Prey availability and foraging activity of grassland bats in relation to urbanization

Author(s): Joanna L. Coleman and Robert M. R. Barclay

Source: Journal of Mammalogy, 94(5):1111-1122. 2013.

Published By: American Society of Mammalogists

URL: http://www.bioone.org/doi/full/10.1644/12-MAMM-A-217.1

Journal of Mammalogy, 94(5):1111–1122, 2013

Prey availability and foraging activity of grassland bats in relation to urbanization

JOANNA L. COLEMAN* AND ROBERT M. R. BARCLAY

Department of Biological Sciences, University of Calgary, 2500 University Drive NW, Calgary, Alberta T2N 1N4, Canada

* *Correspondent: dbscmj@nus.edu.sg*

In general, urbanization negatively impacts wildlife, including bats. However, most urban ecology studies have been conducted in forested biomes and responses of grassland fauna to urbanization are poorly understood. Grasslands are flat, largely treeless, and represent challenging environments to insectivorous bats, which need vertical landscape elements for roosts and often prefer to forage in clutter or along edges. Grasslands may be even less hospitable to bats where agriculture is the dominant land use, as in the Great Plains of North America where intensive pesticide use and livestock grazing are likely detrimental to insects. Compared to agricultural areas that surround them, cities in the Great Plains offer greater structural complexity and an absence of agriculture. We investigated the hypothesis that urbanization benefits bats in the Canadian Prairies by increasing access to insect prey and foraging habitat. In 2007 and 2008, we used sticky traps to sample availability of nocturnal insects, and echolocation detectors to record foraging activity by bats, in and around the city of Calgary, Alberta, Canada. Our data did not support our predictions. Insect biomass and diversity were greatest in rural areas, and foraging activity by bats was influenced more by temperature than by urbanization. Although urbanization does not seem to benefit insects or their bat predators, we found no evidence that it is detrimental to bats in prairie grasslands.

Key words: Alberta, Canadian Prairies, Chiroptera, feeding, grasslands, insects, urban

DOI: 10.1644/12-MAMM-A-217.1

Urbanization, arguably the most destructive human agent of habitat change (McIntyre and Hobbs 1999), is a top contributor to biodiversity loss (Czech et al. 2000), resulting in a growing interest in the ecology of urban wildlife (Shochat et al. 2006). However, the field of urban wildlife ecology retains several key biases. Most studies have been conducted in forested biomes, with few in other regions, notably grasslands (e.g., Marzluff et al. 2001). This is a major gap in North American research on urbanization because the Great Plains has an especially high rate of urbanization (Cromartie 1998). Because urbanization in grasslands increases both tree cover and structural complexity of habitat, the opposite of the process in forested areas (van der Ree and McCarthy 2005), it may affect species in grasslands in unique ways (Gehrt and Chelsvig 2003). Most studies also address synecological questions (Adams 2005), for example, comparing urban and nonurban biodiversity. Autecological studies are required to expose the mechanisms behind urbanization-related changes in community composition (Marzluff et al. 2001; Shochat et al. 2006). Finally, more research has focused on birds than on other vertebrates (Garden et al. 2006). Among studies of mammalian responses to urbanization, few have examined bats (e.g., Garden et al. 2006) despite their importance to mammalian diversity and the ecosystem services they provide (Kunz and Fenton 2003). Also, the slow life histories of bats (i.e., long life span and slow reproductive rate—Barclay and Harder 2003) make bats slow to recover from habitat change (Racey and Entwistle 2003) and useful bioindicators of habitat quality (Jones et al. 2009).

Observations of reduced bat abundance and diversity in response to urbanization (Geggie and Fenton 1985; Gaisler et al. 1998; Avila-Flores and Fenton 2005; Hourigan et al. 2006; Duchamp and Swihart 2008) suggest that urbanization is detrimental to most bats. Urban bat assemblages are usually dominated by species that readily use artificial roosts (Duchamp and Swihart 2008), and decreased diversity of bats in urban areas in forested ecoregions has been attributed to reduced availability of natural roosts (van der Ree and McCarthy 2005). Urbanization in a more homogeneous grassland landscape likely improves access to trees and buildings in which most bats roost, and could thus enhance bat diversity. Landscape heterogeneity and roost diversity are key factors in the distribution and diversity of Nearctic bats (Humphrey 1975). However, most Nearctic bats are insectivorous, and availability of insects influences local distribution patterns, abundance, and diversity of bats (e.g., Avila-Flores and Fenton 2005).

We assessed the hypothesis that urbanization benefits grassland bats (in the Canadian Prairies) by improving conditions for foraging by increasing availability of prey and density of trees. Although urbanization can negatively affect insects (McIntyre 2000), most knowledge about how insects respond to urbanization comes from work in forested biomes (e.g., Morse et al. 2003; Dodds et al. 2004). If riparian tree cover mitigates effects of urbanization on macroinvertebrates (Moore and Palmer 2005), then insects in prairies may respond differently given increased tree density in prairie cities. In addition, intensive agriculture in the Prairies is detrimental to many insects through effects of cattle grazing (e.g., Rambo and Faeth 1999) and use of agricultural pesticides (e.g., Wickramasinghe et al. 2004). These pressures are absent in cities.

By increasing tree density, urbanization in the Prairies should also increase foraging activity by bats. Trees are important to foraging bats, especially in natural or cultivated grasslands (Lumsden and Bennett 2005). Trees provide edges, which some bats prefer (e.g., Patriquin and Barclay 2003), and cover, which may reduce flight costs and predation risk (e.g., Verboom and Spoelstra 1999). We therefore predicted that insects are more abundant and diverse in urban than in nonurban areas in the Prairies, and that urban bats have higher rates of feeding than do nonurban bats.

Materials and Methods

Study area and species.—Our study was in the South Saskatchewan River basin, with Calgary, Alberta, Canada (51°02′45″N, 114°03′27″W), as our focal city. Eight species of insectivorous bats occurred in our study area. *Eptesicus fuscus*, *Myotis ciliolabrum*, *M. evotis*, *M. lucifugus*, and *M. volans* are year-round residents that hibernate locally. *Lasionycteris noctivagans*, *Lasiurus borealis*, and *Lasiurus cinereus* are migratory and are most abundant during late-summer migration (Coleman and Barclay 2012). All species exhibit dietary flexibility according to temporal and spatial fluctuations in prey availability (Whitaker 2004). All but 1 species capture prey by aerial hawking (Saunders and Barclay 1992; Fenton and Bogdanowicz 2002). Of these, the 4 largest (*L. cinereus*, *L. borealis*, *L. noctivagans*, and *E. fuscus*) forage in the open or along edges (Patriquin and Barclay 2003), and *E. fuscus* and both *Lasiurus* species may show a propensity for hunting around streetlights (Furlonger et al. 1987). *Myotis* species can forage in more cluttered habitat types or low over water (Fenton and Bogdanowicz 2002). *M. evotis* hunts by gleaning insects from surfaces and catching them in the air (Faure and Barclay 1994).

Study sites.—We were interested in effects of urbanization, not those of habitat per se. Thus, given that foraging prairie bats are largely restricted to treed, riparian habitat (Holloway and Barclay 2000), all sites were located along rivers and tributaries within the Bow, Red Deer, and Oldman rivers subbasins. We divided our study area into 3 zones: rural, transition, and urban. Urban sites ($n = 10$) were within Calgary city limits and completely surrounded by urban development, rural sites ($n = 9$) were ≥ 40 km from city limits, and transition sites ($n = 10$) were either in the city, but not bounded on all sides by development, or between city limits and the rural zone (Figs. 1 and 2, and Supporting Information S1, DOI: 10.1644/12-MAMM-A-217.S1). Our study sites and selection process are described in detail elsewhere (Coleman and Barclay 2012).

Insect sampling.—In 2007 and 2008, we assessed abundance and diversity of nocturnal aerial insects. From early June through late August, we sampled insects at 1 site per night (weather permitting), alternating zones each night, 3 nights per week, to give roughly equal sampling effort in all 3 zones. We aimed to sample all sites once each year, but sampled some ($n = 7$) only once over both years and others ($n = 10$) more than once within a year, with at least 5 weeks between subsequent visits. Because levels of replication varied among sites, we did not use repeated-measures analysis, but instead treated each sampling night as an independent observation. This is justified given within-site variation in prey availability for insectivorous bats (Whitaker et al. 2009).

To capture insects, we used sticky traps (described by Barclay [1985]). Each night, from sunset to sunrise, we set up 3 traps; 2 suspended above the ground (2 m and 4 m) and 1 floating on the water. One of us (JLC) identified each specimen to order (to family when possible). Length was measured (with a ruler, under a microscope) from the head (not including antennae) to the tip of the abdomen (not including cerci) to the nearest 0.25 mm. Body length data were used to estimate biomass of each insect using order- and family-specific formulae (Sample et al. 1993; Hódar 1996). We only considered specimens 2–29 mm in body length, because smaller insects are unlikely to be detected by bats (Anthony and Kunz 1977) and larger ones are unlikely to be consumed (Barclay 1985). We calculated mean biomass per trap per night as a measure of prey abundance.

Bat foraging activity.—We recorded echolocation activity on Anabat II bat detectors (division ratio set to 16; Titley Electronics, New South Wales, Australia) coupled to zero-crossing analysis interface modules and, in 2007, also on Anabat SD1 detectors (Titley Electronics), from late May through mid-September each year. Detectors recorded continuously from before sunset until after sunrise. We minimized biases inherent in the Anabat system following Larson and Hayes (2000) and Fischer et al. (2009).

During each sampling week in 2007, we simultaneously monitored 3 sites (1 per zone) on 4 nights and in our insect sampling site only on 2 nights, rotating among sites within each zone to give a roughly equal number of sampling nights per site. In 2008, we monitored activity simultaneously in all 3

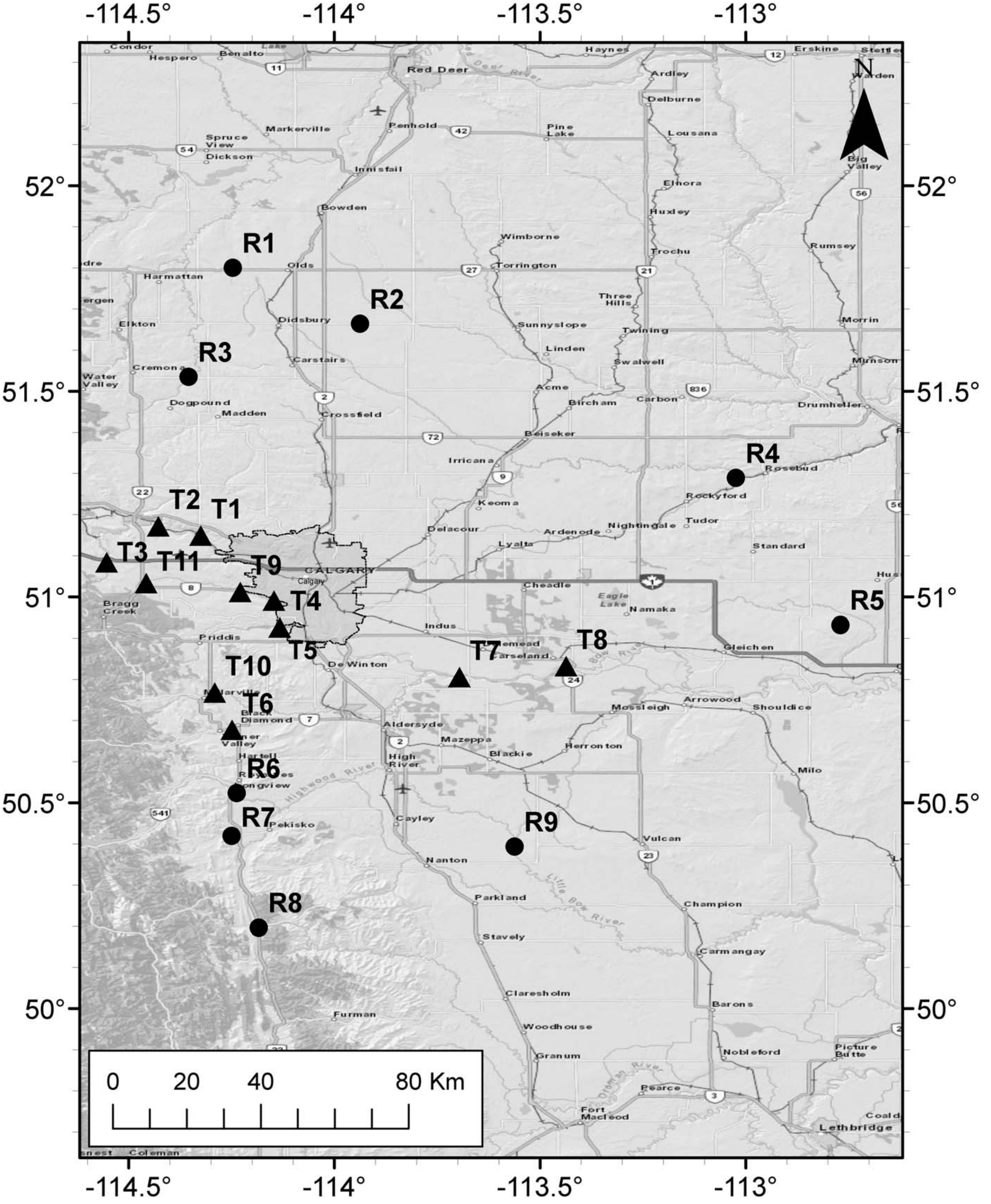

FIG. 1.—Map showing locations of all rural (circles) and transition (triangles) sites in the vicinity of Calgary, Alberta, Canada.

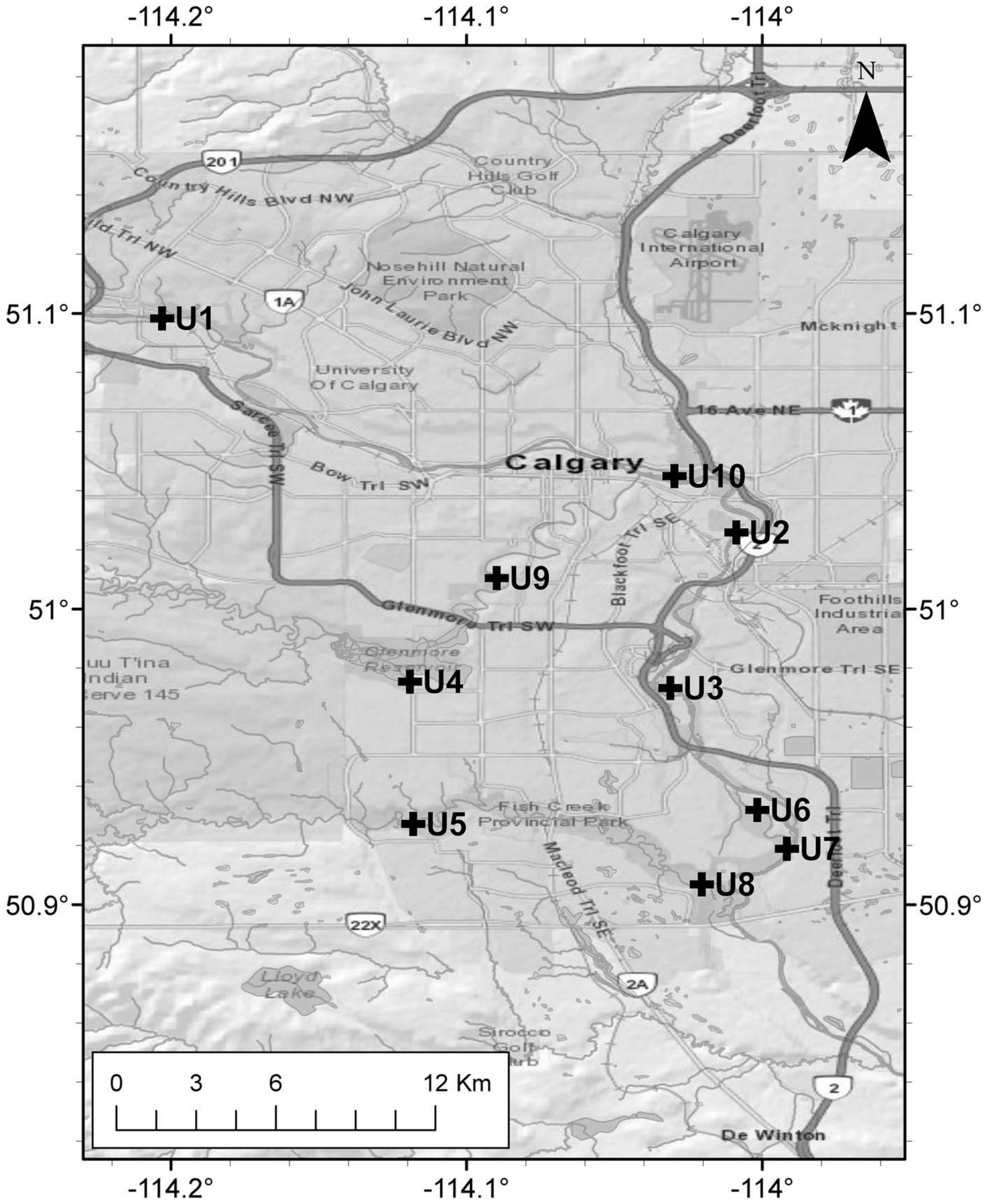

Fig. 2.—Map showing locations of all urban (plus signs) sites in Calgary, Alberta, Canada.

zones on nights when we sampled insects in the rural zone, and only in our insect sampling site on other nights.

Environmental variables.—To account for potential effects of weather on insect availability and bat activity, we recorded wind speed every 30 min while insect traps were being operated using a Kestrel 4000 weather meter (Nielsen-Kellerman, Boothwyn, Pennsylvania). We hung Hobo UA-002-08 data loggers (Onset Computer Corporation, Pocasset, Massachusetts) above each bat detector to record temperature every 30 min. We obtained sunset, sunrise, and civil twilight times, and moon illumination information for our study area from the United States Naval Observatory (2009).

Acoustic data analyses.—One of us (JLC) analyzed acoustic data using Anamusic 3.4 (Corben 2000) to convert digital files to audio files, allowing each one to be heard in Winamp 5.31 (Nullsoft, Inc. 2006) while viewing it in Analook for DOS 4.9j (Corben 2004). We defined a bat pass as a sequence of at least 2 echolocation calls (Thomas 1988) separated by no more than 2 s (for *L. cinereus*) or 1 s (for other species). For each file, we recorded number of passes and assigned each to 1 of 5 categories of bats: *L. cinereus*, *E. fuscus*/*L. noctivagans*, *L. borealis*, *Myotis* spp., and unknown, using qualitative and quantitative methods (described by Coleman and Barclay [2012]). We counted feeding buzzes (sequences of calls having increasing pulse repetition rates, culminating in a rapid burst of calls as the animal closes in on its target [Griffin et al. 1960]) as a measure of feeding activity.

Statistical analyses.—To compare prey availability among zones, we used a general linear model (version 7.0; SAS Institute Inc., Cary, North Carolina) with biomass per trap-night (hereafter, insect biomass) as the dependent variable. For this and all other analyses, we used a 2-tailed test and a rejection criterion of 0.05. Preliminary tests revealed that insect biomass was unaffected by illuminated fraction of the moon or by average wind speed. Thus, our model included zone and year as fixed factors and average nightly temperature as a covariate. We transformed the dependent variable (ln[biomass per trap + 1]) and covariate (ln-temperature) to improve linearity. For this and all other regression analyses, we removed nonsignificant interaction terms sequentially from the saturated model to obtain a reduced model with no nonsignificant interactions (Engqvist 2005). For all significant effects, we conducted post hoc Tukey's honestly significant difference tests (Zar 1999). Because *M. lucifugus* was the most common bat in our study area (Coleman and Barclay 2012), we repeated the analysis from the perspective of this species by only considering insects $\leq$ 10 mm in body length (the prey available to it—Anthony and Kunz 1977).

We calculated 5 measures of insect-assemblage diversity for each zone (Coleman 2010), using the program Species Diversity and Richness 4.1.2 (Seaby and Henderson 2006). However, because results and conclusions were consistent for all measures, we present only 2 here: order richness (O_{obs}; number of orders captured, averaged across nights), and the Shannon–Wiener index (H), incorporating species richness and evenness (Stevens and Willig 2002). We estimated jackknifed standard errors for H for each zone across nights, and ran paired randomization tests (Solow 1993) to determine whether zones differed significantly. We compared O_{obs} among zones with a 1-way analysis of variance in JMP (version 7.0; SAS Institute Inc.), with post hoc Tukey's honestly significant difference tests for significant effects.

To further assess among-zone variation in insect diversity, we used contingency table analyses of the association between zone and insect category in SPSS (version 16.0; SPSS, Inc., Chicago, Illinois). Each analysis had 5 insect categories: the 4 most commonly trapped orders and a category containing all others. The 3rd and 4th most common orders differed between years, so we performed separate analyses for each year. In 2008, we combined Coleoptera and Hemiptera because they were tied for the 4th most common order. Because chironomids (Diptera) are useful indicators of effects of urbanization on stream integrity (e.g., Gresens et al. 2007), and are important in the diet of *M. lucifugus* (e.g., Belwood and Fenton 1976), we performed a hierarchical 3-way log-linear analysis considering effects of zone and year on chironomid proportions.

We assessed variation in foraging activity by bats (total number of buzzes per night), using PROC GENMOD (version 9.2; SAS Institute Inc.). We fitted 2 regression models that had zone and year as fixed factors, but each had different covariates. Model 1 assessed hourly foraging rates, that is, controlled for night length. Model 2 assessed foraging rates in relation to nightly bat activity, that is, controlled for number of passes per night. We included average nightly temperature (untransformed) as a covariate in model 1, but not in model 2. Given the strong, positive correlation between temperature and bat activity (Coleman 2010), including both covariates would violate the no multicolinearity assumption. We analyzed both models considering 1st the whole bat assemblage and then each bat category (except unknowns) separately, to determine if variation in foraging activity among zones was taxon-specific. We conducted each of the full factorial models with a Poisson or a negative binomial distribution (and a log-link function), and compared the results in terms of deviance/*d.f.* (Pedan 2001), and Akaike's information criterion. Negative binomial regression models consistently gave better fit. Because we measured foraging activity more than once at most sites, we evaluated the appropriateness of repeated-measures analysis. We tested effect of site on buzzes per hour and per pass with random effects models in JMP (version 7.0; SAS Institute Inc.), repeating each test for all bats and for each bat category. In every case, site was not significant, so we removed the term.

RESULTS

We captured 3,546 insects belonging to 12 orders (Table 1) and collected 161 nights of acoustic data. All nights had bat activity (47,939 passes total) and 124 had feeding buzzes (3,555 total).

Insects.—Mean insect biomass was higher in the rural zone than in the transition zone (model $R^2_{\text{adj}} = 0.60$, $F = 19.53$, $P < 0.0001$, $n = 50$ nights; zone: $F_{2,45} = 4.49$, $P = 0.02$; Fig. 3).

TABLE 1.—Number and type of insects captured in each zone (number of sampling nights), and measures of insect-assemblage diversity (2007–2008) in and near Calgary, Alberta, Canada, in relation to urbanization. Standard errors are jackknifed values except order richness. Different superscript letters indicate significant differences among zones based on randomization tests, with *P*-values < 0.01 in all cases. Note that diversity analyses only considered 14 nights in the urban zone.

	Rural (18)	Transition (16)	Urban (16)
Order			
Diptera (flies)	794	381	1,146
Trichoptera (caddisflies)	339	31	618
Hemiptera (bugs)	37	41	16
Ephemeroptera (mayflies)	26	3	9
Coleoptera (beetles)	29	3	7
Lepidoptera (moths)	22	7	5
Hymenoptera (ants, bees, and wasps)	13	2	1
Plecoptera (stoneflies)	4	0	0
Neuroptera (lacewings)	4	0	0
Psocoptera (booklice and barklice)	0	0	2
Dermaptera (earwigs)	0	0	1
Diversity indexes			
Least-squares mean order richness (O_{obs}) ± *SE*	4.33 ± 0.40^{a}	2.56 ± 0.42^{b}	$3.14 \pm 0.45^{a,b}$
Shannon–Wiener diversity (*H*) ± *SE*	1.07 ± 0.08^{a}	0.71 ± 0.18^{b}	0.70 ± 0.21^{b}

Variation in insect biomass was best explained by temperature, which had a strong positive effect ($F_{1,45} = 57.09$, $P < 0.0001$). The reduced model ($R^2_{adj} = 0.53$, $F = 15.01$, $P < 0.0001$, $n = 50$ nights) considering the subset of insects available to *M. lucifugus* indicated that insect biomass did not differ among zones ($F_{2,45} = 2.44$, $P = 0.10$; Fig. 3). Insect biomass was strongly influenced by temperature ($F_{1,45} = 48.28$, $P < 0.0001$), and was higher in 2008 than in 2007 ($F_{1,45} = 6.47$, $P = 0.01$; Fig. 3).

The most commonly captured insects were dipterans (especially chironomids), whose numbers exceeded those of all other orders combined, followed by trichopterans (Table 1). This was true in all zones and on most nights. We captured more orders of insects in rural and urban zones (9) than in the transition zone (7; Table 1), and the rural zone had the most diverse insect assemblage (see also Coleman 2010). Mean richness of orders was higher there (4.33 ± 0.40) than in the other 2 zones (transition 2.56 ± 0.42; urban 3.14 ± 0.45), significantly so compared to the transition zone (Table 1). The diversity index (*H*) was higher in the rural zone (1.07 ± 0.08) than in the other 2 zones (transition 0.71 ± 0.18; urban 0.70 ± 0.21), which did not differ (Table 1).

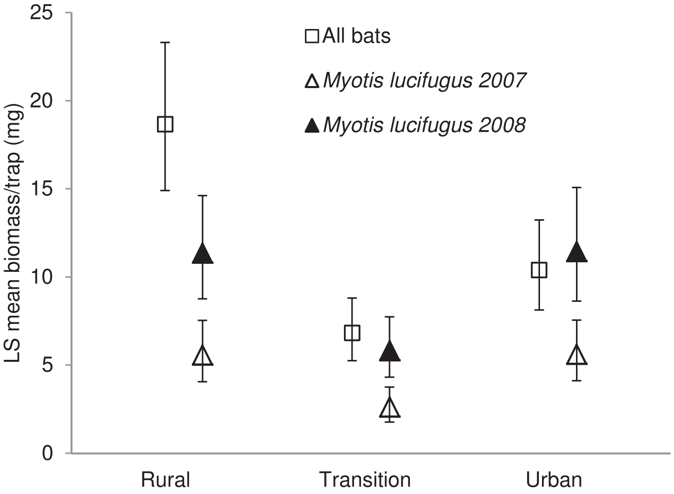

FIG. 3.—Variation in mean insect abundance (biomass/trap*night) considering insects potentially available to all bats and to *Myotis lucifugus* among zones and, for *M. lucifugus*, between years, near Calgary, Alberta, Canada. Points represent back-transformed least-squares means and bars represent back-transformed standard errors, thus resulting in asymmetrical error bars.

Zone affected distribution of insect categories ($\chi^2_8 > 37.0$, $P < 0.001$, in each year), and all pairwise comparisons of zones were significant (Table 2). Proportion of dipterans differed among zones in 2007 ($\chi^2_2 = 71.20$, $P < 0.001$) and 2008 ($\chi^2_2 = 10.20$, $P = 0.006$), and was lowest in the rural zone (Fig. 4). Proportion of trichopterans differed among zones in 2007 ($\chi^2_2 = 122.0$, $P < 0.001$) and 2008 ($\chi^2_2 = 7.29$, $P = 0.03$), and was lowest in the transition zone (Fig. 4). In 2007, zones differed in proportion of hemipterans ($\chi^2_2 = 25.22$, $P < 0.001$), which was lowest in the rural zone (Fig. 4), but not in proportion of beetles ($\chi^2_2 = 5.09$, $P = 0.08$; Fig. 4). In 2008, zones differed in proportion of ephemeropterans ($\chi^2_2 = 10.36$, $P = 0.006$), which were most abundant in the rural zone (Fig. 4). Proportion of hemipterans and coleopterans (combined) differed among zones in 2008 ($\chi^2_2 = 10.74$, $P = 0.005$), when they were least abundant in the urban zone (Fig. 4).

The log-linear analysis of chironomid proportions produced a final model that retained all effects, because the zone*year*-insect-category interaction was significant ($\chi^2_2 = 23.14$, $P < 0.001$). We decomposed the 3rd-order term into 2-way tables for each year, and the zone*insect category interaction was significant in both ($\chi^2_2 > 23.0$, $P < 0.001$), as were all pairwise comparisons of zones, except for transition versus urban in 2008 (Table 2). Proportion of chironomids was lowest in the rural zone, and higher in the transition than in the urban zone in 2007, but not in 2008 (Fig. 4).

Table 2.—A) Results of pairwise chi-square tests comparing zones in terms of relative proportions of insects belonging to 5 categories captured in and near Calgary, Alberta, Canada, in 2007 (n = 1,074 individuals) and 2008 (n = 1,409 individuals). Both analyses considered dipterans, trichopterans, and a combined category representing all other orders of insects. Additionally, the 2007 analysis considered hemipterans and coleopterans, and the 2008 analysis considered ephemeropterans and a combined category with coleopterans and hemipterans, which were tied for the 4th most common insect order. B) Results of pairwise chi-square tests comparing zones in terms of relative proportions of chironomids and nonchironomid insects.

	2007		2008	
	Transition	Urban	Transition	Urban
A) Proportions among all orders				
Rural				
χ^2	124.8	41.39	10.39	27.15
d.f.	4	4	4	4
P-value	< 0.001	< 0.001	0.03	< 0.001
Transition				
χ^2		9.11		16.34
d.f.		3[a]		2[b]
P-value		0.03		< 0.001
B) Proportions of chironomids				
Rural				
χ^2	103.4	22.34	6.83	22.60
d.f.	1	1	1	1
P-value	< 0.001	< 0.001	0.009	< 0.001
Transition				
χ^2		10.09		0.68
d.f.		1		1
P-value		0.001		0.41

[a] We omitted 1 category because expected frequencies were less than 5 in > 20% of cells.

[b] We omitted 2 categories because expected frequencies were less than 5 in > 20% of cells.

Foraging activity.—For all bats (reduced model 1; χ^2 = 143.90, *d.f.* = 128, deviance/*d.f.* = 1.23, n = 136 nights), foraging activity increased as a function of night length (χ^2_1 = 6.62, P = 0.01). The significance of zone*temperature (χ^2_2 = 15.42, P = 0.004), indicated that effects of zone and temperature must be interpreted in light of this interaction (Engqvist 2005). At the average level of the covariate (11.7°C), we recorded fewer buzzes per night in the transition zone than in the other 2, between which foraging activity did not differ (Fig. 5a). We estimated ranges of temperatures over which the zone effect was significant by a lack of overlap between the upper individual 95% confidence limits for predicted values of the transition zone, and the lower limits for predicted values in the other 2 zones. Zone had a significant effect when mean nightly temperature was < 12.5°C, and the temperature effect was positive in the transition zone, negligible in the urban zone, and slightly (but not significantly) negative in the rural zone.

Results of the reduced model 1 for *Myotis* spp. (χ^2 = 148.87, *d.f.* = 128, deviance/*d.f.* = 1.20, n = 136 nights) were analogous to those for all bats (year: χ^2_1 = 2.02, P = 0.16, hours: χ^2_1 = 4.56, P = 0.03, zone*temperature: χ^2_2 = 9.73, P = 0.007; Fig. 5a). Model 1 results for *E. fuscus*/*L. noctivagans* (χ^2 = 126.21, *d.f.* = 130, deviance/*d.f.* = 0.86, n = 136 nights) were different in that there was more foraging activity in the urban than in the other 2 zones, between which it did not differ (Fig. 5a), and this was true regardless of temperature. Foraging activity increased with night length (χ^2_1 = 9.60, P = 0.002), but not with temperature (χ^2_1 = 0.48, P = 0.49).

Foraging activity for the entire bat assemblage (reduced model 2; χ^2 = 149.31, *d.f.* = 140, deviance/*d.f.* = 1.15, n = 145 nights) was strongly influenced by bat activity, that is, passes per night (χ^2_1 = 143.21, P < 0.0001). Year and zone effects were not significant (year: χ^2_1 = 0.82, P = 0.37; zone: χ^2_2 = 1.00, P = 0.61; Fig. 5b). Foraging activity by *Myotis* spp. was influenced in a similar manner (reduced model 2; χ^2 = 128.21, *d.f.* = 120, deviance/*d.f.* = 1.11, n = 125 nights). *Myotis* spp. activity was the only variable that explained a significant proportion of the variation in foraging activity (χ^2_1 = 103.52, P < 0.0001). Results for *E. fuscus*/*L. noctivagans* (χ^2 = 131.33, *d.f.* = 139, deviance/*d.f.* = 0.81, n = 144 nights) were again similar in that nightly activity explained most of the variation in foraging activity (χ^2_1 = 63.87, P < 0.0001), and foraging activity did not differ significantly among zones (χ^2_2 = 3.29, P = 0.19; Fig. 5b). However, variation in foraging activity by *E. fuscus*/*L. noctivagans* was distinct in that there was significantly more foraging activity in 2008 than in 2007 (χ^2_1 = 3.99, P = 0.046; Fig. 5b).

In summary, insect availability for all bats was highest in the rural zone and lowest in the transition zone, but not different between the urban and rural or the urban and transition zones. Biomass of insects potentially available to *M. lucifugus* did not vary among zones. The rural insect assemblage was the most diverse, and the one least dominated by dipterans in general and chironomids in particular. Foraging activity by all bats and by *Myotis* spp., controlled for night length, was lowest in the transition zone, but only on cooler nights. Hourly foraging by *E. fuscus*/*L. noctivagans* was highest in the urban zone, regardless of temperature. Zone had no effect on foraging activity after controlling for bat activity.

Discussion

Whether insectivorous bats respond positively or negatively to urbanization should, to some extent, depend on the response of their prey. We hypothesized that urbanization increases the availability of prey to bats in the Prairies, where insects may respond negatively to the dominant land uses. Calgary has riparian buffers that are moderately treed (Clipperton et al. 2003) and fairly continuous (Bow River Basin Council 2005) and lacks agriculture. Therefore, we expected urban assemblages of insects to be more abundant and diverse than those in nonurban areas. Our data do not support either prediction. The lack of a difference in insect biomass between urban and rural zones agrees with previous studies (Jones and Clark 1987; Gresens et al. 2007). Why

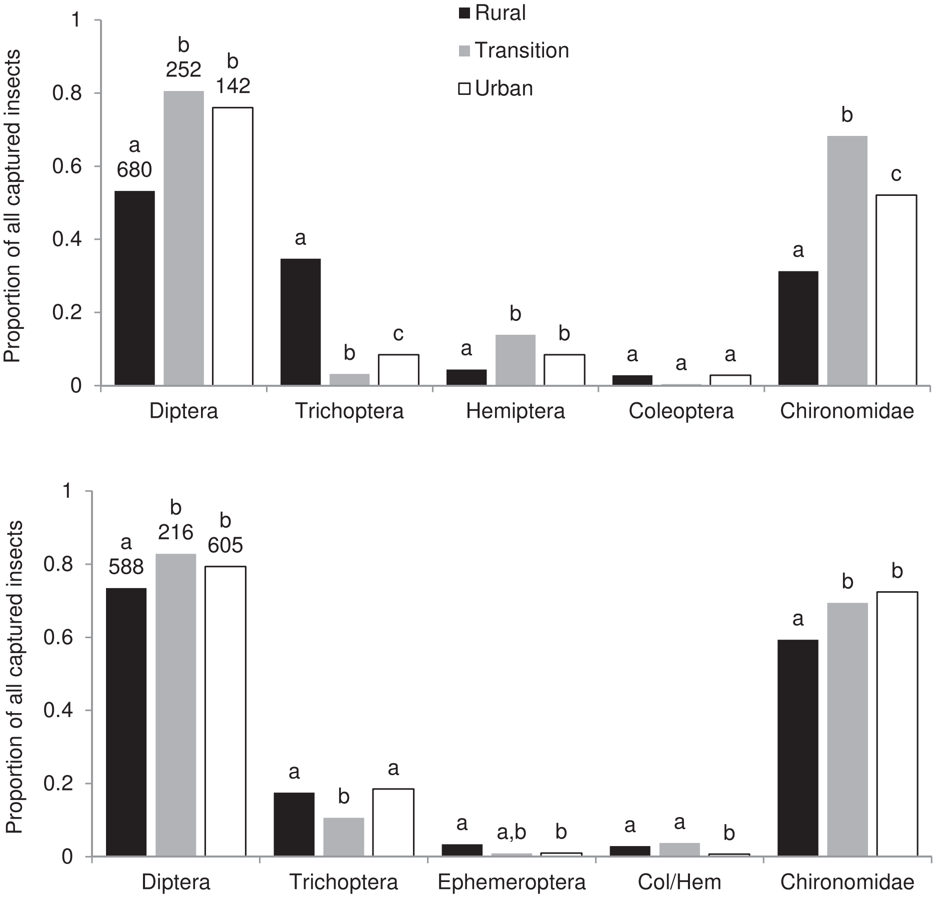

Fig. 4.—Differences among zones in the distribution of the 4 most common categories of insects, and in proportions of chironomids, in 2007 (top panel) and 2008 (bottom panel) near Calgary, Alberta, Canada. Different letters above columns indicate significant differences among zones, with associated *P*-values given in Supporting Information S2 (DOI: 10.1644/12-MAMM-A-217.S2). Numbers are sample sizes. Insects belonging to the "other" category are not shown, so proportions for a zone do not sum to one; Col/Hem is the combined Coleoptera and Hemiptera category.

insects were less abundant in the transition than in the rural zone is harder to explain, because most sites in the transition zone were well outside Calgary, with surrounding development similar to that in rural sites.

Although most urban ecology studies of riparian insects compared urban streams with streams in natural areas, some compared effects of urbanization with those of agriculture, yielding consistent findings. Both land uses similarly affect insect abundance, but urbanization may cause a greater reduction in diversity (Moore and Palmer 2005). Compared to insect assemblages in agricultural or natural areas, assemblages in urban environments are more dominated by chironomids, with fewer other insects, (e.g., Jones and Clark 1987; Morse et al. 2003; Gresens et al. 2007). This is similar to our findings.

Several factors other than deforestation may result in urbanization being more deleterious than agriculture to riparian insects. One is the increase in impervious surface area in urban areas. By 1998, 32% of Calgary's land was covered with impervious surfaces (The City of Calgary 2009), exceeding the 5% threshold above which insect diversity may decline (Morse et al. 2003). Water pollution also is important. Although we expected water quality to be better in Calgary than outside the city, levels of pesticides (e.g., Stackelberg 1997), nitrogen, and phosphorus (Nagumo and Hatano 2000) in urban streams may equal or exceed levels in streams receiving agricultural runoff. There are no recent, long-term data on water quality for the reach of the Bow River that flows through Calgary, but short-term studies revealed increased nutrient and pesticide levels at urban sampling stations (Bow River Basin Council 2005). Sewage effluent is a key source of urban-stream pollutants that can shift composition of prey for insectivorous bats toward pollution-tolerant taxa (e.g., chironomids) and can affect bat foraging (e.g., Kalcounis-Rueppell et al. 2007). We did not assess water quality, but 3 urban and 2 transition sites were downstream from Calgary's wastewater treatment plants. Other urban sites and most transition sites, including those upstream from Calgary, receive storm-water runoff or sewage effluent from small communities (Bow River Basin Council 2005). Thus, reduced abundance of pollution-sensitive ephemeropterans, plecopterans, and trichopterans (Jones and Clark 1987) in the urban and transition zones seems related to water quality.

We hypothesized that increased urban tree cover reduces flight costs and predation risk for foraging bats and increases the amount of edge. Combined with the predicted increase in

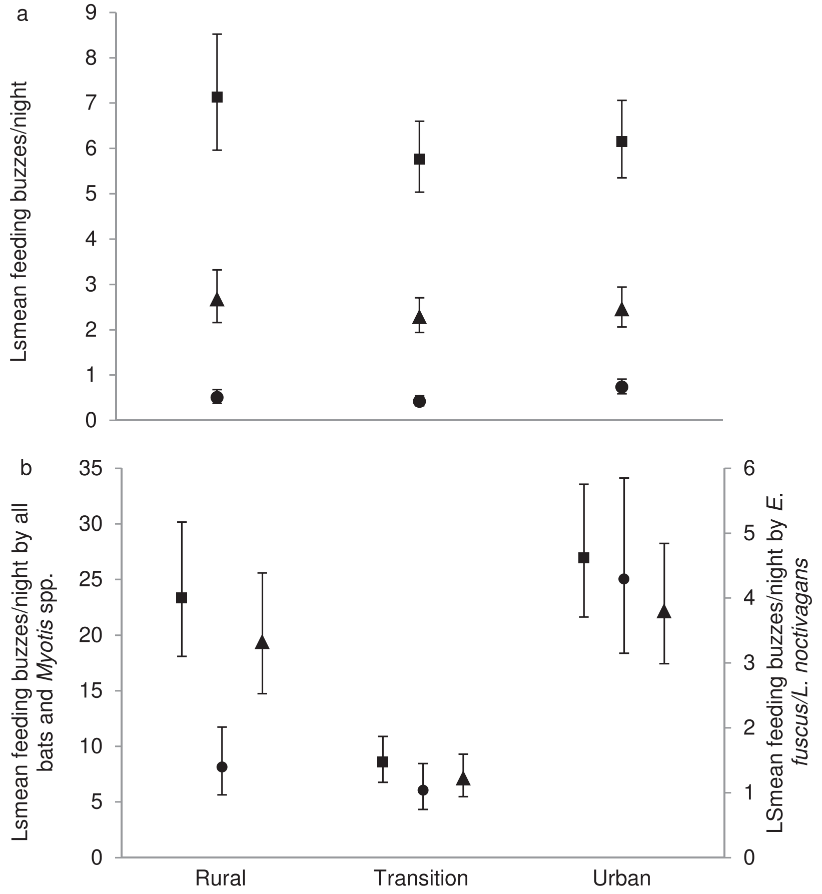

FIG. 5.—Variation in foraging activity, controlling for a) night length or b) bat activity for all bats (squares), for *Myotis* spp. (triangles), and for *Eptesicus fuscus*/*Lasionycteris noctivagans* (circles) among zones in 2007 and 2008 near Calgary, Alberta, Canada. Points are back-transformed least-squares means and bars represent back-transformed standard errors.

prey availability, this would produce greater foraging activity by urban bats. Again, our data do not support this prediction. Hourly foraging activity by all bats differed among zones, but not in the expected direction, and foraging relative to overall bat activity did not vary. In other words, all zones had similar rates of attack per pass, suggesting an effect of urbanization on bat abundance rather than on foraging rates. Indeed, bats were more abundant in the urban zone than in the transition or rural zones (Coleman and Barclay 2012). Inherent in this prediction was our assumption that any benefit of urbanization (i.e., enhanced prey availability and foraging habitat quality) would be evidenced by higher numbers of feeding buzzes by urban bats. However, not all capture attempts are successful (Britton and Jones 1999), and buzzes produced by hunting bats may attract conspecifics to a food patch (Gillam 2007). More bats foraging in a patch could produce higher attack rates while reducing individual hunting success. Such a scenario seems most likely in the urban zone, where bats were most numerous.

The correspondence between patterns of among-zone variation in foraging by all bats and by *Myotis* spp. reflects dominance of *M. lucifugus* throughout our study area (Coleman and Barclay 2012). Among-zone variation in hourly foraging activity of *Myotis* spp. corresponded to among-zone variation in insect biomass, as expected (Scanlon and Petit 2008). The lack of this relationship for *E. fuscus*/*L. noctivagans* may indicate that sticky traps are not particularly effective at sampling the larger, hard-bodied taxa (Kunz 1988) important in the diet of *E. fuscus* (e.g., Brigham and Saunders 1990).

Examination of our data does not indicate that urbanization enhances foraging activity by prairie bats, but contrary to previous studies, they do not suggest a negative effect either. However, comparing our results to those of previous studies is difficult because of differences in research questions and methodologies. Some bats aggregate at streetlights and hunt swarms of phototactic insects (e.g., Furlonger et al. 1987; Rydell 1992), leading to the suggestion that some bats persist in cities by exploiting these concentrations of food (e.g., Gehrt and Chelsvig 2003; Duchamp et al. 2004; Haupt et al. 2006; Hourigan et al. 2006). However, artificial lights attract fewer insects in well-lit (e.g., urban) areas than in darker areas (Frank 2006), and bats may be more likely to forage around lights outside cities than within them (Geggie and Fenton 1985; Furlonger et al. 1987). Furthermore, high- and low-pressure sodium-vapor lamps attract relatively few insects and bats (e.g., Rydell 1992). More than 95% of Calgary streetlights are sodium-vapor lamps (The City of Calgary 2008), and we never saw bats foraging around lights. We reject the idea that urban streetlights help to maintain equal levels of foraging activity by bats between urban and rural areas, and they seem even less relevant to *M. lucifugus*, which rarely hunts at streetlights (Furlonger et al. 1987).

Whether foraging bats prefer or avoid urban habitats, that is, use them more or less than expected based on availability, also has yielded mixed results. Studies in the United States (e.g., Duchamp et al. 2004; Sparks et al. 2005) reported avoidance of urban areas, whereas 2 European studies reported preference (Walsh and Harris 1996; Haupt et al. 2006). However, both European studies considered populated areas with too few inhabitants to be considered cities (McIntyre et al. 2000), so they may indicate a benefit of low levels of development to bats. The studies in the United States focused on the urban–rural interface, and did not compare habitat selection between urban and nonurban bats.

Studies comparing urban and nonurban areas in terms of actual foraging activity by bats also have produced conflicting results. In some, foraging activity did not differ between urban and nonurban habitats (e.g., Vaughan et al. 1997), whereas others reported lower foraging activity in urban areas (Geggie and Fenton 1985; Hourigan et al. 2006).

Our study differs from those described above in that we compared foraging by urban and nonurban bats in the context of food availability, and we are the 1st to examine this in a grassland landscape. Our predictions were largely based on the premise that landscape context modulates impacts of urbanization on insects and on foraging habitat quality for bats, but our findings regarding the structure of insect assemblages resembled those of studies in forested biomes. This suggests that negative effects of urbanization on insect diversity may be fairly universal, although the potential for urbanization to benefit insects and their bat predators in an even more arid ecoregion than the Prairies is worth investigating. For example, increased water use in Phoenix, Arizona, was linked to greater primary productivity (Shochat et al. 2006) and arthropod abundance (Cook and Faeth 2006), and this could in turn benefit insectivorous bats. Despite reduced urban insect diversity, we found no obviously negative impact of urbanization on foraging activity of bats. This likely reflects the fact that *M. lucifugus*, the dominant bat in our study area, has a catholic diet and readily eats chironomids, which are especially abundant in cities. The situation may be different for bats with more specialized feeding behaviors.

ACKNOWLEDGMENTS

For invaluable assistance in the field, we thank N. Boulic, A. Bugajski, A. Goldie, T. Hershon, C. Olson, P. Payette, and especially E. Swerdfeger. Many thanks to R. Longair for help with insect identifications; to J. Talerico for equipment loans; and to R. Cartar, B. Klug, and C. Olson for statistical advice. For facilitating access to our field sites, we gratefully acknowledge Government of Alberta (Tourism Parks and Recreation), the City of Calgary, Parks Canada, and many private landowners. Funding and materials were provided by the Natural Sciences and Engineering Research Council of Canada, Killam Trusts, Bat Conservation International, University of Calgary, and Canadian Tire. We thank P. Moosman and an anonymous reviewer for comments that improved the manuscript.

SUPPORTING INFORMATION

SUPPORTING INFORMATION S1.—Examples of rural (upper), transition (middle), and urban (lower) field sites. All sites were riparian, with mature trees that could potentially be used as day roosts by bats.

Found at DOI: 10.1644/12-MAMM-A-217.S1

SUPPORTING INFORMATION S2.—Results of significant pairwise chi-square tests comparing zones in terms of relative proportions of insects belonging to 5 categories captured in and near Calgary, Alberta, Canada, in 2007 ($n = 1{,}074$) and 2008 ($n = 1{,}409$). Because we compared proportions of the 4 most commonly trapped orders within each year, categories differ somewhat between years.

Found at DOI: 10.1644/12-MAMM-A-217.S2

LITERATURE CITED

ADAMS, L. 2005. Urban wildlife ecology and conservation: a brief history of the discipline. Urban Ecosystems 8:139–156.

ANTHONY, E. L. P., AND T. H. KUNZ. 1977. Feeding strategies of the little brown bat, *Myotis lucifugus*, in southern New Hampshire. Ecology 58:775–786.

AVILA-FLORES, R., AND M. B. FENTON. 2005. Use of spatial features by foraging insectivorous bats in a large urban landscape. Journal of Mammalogy 86:1193–1204.

BARCLAY, R. M. R. 1985. Long- versus short-range foraging strategies of hoary (*Lasiurus cinereus*) and silver-haired (*Lasionycteris noctivagans*) bats and the consequences for prey selection. Canadian Journal of Zoology 63:2507–2515.

BARCLAY, R. M. R., AND L. D. HARDER. 2003. Life histories of bats: life in the slow lane. Pp. 209–253 in Bat ecology (T. H. Kunz and M. B. Fenton, eds.). University of Chicago Press, Chicago, Illinois.

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

BOW RIVER BASIN COUNCIL. 2005. Nurture, renew, protect: a report on the state of the Bow River basin. Bow River Basin Council, Calgary, Alberta, Canada.

BRIGHAM, R. M., AND M. B. SAUNDERS. 1990. The diet of big brown bats (*Eptesicus fuscus*) in relation to insect availability in southern Alberta, Canada. Northwest Science 61:7–10.

BRITTON, A. R., AND G. JONES. 1999. Echolocation behaviour and prey-capture success in foraging bats: laboratory and field experiments on *Myotis daubentonii*. Journal of Experimental Biology 202:1793–1801.

CLIPPERTON, G. K., C. W. KONING, A. G. H. LOCKE, J. M. MAHONEY, AND B. QUAZI. 2003. Instream flow needs determinations for the South Saskatchewan River basin, Alberta, Canada. Alberta Environment and Sustainable Resource Development (Publication T/719), Calgary, Alberta, Canada. www3.gov.ab.ca/env/water/regions/ssrb/IFN_reports.asp. Accessed 21 April 2010.

COLEMAN, J. 2010. The effects of urbanization on prairie bats. Ph.D. dissertation, University of Calgary, Calgary, Alberta, Canada.

COLEMAN, J. L., AND R. M. R. BARCLAY. 2012. Urbanization and the abundance and diversity of prairie bats. Urban Ecosystems 15:87–102.

Cook, W. M., and S. H. Faeth. 2006. Irrigation and land use drive ground arthropod community patterns in an urban desert. Environmental Entomology 35:1532–1540.

Corben, C. 2000. Anamusic WAV file generation utility. Version 3.4. http://www.hoarybat.com. Accessed 22 August 2013.

Corben, C. 2004. Analook bat call analysis system. Version 4.9j. http://www.hoarybat.com. Accessed 22 August 2013.

Cromartie, J. B. 1998. Net migration in the Great Plains increasingly linked to natural amenities and suburbanization. Rural Development Perspectives 13:27–34.

Czech, B., P. R. Krausman, and P. K. Devers. 2000. Economic associations among causes of species endangerment in the United States. BioScience 50:593–601.

Dodds, W. K., K. Gido, M. R. Whiles, K. M. Fritz, and W. J. Matthews. 2004. Life on the edge: the ecology of Great Plains prairie streams. BioScience 54:205–216.

Duchamp, J. E., D. W. Sparks, and J. O. Whitaker, Jr. 2004. Foraging-habitat selection by bats at an urban–rural interface: comparison between a successful and a less successful species. Canadian Journal of Zoology 82:1157–1164.

Duchamp, J. E., and R. K. Swihart. 2008. Shifts in bat community structure related to evolved traits and features of human-altered landscapes. Landscape Ecology 23:849–860.

Engqvist, L. 2005. The mistreatment of covariate interaction terms in linear model analyses of behavioural and evolutionary ecology studies. Animal Behaviour 70:967–971.

Faure, P. A., and R. M. R. 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.

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.

Fischer, J., J. Stott, B. S. Law, M. D. Adams, and R. I. Forrester. 2009. Designing effective habitat studies: quantifying multiple sources of variability in bat activity. Acta Chiropterologica 11:127–137.

Frank, K. D. 2006. Effects of artificial night lighting on moths. Pp. 305–344 in Ecological consequences of artificial night lighting (C. Rich and T. Longcore, eds.). Island Press, Washington, D.C.

Furlonger, C. L., H. J. Dewar, and M. B. Fenton. 1987. Habitat use by foraging insectivorous bats. Canadian Journal of Zoology 65:284–288.

Gaisler, J., J. Zukal, Z. Rehak, and M. Homolka. 1998. Habitat preference and flight activity of bats in a city. Journal of Zoology 244:439–445.

Garden, J., C. McAlpine, A. N. N. Peterson, D. Jones, and H. Possingham. 2006. Review of the ecology of Australian urban fauna: a focus on spatially explicit processes. Austral Ecology 31:126–148.

Geggie, J. F., and M. B. Fenton. 1985. A comparison of foraging by *Eptesicus fuscus* (Chiroptera: Vespertilionidae) in urban and rural environments. Canadian Journal of Zoology 63:263–266.

Gehrt, S. D., and J. E. Chelsvig. 2003. Bat activity in an urban landscape: patterns at the landscape and microhabitat scale. Ecological Applications 13:939–950.

Gillam, E. H. 2007. Eavesdropping by bats on the feeding buzzes of conspecifics. Canadian Journal of Zoology 85:795–801.

Gresens, S. E., K. T. Belt, J. A. Tang, D. C. Gwinn, and P. A. Banks. 2007. Temporal and spatial responses of Chironomidae (Diptera) and other benthic invertebrates to urban stormwater runoff. Hydrobiologia 575:173–190.

Griffin, D. R., F. A. Webster, and C. R. Michael. 1960. The echolocation of flying insects by bats. Animal Behaviour 8:141–154.

Haupt, M., S. Menzler, and S. Schmidt. 2006. Flexibility of habitat use in *Eptesicus nilssonii*: does the species profit from anthropogenically altered habitats? Journal of Mammalogy 87:351–361.

Hódar, J. A. 1996. The use of regression equations for estimation of arthropod biomass in ecological studies. Acta Oecologica 17:421–433.

Holloway, G. L., and R. M. R. Barclay. 2000. Importance of prairie riparian zones to bats in southeastern Alberta. Ecoscience 7:115–122.

Hourigan, C. L., C. Johnson, and S. K. A. Robson. 2006. The structure of a micro-bat community in relation to gradients of environmental variation in a tropical urban area. Urban Ecosystems 9:67–82.

Humphrey, S. R. 1975. Nursery roosts and community diversity of Nearctic bats. Journal of Mammalogy 56:321–346.

Jones, G., D. S. Jacobs, T. H. Kunz, M. R. Willig, and P. A. Racey. 2009. Carpe noctem: the importance of bats as bioindicators. Endangered Species Research 8:93–115.

Jones, R. C., and C. C. Clark. 1987. Impact of watershed urbanization on stream insect communities. Journal of the American Water Resources Association 23:1047–1055.

Kalcounis-Rueppell, M. C., V. H. Payne, S. R. Huff, and A. L. Boyko. 2007. Effects of wastewater treatment plant effluent on bat foraging ecology in an urban stream system. Biological Conservation 138:120–130.

Kunz, T. H. 1988. Methods of assessing the availability of prey to insectivorous bats. Pp. 191–210 in Ecological and behavioral methods for the study of bats (T. H. Kunz, ed.). Smithsonian Institution Press, Washington, D.C.

Kunz, T. H., and M. B. Fenton (eds.). 2003. Bat ecology. University of Chicago Press, Chicago, Illinois.

Larson, D. J., and J. P. Hayes. 2000. Variability in sensitivity of Anabat II bat detectors and a method of calibration. Acta Chiropterologica 2:209–213.

Lumsden, L. F., and A. F. Bennett. 2005. Scattered trees in rural landscapes: foraging habitat for insectivorous bats in south-eastern Australia. Biological Conservation 122:205–222.

Marzluff, J. M., R. Bowman, and R. Donnelly. 2001. A historical perspective on urban bird research: trends, terms, and approaches. Pp. 1–18 in Avian ecology and conservation in an urbanizing world (J. M. Marzluff, R. Bowman, and R. Donnelly, eds.). Kluwer Academic Publishers, Norwell, Massachusetts.

McIntyre, N. E. 2000. Ecology of urban arthropods: a review and a call to action. Annals of the Entomological Society of America 93:825–835.

McIntyre, N. E., K. Knowles-Yánez, and D. Hope. 2000. Urban ecology as an interdisciplinary field: differences in the use of “urban” between the social and natural sciences. Urban Ecosystems 4:5–24.

McIntyre, S., and R. Hobbs. 1999. A framework for conceptualizing human effects on landscapes and its relevance to management and research models. Conservation Biology 13:1282–1292.

Moore, A. A., and M. A. Palmer. 2005. Invertebrate biodiversity in agricultural and urban headwater streams: implications for conservation and management. Ecological Applications 15:1169–1177.

Morse, C. C., A. D. Huryn, and C. Cronan. 2003. Impervious surface area as a predictor of the effects of urbanization on stream insect communities in Maine, U.S.A. Environmental Monitoring and Assessment 89:95–127.

Nagumo, T., and R. Hatano. 2000. Impact of nitrogen cycling associated with production and consumption of food on nitrogen pollution of stream water. Soil Science and Plant Nutrition 46:325–342.

Nullsoft, Inc. 2006. Winamp media player. Version 5.31. http://www.winamp.com/. Accessed 22 August 2013.

Patriquin, K. J., and R. M. Barclay. 2003. Foraging by bats in cleared, thinned and unharvested boreal forest. Journal of Applied Ecology 40:646–657.

Pedan, A. 2001. Analysis of count data using the SAS system. 26th International SAS Conference. SUGI; 247-26:1–6..

Racey, P. A., and A. C. Entwistle. 2003. Conservation ecology of bats. Pp. 680–743 in Bat ecology (T. H. Kunz and M. B. Fenton, eds.). University of Chicago Press, Chicago, Illinois.

Rambo, J. L., and S. H. Faeth. 1999. Effect of vertebrate grazing on plant and insect community structure. Conservation Biology 13:1047–1054.

Rydell, J. 1992. Exploitation of insects around streetlamps by bats in Sweden. Functional Ecology 6:744–750.

Sample, B. E., R. J. Cooper, R. D. Greer, and R. C. Whitmore. 1993. Estimation of insect biomass by length and width. American Midland Naturalist 129:234–240.

Saunders, M. B., and R. M. R. Barclay. 1992. Ecomorphology of insectivorous bats: a test of predictions using two morphologically similar species. Ecology 73:1335–1345.

Scanlon, A., and S. Petit. 2008. Biomass and biodiversity of nocturnal aerial insects in an Adelaide city park and implications for bats (Microchiroptera). Urban Ecosystems 11:91–106.

Seaby, R. M., and P. A. Henderson. 2006. Species Diversity and Richness. Version 4.1.2. Pisces Conservation Ltd., Lymington, United Kingdom.

Shochat, E., P. S. Warren, S. H. Faeth, N. E. McIntyre, and D. Hope. 2006. From patterns to emerging processes in mechanistic urban ecology. Trends in Ecology & Evolution 21:186–191.

Solow, A. R. 1993. A simple test for change in community structure. Journal of Animal Ecology 62:191–193.

Sparks, D. W., C. M. Ritzi, J. E. Duchamp, and J. O. Whitaker, Jr. 2005. Foraging habitat of the Indiana bat (*Myotis sodalis*) at an urban–rural interface. Journal of Mammalogy 86:713–718.

Stackelberg, P. E. 1997. Presence and distribution of chlorinated organic compounds in streambed sediments, New Jersey. Journal of the American Water Resources Association 33:271–284.

Stevens, R. D., and M. R. Willig. 2002. Geographical ecology at the community level: perspectives on the diversity of New World bats. Ecology 83:545–560.

The City of Calgary. 2008. Envirosmart streetlight retrofit FAQs. Calgary, Alberta, Canada. http://content.calgary.ca/CCA/City+Hall/Business+Units/Roads/Streetlights/EnviroSmart+Streetlight+Retrofit/FAQs.htm. Accessed 15 April 2010.

The City of Calgary. 2009. Calgary transportation plan. City of Calgary, Calgary, Alberta, Canada.

Thomas, D. W. 1988. The distribution of bats in different ages of Douglas-fir forests. Journal of Wildlife Management 52:619–626.

United States Naval Observatory. 2009. United States Naval Observatory astronomical applications. http://www.usno.navy.mil/USNO/astronomical-applications. Accessed 13 December 2009.

van der Ree, R., and M. A. McCarthy. 2005. Inferring persistence of indigenous mammals in response to urbanisation. Animal Conservation 8:309–319.

Vaughan, N., G. Jones, and S. Harris. 1997. Habitat use by bats (Chiroptera) assessed by means of a broad-band acoustic method. Journal of Applied Ecology 34:716–730.

Verboom, B., and K. Spoelstra. 1999. Effects of food abundance and wind on the use of tree lines by an insectivorous bat, *Pipistrellus pipistrellus*. Canadian Journal of Zoology 77:1393–1401.

Walsh, A. L., and S. Harris. 1996. Foraging habitat preferences of vespertilionid bats in Britain. Journal of Applied Ecology 33:508–518.

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

Whitaker, J. O., Jr., G. F. McCracken, and B. M. Siemers. 2009. Food habits analysis of insectivorous bats. Pp. 567–592 in Ecological and behavioral methods for the study of bats (T. H. Kunz and S. Parsons, eds.). 2nd ed. Johns Hopkins University Press, Baltimore, Maryland.

Wickramasinghe, L. P., S. Harris, G. Jones, and N. V. Jennings. 2004. Abundance and species richness of nocturnal insects on organic and conventional farms: effects of agricultural intensification on bat foraging. Conservation Biology 18:1283–1292.

Zar, J. H. 1999. Biostatistical analysis. 4th ed. Prentice Hall, Upper Saddle River, New Jersey.

Submitted 28 August 2012. Accepted 29 March 2013.

Associate Editor was Richard D. Stevens.