Spiders (Araneae) and mites (Acari) were the only noninsect and the only nonvolant taxa consumed.

Differences in diet composition were evident among species of bats (Tables 2 and 3). Three pairs of species exhibited a great degree of overlap in food habits, as evidenced by short internode distances in the dendrogram produced by the cluster analysis (Pielou 1984; Fig. 1): *M. lucifugus* with *M. yumanensis*, *M. californicus* with *Lasionycteris noctivagans*, and *M. evotis* with *M. thysanodes*. Moreover, the long internodal distances in the dendrogram indicate that bats clustered into 3 broad groups (Pielou 1984; Fig. 1). *C. townsendii* and *M. volans* clustered together, reflecting specialization on Lepidoptera. *Lasiurus cinereus*, *M. evotis*, *M. thysanodes*, and *E. fuscus* clustered together, reflecting a generalist feeding strategy with large volumes of terrestrial

TABLE 3.—Frequency of occurrence of food items identified in fecal pellets of bats in the Oregon Coast Range, summers 2002–2004. Abbreviations are as in Table 2. Sample sizes (no. samples per species) are given in parentheses.

	COTO (4)	EPFU (67)	LACI (2)	LANO (4)	MYCA (15)	MYEV (23)	MYLU (26)	MYTH (20)	MYVO (106)	MYYU (70)
Acari	0	3	0	0	0	0	12	0	0	17
Araneae	75	3	50	0	40	91	50	90	42	59
Coleoptera	25	91	100	100	53	78	23	75	10	10
Diptera	0	42	0	100	100	61	96	65	37	94
Ephemeroptera	0	0	0	0	0	0	0	0	0	1
Hemiptera	0	79	100	100	47	57	27	40	33	31
Homoptera	0	7	50	0	7	4	12	40	5	9
Hymenoptera	0	22	50	50	40	9	15	15	5	16
Isoptera	0	28	50	25	7	13	15	10	19	26
Lepidoptera	100	97	100	100	100	100	77	90	100	83
Neuroptera	0	57	50	100	73	35	38	25	14	17
Orthoptera	0	0	0	0	0	17	0	30	0	0
Plecoptera	0	0	0	0	0	0	4	0	0	1
Psocoptera	0	0	0	0	7	4	0	0	0	3
Trichoptera	0	28	50	100	67	35	96	15	3	90

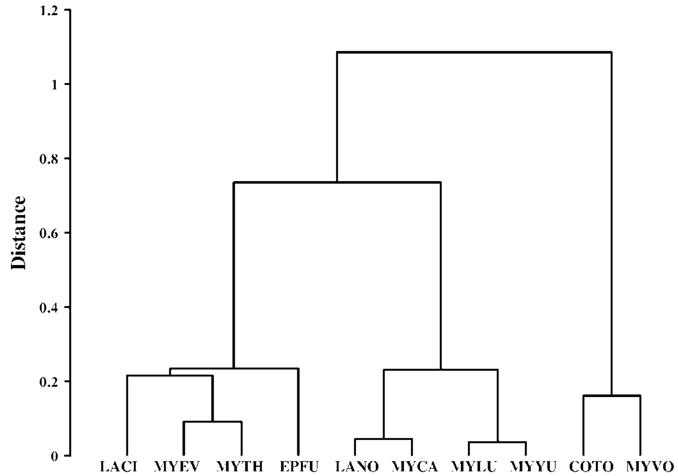

Fig. 1.—Dendrogram resulting from cluster analysis of diet composition of bats in the Oregon Coast Range, summers 2002–2004. (LACI = *Lasiurus cinereus*, MYEV = *Myotis evotis*, MYTH = *M. thysanodes*, EPFU = *Eptesicus fuscus*, LANO = *Lasionycteris noctivagans*, MYCA = *M. californicus*, MYLU = *M. lucifugus*, MYYU = *M. yumanensis*, COTO = *Corynorhinus townsendii*, MYVO = *M. volans*).

insects (Lepidoptera, Araneae, Coleoptera, and Hemiptera). *Lasionycteris noctivagans*, *M. californicus*, *M. lucifugus*, and *M. yumanensis* clustered together, reflecting a generalist strategy with large volumes of insects likely of aquatic origin (Diptera and Trichoptera).

Bat activity and insect captures.—We captured a mean of 815 insects per stream reach per night (*SE* = 116.5). The most commonly captured orders were Diptera (74.5% of individuals), Trichoptera (12.2%), and Lepidoptera (11.9%; Table 4). Body lengths of insects ranged from 1 to 50 mm, with a distribution skewed heavily toward smaller sizes ($\bar{X}$ = 3.8 mm, median = 2 mm). Distributions of body lengths varied greatly among orders of insects (Fig. 2).

Bat activity varied among stream reaches and species. Activity within a single stream reach varied from 3 to 524 min per night ($\bar{X}$ = 169 ± 6.1 min). The majority of activity was by bats in the 2 phonic groups containing small *Myotis* species, MYCA/MYYU ($\bar{X}$ = 111 ± 9.8 min; range = 0–411 min) and MYLU/MYVO ($\bar{X}$ = 32 ± 6.1 min; range = 0–470 min). Little activity was recorded from bats in the remaining phonic groups: MYEV/MYTH ($\bar{X}$ = 2 ± 0.3 min; range = 0–21 min), COTO ($\bar{X}$ = 0.3 ± 0.1 min; range = 0–6 in), and EPFU/LANO/LACI ($\bar{X}$ = 0.9 ± 0.2 min; range = 0–18 min).

The relationship between bat activity and total number of insects captured was relatively weak for all phonic groups (Table 5), indicating that bat activity is more strongly associated with abundance of a subset of insects than with abundance of all insects. Models for the MYCA/MYYU and MYLU/MYVO phonic groups containing explanatory variables pertaining to number of captures of insects in the small size class had the lowest AIC$_c$ scores (Table 5; Fig. 3). For the MYLU/MYVO phonic group, the model with number of captures of small insects was >3 times more likely to be the best model than the next highest ranked model and >11 times more likely than any remaining model. The top-ranked model for this phonic group explained 47 percent of the variation. For the MYCA/MYYU phonic group, the model with number of captures of small insects was 2.5 times more likely to be the best model than the model with abundance of Diptera, >5 times more likely than the model with number of captures of all insects, and >14 times more likely than any remaining model. The model with number of captures of small insects explained 26% of the variation for this phonic group, and the model with number of captures of Diptera explained 21% of the variation.

Table 4.—Number of individuals of common orders of insects captured per stream reach per night in blacklight traps in the Oregon Coast Range, summers 2003 and 2004.

	No. individuals		
Order	$\bar{X}$	*SE*	Range
Coleoptera	5.4	0.66	0–43
Diptera	627.1	115.66	7–9,969
Ephemeroptera	29.6	6.51	0–437
Hemiptera	0.2	0.05	0–3
Homoptera	3.3	0.49	0–29
Hymenoptera	5.1	0.53	0–40
Lepidoptera	68.1	6.66	1–420
Neuroptera	0.1	0.04	0–3
Plecoptera	3.8	1.24	0–135
Trichoptera	79.9	8.92	1–605

For the remaining phonic groups (MYEV/MYTH, COTO, and EPFU/LANO/LACI), the null model had ΔAIC$_c$ < 2 (Table 5). This indicates that none of the explanatory variables we investigated were strongly related to activity of these bats or

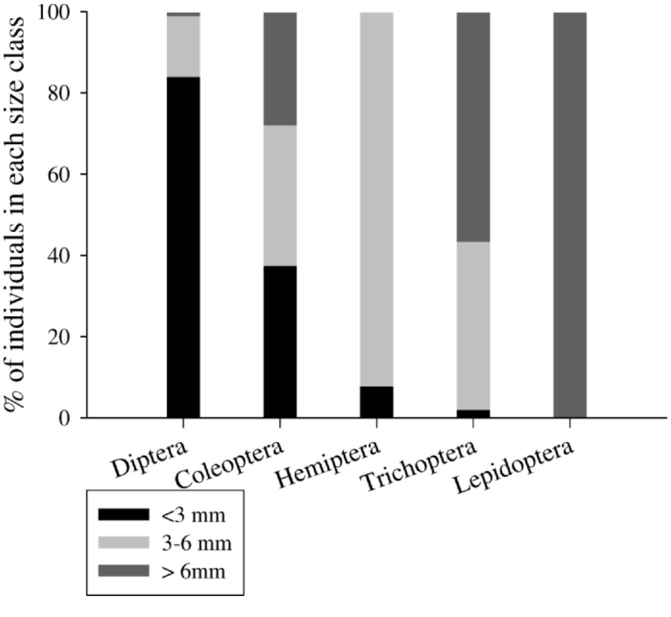

Fig. 2.—Percentage of individuals within each of 3 size classes for nocturnal insects captured in blacklight traps in riparian areas of the Oregon Coast Range, summers 2003 and 2004.

TABLE 5.—Akaike information criterion for small sample sizes (ΔAIC_c) and weight of evidence (w_i) for each candidate model relating activity of bat phonic groups to number of insects captured in riparian areas of the Oregon Coast Range, summers 2003 and 2004. Models receiving substantial empirical support ($\Delta AIC_c \leq 2.0$) are in boldface type.[a]

Explanatory variable in model	MYLU/MYVO		MYCA/MYYU		MYEV/MYTH		COTO		EPFU/LANO/LACI	
	ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i
No. small insects	**0**	**0.67**	**0**	**0.58**	2.5	0.09	3.2	0.08	2.4	0.08
No. medium insects	13.5	0	7.7	0.01	**2.0**	**0.11**	**0**	**0.39**	2.6	0.08
No. large insects	13.6	0	6.8	0.02	2.6	0.08	**1.5**	**0.19**	2.6	0.08
No. Coleoptera	NA	NA	NA	NA	**1.2**	**0.16**	NA	NA	2.6	0.08
No. Diptera	2.2	0.22	**1.9**	**0.23**	NA	NA	NA	NA	NA	NA
No. Hemiptera	NA	NA	NA	NA	2.6	0.08	NA	NA	**0**	**0.27**
No. Lepidoptera	16.5	0	7.5	0.01	2.1	0.10	3.9	0.05	2.6	0.07
No. Trichoptera	10.8	0	7.3	0.01	NA	NA	NA	NA	NA	NA
No. all insects	3.6	0.11	3.6	0.09	2.6	0.08	2.3	0.12	2.6	0.07
Null model	14.0	0	5.3	0.04	**0**	**0.30**	**1.7**	**0.17**	**0**	**0.27**

[a] MYLU = *Myotis lucifugus*; MYVO = *Myotis volans*; MYCA = *Myotis californicus*; MYYU = *Myotis yumanensis*; MYEV = *Myotis evotis*; MYTH = *Myotis thysanodes*; COTO = *Corynorhinus townsendii*; EPFU = *Eptesicus fuscus*; LANO = *Lasiurus cinereus*; LACI = *Lasionycteris noctivagans*. NA indicates that models with this explanatory variable were not included in the candidate set for a particular phonic group.

that activity levels of these bats were too low to arrive at conclusive results.

DISCUSSION

Diets of bats.—Overall, food habits of bats in the Oregon Coast Range were similar to those reported for the same species in other geographic locations. For example, studies across North America have reported that the diet of *E. fuscus* consists of a large proportion of Coleoptera, that *M. lucifugus* feeds on a variety of insects including Diptera and Trichoptera, and that *C. townsendii*, *M. volans*, and *M. evotis* feed predominantly on Lepidoptera (Barclay 1991; Belwood and Fenton 1976; Black 1974; Brigham et al. 1992; Brigham and Saunders 1990; Syme et al. 2001; Whitaker 1972, 2004; Whitaker et al. 1977, 1981). However, we found that Lepidoptera were more prominent in the diet of some species than has been typically reported. For example, *M. lucifugus* (Adams 1997; Barclay 1991; Buchler 1976; Syme et al. 2001) and *E. fuscus* (Brigham and Saunders 1990; Hamilton and Barclay 1998; Whitaker 1972, 1995, 2004) rarely consume Lepidoptera elsewhere but did so in our study area. The prevalence of Lepidoptera in diets in the Oregon Coast Range may be due to their preponderance; Lepidoptera ranked 1st in biomass (Ober 2007) and 3rd in number of captures of orders of insects captured via blacklight traps (Table 4). Spiders comprised a greater amount of the diet of bats in our study than from other areas for almost all species we examined. Moreover, we found that spiders comprised a sizeable proportion of the diets of several species considered to be aerial insectivores (Verts and Carraway 1998). Because spiders are flightless, evidence of their presence in bat diets could have been the result of specific foraging strategies employed by bats in our study area (Faure and Barclay 1994; Fenton 1990; Fenton and Bell 1979; Ratcliffe and Dawson 2003).

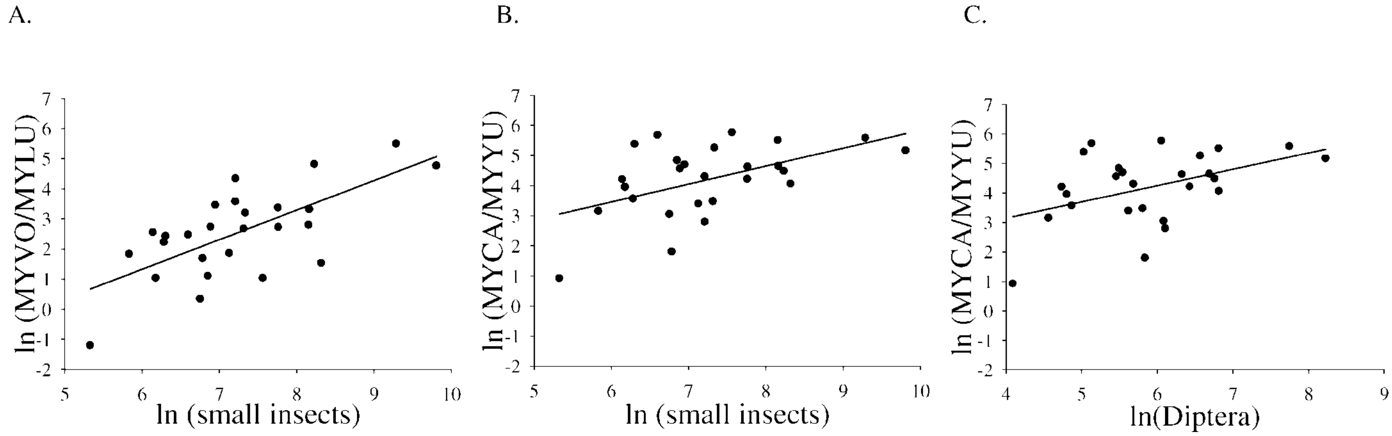

FIG. 3.—Relationships between bat activity and number of captures of nocturnal insects in riparian areas of the Oregon Coast Range for models that received substantial support ($\Delta AIC_c \leq 2.0$). The x-axes portray mean number of insects captured per stream reach per night, ln-transformed. The y-axes portray mean number of minutes during which bat activity was recorded per stream reach per night, ln-transformed. A) Activity of the phonic group consisting of little brown and long-legged myotis versus number of captures of small insects. B) Activity of the phonic group consisting of California and Yuma myotis versus number of captures of small insects. C) Activity of the phonic group consisting of California and Yuma myotis versus number of captures of Diptera.

Alternatively, spiders that are ballooning or suspended in open areas (Best et al. 1997; Schulz 2000) may be more vulnerable to predation by bats in the Pacific Northwest than in other regions.

Isoptera ranked 4th in percent volume and 8th in frequency of occurrence across all species of bats combined. This implies that Isoptera were not consumed by many individual bats, but those bats that did eat Isoptera consumed large quantities. The tendency of winged termites from all colonies in an area to leave nests simultaneously promotes outbreeding in termites (Weesner 1965) and provides an opportunistic food resource for bats (Redford and Dorea 1984). Although bats may rarely encounter these aggregations, they appear to take advantage of profitable feeding opportunities during these rare events (Gould 1978). Isoptera consumption was detected in the diets of only 26 bats collected during 2003, but 22 of these samples were collected over 4 consecutive nights in August and the average volume of Isoptera in these samples exceeded 50%.

In contrast, Hemiptera ranked 7th in percent volume and 3rd in frequency of occurrence across all species of bats combined. This suggests that Hemiptera were consumed by more individual bats than were most orders of insects, but usually in small quantities. Hemiptera were not abundant among captures by blacklight traps. Although blacklight traps may not have effectively sampled Hemiptera, the high frequency of occurrence but low volume of occurrence suggests that bats may have a preference for these insects, regularly consuming them when they are encountered. High nitrogen content relative to other insect orders (Fagan et al. 2002; Studier and Sevick 1992) may make Hemiptera a particularly valuable food resource.

One means by which resources are partitioned among species within a community is through dietary specialization (Hutchinson 1959; Schoener 1974). By grouping species according to similarities in food resource selection, community structure and similarities in foraging adaptations among species becomes clearer. The cluster analysis partitioned the 10 species of bats that use riparian areas in western Oregon into 3 foraging guilds (Fig. 1). Diets of bats from the 2 larger foraging guilds (those containing 4 species each) were generalist in nature and differed from one another in composition. Bats in 1 of these groups fed primarily on insects of terrestrial origin, and bats in the other fed mostly on insects likely of aquatic origin. The guild with only 2 species of bats, *C. townsendii* and *M. volans*, was distinguished from the others by a high degree of specialization on a single order of insects, Lepidoptera.

Bat activity and insect captures.—Morphology, flight patterns, echolocation call structure, and feeding behavior of bats are strongly linked (Barclay and Brigham 1991; Bogdanowicz et al. 1999; Norberg and Rayner 1987; Schnitzler and Kalko 2001). Morphology influences flight capabilities, which in turn constrain the ecological roles bats can fill by limiting their ability to forage in certain habitats (Norberg and Rayner 1987). Similarly, body size influences the frequency of echolocation calls bats produce, which in turn constrains both the size of prey bats can detect and the range over which they can detect them (Barclay and Brigham 1991; Bogdanowicz et al. 1999; Jones and Rydell 2003; Schnitzler and Kalko 2001). These ecomorphological relationships are consistent with many of the patterns we observed between bat and insect activity.

Activity by the smallest species in the bat community of the Oregon Coast Range (*M. californicus*, *M. yumanensis*, and *M. lucifugus*) was most strongly associated with captures of insects in the small size class. Low wing loading, low aspect ratios, and rounded wing tips allow these species to perform maneuverable flight (Norberg and Rayner 1987) and more effectively pursue small insects (Dudley 2002; Nachtigall 1968). The high-frequency echolocation calls of these species are best suited for locating small targets at close range (Jones and Rydell 2003; Schnitzler and Kalko 2001). The relatively small size of the heads and gapes of these species also limits the size of prey they can successfully capture (Fenton 1989). Thus, these species possess a combination of traits that predisposes them to specialize on small prey. In our traps, 99% of the insects in the small size class (0–2 mm) were Diptera, so it is not surprising that activity of these species was also highly correlated with number of captures of Diptera. The fact that insects in the small size class were nearly exclusively Diptera indicates that bats morphologically constrained to foraging on small insects have little choice but to feed on insects of this order, and the high correlation ($r = 0.968$) between captures of Diptera and of small insects limited our ability to distinguish prey selection based on size or taxon for these species.

The 4th species of bat in the 2 phonic groups whose activity was highly correlated with number of captures of small insects, *M. volans*, differs from the other 3 in diet and morphology. Given the greater affinity for *M. lucifugus* to riparian areas and the greater dietary dependence of *M. lucifugus* on insects of aquatic origin, we suspect that *M. volans* produced a small proportion of the calls we recorded for the MYLU/MYVO phonic group.

Activity of the remaining species of bats, *C. townsendii*, *M. evotis*, *M. thysanodes*, *E. fuscus*, *Lasionycteris noctivagans*, and *Lasiurus cinereus*, was extremely low in the riparian habitats of our study area, limiting our ability to elucidate relationships between bat activity and insect abundance. Furthermore, blacklight traps may not be an effective means of sampling insects consumed by some of these species, for example, *M. evotis* and *M. thysanodes* often glean prey from canopy foliage (Barclay 1991; Faure and Barclay 1994; Whitaker et al. 1977). Finally, the disparity in food selection among bat species in the EPFU/LANO/LACI phonic group may be responsible for the absence of strong associations between activity of these bats and number of captures of any insect taxon. Associations may have been more likely to emerge if we were able to distinguish echolocation calls made by each of these 3 species, and conduct an independent analysis for each.

It has been suggested that the morphology and echolocation calls of larger species, such as *E. fuscus*, *Lasionycteris noctivagans*, and *Lasiurus cinereus*, should predispose them to specialize on larger prey items (Barclay 1985; Barclay and Brigham 1991; Jones and Rydell 2003). If these species select larger prey, the number of prey items required to meet energetic demands may be low enough that it is not profitable for these species to expend energy searching for areas with high prey concentrations, in contrast to those species that feed on smaller prey items that provide so little energy per unit that bats specializing on them must locate areas with high abundances of prey to meet energetic demands (Aldridge and Rautenbach 1987). Alternatively, the fast flight of these larger species may facilitate a relatively high encounter rate with insects such that these bats are able to maintain energy balance in habitats with lower insect abundances than is possible for slower-flying bats with lower insect encounter rates (Aldridge and Rautenbach 1987). The greater distances these larger species fly per night (Arbuthnott and Brigham 2007; Brigham 1991; Campbell et al. 1996; Mattson et al. 1996) may lead to less localization of foraging effort than is typical of smaller, slower-flying species that use smaller nightly ranges (Brigham et al. 1997; Waldien et al. 2000; Weller and Zabel 2001). This would in turn lead to weaker correlations between activity of these larger bats and local insect abundance than is typical of smaller bats.

Although activity by bats in every phonic group was more strongly associated with number of captures of a subset of insects than with number of captures of all insects, we found only partial support for our hypothesis that high mobility and high energetic demands of bats would result in strong correlations between use of stream reaches and abundance of potential invertebrate prey. Although we found strong associations between activity of small *Myotis* bats and number of captures of small insects, activity by larger *Myotis* and non-*Myotis* species was not associated with number of captures of insects of any category investigated. This lack of association may be due in part to shortcomings inherent to the methodologies employed to investigate bat diets, insect activity, and bat activity. For example, diet analyses based on prey remains identified in guano may be biased toward more-chitinous insects (Rabinowitz and Tuttle 1982), bats may select prey according to greater taxonomic resolution than we were able to discern, and the lumping of bat species with dissimilar diets into phonic groups with similar echolocation calls may have contributed to a lack of clear associations. We recommend that future studies employ different methodologies to investigate the relative importance of prey size versus prey taxon in prey selection by bats.

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