Urbanization and the abundance and diversity of Prairie bats

Joanna L. Coleman · Robert M. R. Barclay

Abstract The effects of urbanization on biodiversity are generally considered to be negative, but the potential for landscape context to modulate these effects has not been adequately examined because most urban ecology research has been conducted in one biome: the temperate forest. This bias also applies to studies of the urban ecology of bats, whose diversity is correlated with habitat heterogeneity. We investigated the hypothesis that in the fairly flat, homogeneous Prairies, urbanization, by creating structurally complex islands, benefits bats by increasing access to the vertical landscape elements (buildings and trees) in which they roost. From 2006 to 2008, we surveyed bat assemblages in and around Calgary, Alberta, using mist nets to capture them and bat detectors to record their echolocation activity. Our data supported the prediction that urbanization increases the abundance of Prairie bats, but not the prediction that it increases their diversity. Instead, the urban bat assemblage was less diverse, and exhibited decreased species evenness compared to non-urban assemblages. Although *Myotis lucifugus* dominated bat assemblages throughout our study area, this was most evident in the city, and this species drove the increased urban abundance of bats. Ultimately, we reject our hypothesis and conclude that urbanization in the Prairies may create attractive habitat for one synanthropic bat, but is detrimental to others.

Keywords Urbanization · Chiroptera · Abundance · Diversity · Landscape · Grassland

Introduction

Among anthropogenic agents of habitat change, none so profoundly alters natural landscapes as urbanization (McIntyre and Hobbs 1999). Its impact on wildlife is therefore disproportionately large (Marzluff and Ewing 2001) given the small proportion (<1%) of the Earth's land surface occupied by urban areas (Potere et al. 2009). Indeed, urbanization is

J. L. Coleman (✉) · R. M. R. Barclay
Department of Biological Sciences, University of Calgary, 2500 University Drive NW, Calgary, Alberta T2N 1N4, Canada
e-mail: jcoleman@ucalgary.ca

a key factor in the global biodiversity crisis and may be the leading cause of species' endangerments (Czech et al. 2000). The need to study how urbanization affects wildlife and use the results to develop sound management plans is pressing: today's urban population is ten times that of 100 years ago and is expected to nearly double by 2050, when it should reach 6.4 billion, or 70% of all people on Earth (United Nations 2008).

Not surprisingly, the field of urban ecology has grown considerably in recent decades (Niemelä 1999), but it remains biased in several ways. One is that most research has been conducted in forested biomes, whereas other biomes, notably grasslands, have been largely ignored (Chace and Walsh 2006). In North America, this is a major oversight because, of all the continent's biomes, the Great Plains has experienced the most extensive habitat destruction (Samson and Knopf 1994), despite a fairly recent history of human settlement (Lemmen et al. 1997). Also, for a region where agriculture is the main human activity, urbanization has strongly influenced the landscape, and occurs at a higher rate in the Great Plains than in any other biome (Cromartie 1998).

Urban ecology is also biased in that birds have received most of the research attention (Garden et al. 2006). How other vertebrate classes respond to urbanization is less well-understood. Among studies of mammals in urban areas, most have considered easily-observed and charismatic species, whereas taxa that are cryptic, difficult to work with, or have less public appeal, such as bats, are underrepresented (Gehrt and Chelsvig 2003; Garden et al. 2006). Yet there are good reasons to study the urban ecology of bats besides the fact that they provide key ecosystem services, e.g., control of insect populations (Kunz and Fenton 2003). Because bats have slow life histories (Barclay and Harder 2003) and are slow to recover from habitat change (Racey and Entwistle 2003), they are useful bioindicators of habitat quality in general and are responsive to urbanization (Fenton 2003).

Urbanization poses at least three specific challenges to vertebrates that may be less problematic for bats. First, inhospitable elements of the urban matrix, e.g., roads, are often barriers to dispersal and sources of mortality, especially for terrestrial fauna (Forman and Alexander 1998). Second, small urban animals may face increased predation by exotics and mesopredators which often attain unnaturally high densities in cities (Crooks and Soulé 1999). Third, some urban animals respond to increased disturbance with costly behavioral adjustments, e.g., becoming crepuscular or nocturnal (e.g., Ticer et al. 1998). However, all bats fly and are nocturnal, and for most, predation is not a limiting factor (Fenton and Fleming 1976). Thus, bats may be better-suited than other mammals for studies of the effects of urbanization purely as they relate to habitat change.

Of studies that examined the effects of urbanization on the composition of bat assemblages, most found reduced abundance, species richness, evenness and/or diversity, and/or disappearance of rarer species (Geggie and Fenton 1985; Kurta and Teramino 1992; Bredt and Uieda 1996; Gaisler et al. 1998; Kirsten and Klomp 1998; Avila-Flores and Fenton 2005; Hourigan et al. 2006; Rainho 2007; Duchamp and Swihart 2008; Loeb et al. 2009). This is similar to what is often observed for wildlife in general (Shochat et al. 2006). Given evidence that the diversity of available roosts largely governs bat diversity, at least in the temperate zone (Humphrey 1975), it makes sense that reduced availability of natural roosts, e.g., trees with cavities (Bate et al. 2007), is among the proposed explanations for reduced diversity of urban bats (van der Ree and McCarthy 2005). Even species that often roost in human structures, e.g., buildings and bridges, and may benefit from urbanization (Agosta 2002; Duchamp and Swihart 2008) may still prefer to use trees in urban areas (Evelyn et al. 2004).

Most urban-ecology studies, including those of bats, have taken place in treed ecoregions, where urban development implies deforestation and habitat simplification

(van der Ree and McCarthy 2005). Thus, the role of landscape context in shaping how animals respond to urbanization is unclear. However, given the importance of vegetation to wildlife in general and of vertical landscape elements to bats in particular, locale may influence the outcome of urban ecology studies (Chace and Walsh 2006). Interestingly, the only study that found a positive effect of urbanization on the diversity of temperate-zone bats (Gehrt and Chelsvig 2004) was conducted in a matrix of open, agricultural land, which bats avoided, a tendency also documented elsewhere (e.g., Walsh and Harris 1996a).

To address the research gaps outlined above, we studied the effects of urbanization on the composition of the bat assemblage in the Canadian Prairies. Because humans maintain a rather uniform, moderate level of tree cover in all cities, urbanization in the Prairies implies significant forestation (McKinney 2006). This proliferation of trees along with the abundance of buildings and other human structures contributed to our view of Prairie cities as structurally complex islands in a relatively homogeneous landscape. For animals such as bats that need vertical landscape elements and for which the key extrinsic determinant of diversity may be habitat complexity (Humphrey 1975), whether urbanization positively or negatively affects them may depend on whether it increases or decreases landscape heterogeneity (see also Gehrt and Chelsvig 2004). Our hypothesis was that urbanization benefits Prairie bats, especially species that roost in trees and/or human structures, and we predicted that bat abundance and diversity are highest in urban areas.

Methods

Study area and species

Our study area was located in the South Saskatchewan River basin (SSRB), with Calgary, Alberta (city centre 51°02′45″N, 114°03′27″W) and the surrounding area as the focal point. Calgary is situated within the Bow River sub-basin, in the ecotone between the Aspen Parkland and Fescue Grassland ecoregions of the Prairies ecozone (Gauthier and Wiken 2003). In general, Prairie winters are long and cold, and summers are short and dry (Lac and Colan 2004), with nocturnal temperatures often below 5°C. In its natural state, the region is typified by grasses in drier areas, and poplar (*Populus* spp.)-dominated stands in low-lying, mesic and riparian areas (Moss 1932). However, the Prairies have sustained considerable habitat loss (Samson and Knopf 1994), especially in the Aspen Parkland (Vujnovic et al. 2002), and the SSRB is heavily urbanized, with 85% of the human population living in urban areas (Lac and Colan 2004). Calgary, situated in a high-intensity agriculture zone (Alberta Environmental Protection 1997), is surrounded by a mosaic of acreages and land converted to crop and livestock production.

Among major Canadian cities, Calgary (incorporated in 1893) is one of the youngest (Wickett 1900) and the fastest-growing one, with just over 1,000,000 inhabitants in 2006 (a 13% increase over 2001; Statistics Canada 2007). In 2007, Calgary was also Canada's largest city (726.5 km^2; Statistics Canada 2007). Compared to other North American cities, Calgary's level of urban fragmentation is low, i.e., >90% of the census metropolitan area's population lives within city limits (Ghitter and Smart 2009). However, Calgary is considered to have the worst urban sprawl in Canada (Sun et al. 2007) because urban development has largely consisted of low-density, single-use suburbs, with a maximum density of 15–17 units per ha (B. Sandalack, pers. comm.).

Eight bat species occur in our study area. All are insectivorous, three are migratory and five are year-round residents that hibernate over the winter. All three migratory bats hunt by

aerial hawking (Barclay 1993). They include *Lasiurus cinereus* and *L. borealis*, which are solitary and roost in tree foliage (Willis and Brigham 2005), and *Lasionycteris noctivagans*, which roosts in tree cavities and bark (Fenton 2003). *Myotis evotis* hunts mainly by gleaning and usually roosts in tree cavities and rock crevices, but also uses buildings (Solick and Barclay 2007). The other *Myotis*: *M. ciliolabrum*, *M. lucifugus* and *M. volans*, are primarily aerial hawkers (Barclay 1993). *M. lucifugus* uses diverse roosts, including tree cavities and often buildings (Davis and Hitchcock 1965). The ecology of *M. volans* in Alberta is poorly known, but elsewhere this species is similar to *M. lucifugus* (Ormsbee and McComb 1998). *M. ciliolabrum* roosts mainly in rock and ground crevices, and rarely in human structures (Holloway and Barclay 2001). Finally, *Eptesicus fuscus*, strictly an aerial hawker (Barclay 1993), is the most common North American bat, with the most diverse roost types, e.g., rock crevices, trees, and especially buildings (Agosta 2002).

Study sites

Given the importance of treed, riparian habitat to Prairie bats (Holloway and Barclay 2000), all sites were located along rivers and tributaries within the Bow, Red Deer and Oldman River sub-basins. We wanted to isolate the effects of urbanization from those of habitat, so all field sites had flowing water and native trees, particularly poplars, that could potentially be used by bats as roosts. Water flow varied both within sites (depending on precise location and date) and among them, but all zones contained similar numbers of sites with riffles and still water. Although we did not obtain precise data on stand age in our sites, all contained mature (i.e. ≥50 years old) *P. deltoides*, *P. balsamifera*, and/or *P. tremuloides* according to criteria in Lauriault (1989), with at least some individuals bearing holes that could potentially be used by cavity-roosting bats. Many sites also contained conifers (*Picea* and *Abies* spp.) on north-facing aspects. The width of the riparian zone varied both within sites (depending on precise location) and among them, and varied equally among zones. Sites were located in municipal and provincial parks, provincial natural recreation areas, on municipal and private property and in one national historic site.

We divided our study area into three zones. Urban sites were within city limits and bounded on all sides by human development, i.e., not on city edges. Rural sites were ≥40 km from city limits. This represents twice the maximum distance traveled by reproductive female hoary bats (*L. cinereus*), the largest species in our study area, from day roosts to foraging areas (Barclay 1989). We chose this distance to effectively separate urban and rural bat assemblages. However, because individuals could potentially roost in the city and forage outside (or vice versa), we established a transition zone as a buffer between urban and rural assemblages. Transition sites were either within city limits but not completely surrounded by urban development, or between city limits and the rural zone. In total, we had at least nine replicate sites per zone, but the exact number varied among and within years when access was limited (e.g., due to flooding). Although transition sites were situated in all cardinal directions from Calgary, there were no rural sites to the west, because the Boreal Plains and Montane Cordillera (Eastern Foothills) ecozones meet the Prairies <40 km west of city limits (Ecological Stratification Working Group 1995). No two sites within a zone were less than 1 km apart.

Field methods

From 2006 through 2008, we assessed bat assemblage structure in all three zones. However, in 2006, we only worked in the urban and transition zones and used a slightly different

protocol, so we mainly present 2006 data as appropriate to support overall trends. To gain as complete a picture as possible of bat abundance and diversity, we combined two field methods: acoustic monitoring and mist netting (Kunz et al. 2009).

Mist netting

From late May through mid-September, we netted in one site per night, alternating nights among zones, six nights per week (weather permitting). Each night we set between three and eight 38-mm mesh mist nets (Avinet, Dryden, NY, USA) of varying lengths (6–18 m), at ground-level (top of net 3 m high) and raised (4.5 m high). We generally left nets open all night but closed them early when (1) temperatures fell below 0°C or it was raining, (2) we had too many captures to monitor nets effectively, or (3) we had not captured bats or heard any (on a handheld bat detector) for at least an hour. We identified captured individuals to species and marked them with numbered, split-ring arm bands before releasing them.

Passive acoustic monitoring

From late May through 31-August each year, we recorded bat activity on Anabat II bat detectors (division ratio set to 16) coupled to zero-crossing analysis interface modules and, in 2007, also on Anabat SD1 detectors (Titley Electronics, New South Wales, Australia). The devices recorded continuously from before sunset until after sunrise.

In 2006, we recorded bat activity at our netting site each night, with the detector at least 100 m from any net. In 2007, we simultaneously monitored three sites (one per zone, including our netting site) on four nights a week and our mist netting site only on the other two nights, rotating among sites within each zone to give a roughly equal number of sampling nights per site. In 2008, we simultaneously monitored activity in all three zones on nights when we netted in the rural zone and in our netting site only on other nights.

To minimize the effects of bias, we calibrated detectors at the beginning of each field season (Larson and Hayes 2000) and rotated them among zones (Fischer et al. 2009). We were also consistent in how we placed detectors relative to habitat features: we raised each box 1 m above the ground and put it in an open area ≤30 m from the water's edge, with the microphone facing the water and upward at 45°. We changed the exact location of the detector within a site on subsequent sampling nights (Fischer et al. 2009).

Environmental variables

In 2007 and 2008, to account for the potential effects of weather on capture success, we recorded temperature and wind speed every 30 min while nets were open using a Kestrel 4,000 weather meter (Nielsen-Kellerman, Boothwyn, PA, USA). We also hung Hobo UA-002-08 data loggers (Onset Computer Corporation, Pocasset, MA, USA) above each bat detector to record temperature (every 30 min). We obtained sunset, sunrise, and civil twilight times as well as moon illumination information for our study area from the U.S. Naval Observatory (www.usno.navy.mil/USNO).

Data analyses

We recorded the time (to the nearest 5 min) at which we opened and closed each net; the sum of hours during which each net was open is the total number of net-hours. We used capture success, in terms of captures per net-hour, as a measure of bat abundance.

We used Anamusic 3.4 (Corben 2000) to convert digital files from the detectors to audio files so we could listen to each file in Winamp 5.31 (Nullsoft, Inc.) while viewing it in Analook for DOS 4.9j (Corben 2004). We defined a bat pass as a sequence of at least two echolocation calls (Thomas 1988) separated by no more than two seconds (for *L. cinereus*) or one second (other species), and considered each pass to be an independent event. Acoustic monitoring does not allow direct assessment of abundance (Thomas and LaVal 1988). In effect, we measured bat activity and used it as an abundance index. For each file, we recorded the number of separate passes and quantified activity in terms of passes per hour from sunset to sunrise.

To examine bat diversity, one of us (J.C.) visually inspected high-quality search-phase calls and assigned each pass to one of five bat categories based on our knowledge of species in our study area: (1) *L. cinereus*, (2) *E. fuscus*/*L. noctivagans*, (3) *L. borealis*, (4) *Myotis* spp., and (5) unknown. The first two categories are low-frequency (LF) bats, whose calls usually have minimum frequencies <35 kHz; the third and fourth are high-frequency (HF) bats, whose calls are typically ≥35 kHz. We distinguished among pairs of LF and HF categories qualitatively and quantitatively (see Coleman 2010) and did not distinguish among the four *Myotis* bats in our study area.

Bat abundance

We used hierarchical linear mixed models (REML estimation of variance components) to analyze variance in captures/net-hour (hereafter capture success) and passes/hour (hereafter activity), using 2007 and 2008 data in JMP 7.0 (SAS Institute Inc., Cary, NC, USA). For this analysis (and all others), we used two-tailed tests and a rejection criterion of 0.05. We transformed data as appropriate to meet the assumptions of statistical tests. Preliminary analyses revealed that illuminated fraction of the moon did not affect activity or capture success (see also Hayes 1997), that average wind speed did not affect capture success, and that both dependent variables were correlated with average nightly temperature more than with maximum or minimum temperature. Both models included zone and year as fixed factors, site (nested in zone) as a random factor, and average temperature (ln-transformed) as a covariate. Our activity model also included (ln-transformed) Julian day as a covariate, but date did not affect capture success (as a covariate or a random factor). For both dependent variables, we started with saturated models, removing non-significant interaction terms sequentially (Engqvist 2005). For all significant fixed effects, we conducted post-hoc Student's t or Tukey's HSD tests.

Bat diversity

We used capture data to calculate four measures of bat diversity in each zone. These included: species richness (S_{obs}), or the total number of species captured, averaged across sites, Simpson's evenness index (E), which weights common and rare species equally, Fisher's alpha-diversity (α), which incorporates richness and evenness, and the Berger-Parker index (d), one of the best measures of dominance (Magurran 2004). We estimated parameters (except S_{obs}) with the program Species Diversity and Richness 4.1.2 (SDR; Seaby and Henderson 2006). SDR allowed us to compute jackknifed standard errors across replicate sites and run paired randomization tests (see Solow 1993) to assess whether zones differed significantly in terms of E and d. SDR does not perform such testing for α, so we estimated statistical significance by lack of overlapping standard errors. We compared zones in terms of S_{obs} with a Student's *t*-test or one-way ANOVA, as appropriate. We performed all calculations considering all individuals but no recaptures separately for 2007–2008 (*n*=

1,497) and for 2006 (n=369). We followed the same procedure with 2007–2008 acoustic data (excluding unknowns) but assessed bat-category diversity, rather than species diversity, and did not calculate bat category richness.

We ran a hierarchical three-way loglinear analysis in SPSS 16.0 (SPSS, Inc., Chicago, IL, USA) on 2007–2008 acoustic data (years combined), considering the effects of zone and migration period (before and during) on the distribution of all recorded passes among bat categories (excluding unknowns), after ensuring roughly equal sample size among groups, as follows. The beginning of fall migration (14-July) coincided with the midpoint of our field seasons, so sample sizes were equal between periods. However, they were unequal among zones, with fewer nights of data for the rural zone than for the other two. Thus, we omitted nights when we did not monitor activity simultaneously in all three zones, giving a final sample size of 35,093 passes distributed across 122 nights (40 rural, 41 transition, 41 urban). We broke down significant three-way interactions into two-way contingency tables to examine them in greater detail.

Results

In three summers, we captured 1,974 bats over 152 nights (41 in 2006, 65 in 2007 and 46 in 2008). In all, we collected 190 nights of useable acoustic data (34 in 2006, 115 in 2007 and 41 in 2008) and recorded 52,645 bat passes. We classified 2,428, or <5%, of all passes as unknown.

Bat abundance

The reduced mixed ANCOVA (R^2_{adj}=0.65, P<0.0001, n=111 netting nights) revealed that although mean capture success tended to be highest in the urban zone, intermediate in the rural zone and lowest in the transition zone, the zone effect was not significant ($F_{2, 25.23}$=2.85, P=0.09; Fig. 1). Capture success increased on warmer nights ($F_{1, 91.97}$=8.03, P=0.006) and tended to be higher in 2008 (0.65, +0.08, −0.06 bats/net*hour) than in 2007 (0.57, +0.05, −0.03 bats/net*hour), but not significantly (year: $F_{1, 86.55}$=2.86, P=0.09). Capture success varied significantly among sites (within zone), with site accounting for 49.5% of the variance (Wald Z=2.67, P=0.008). The reduced mixed ANCOVA (R^2_{adj}=0.62, P<0.0001, n=156 detector nights) revealed that zone affected mean activity ($F_{2, 25.31}$=3.50, P=0.046), which was higher in the urban than in the rural zone (Fig. 2). Activity increased as summer progressed ($F_{2, 125}$=12.64, P=0.0005), and when it was warmer ($F_{1, 126.2}$=20.74, P<0.0001), although the model retained an interaction between year and temperature ($F_{1, 124.4}$=4.46, P=0.04). At the average level of the covariate (10.85°C), activity tended to be higher in 2007 (LSmean=12.22, +2.99, −2.40 passes/hour) than in 2008 (LSmean=9.08, + 2.81, −2.14 passes/hour), but not significantly ($F_{1, 126.7}$=2.00, P=0.16). The JMP 7.0 prediction profiler revealed that the year effect was not significant over the range of temperatures, and that the temperature effect, while significant in both years, was stronger in 2008 than in 2007. Activity varied significantly among sites (within zone), with site accounting for 50.7% of the variance (Wald Z=2.89, P=0.004).

Bat diversity

In all three years, *M. lucifugus* was the most commonly captured bat. This was true in all zones, in all sites (except for one rural site), and on most nights. Relative abundance of *M.*
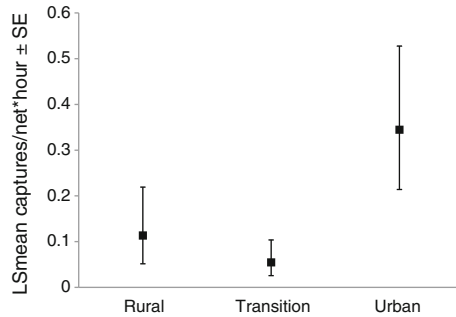
Fig. 1 Variation in mean bat abundance (capture success) among rural, transition and urban zones in 2007 and 2008 near Calgary, Alberta. Points represent back-transformed least squares means and bars represent back-transformed standard errors, resulting in asymmetrical error bars

lucifugus was consistently higher in the urban zone (80% and 91% of captures in 2006 and 2007–2008, respectively) than in the transition zone (70% and 82% of captures in 2006 and 2007–2008, respectively), and was lowest in the rural zone in 2007 and 2008 (71% of captures). Acoustic data revealed a similar pattern of dominance by *Myotis* spp. in 2007 and 2008, especially in the urban zone, and least of all in the transition zone (73%, 67% and 76% of all passes in the rural, transition and urban zones, respectively).

In all, we captured eight species in the rural zone, six in the urban zone and five in the transition zone (Table 1). Mean captured bat species richness tended to be highest in the rural zone, intermediate in the transition zone and lowest in the urban zone in 2007 and 2008, and higher in the transition than in the urban zone in 2006, but the zone effect was not significant (Table 1). Alpha-diversity tended to be higher in the rural zone than in the other two in 2007 and 2008, and higher in the urban than in the transition zone in 2006, but differences among zones were not significant (Table 1). Whereas evenness was similar in the urban and rural zones and tended to be higher (but not significantly) in the transition zone in 2007 and 2008, it was significantly higher in the transition zone than in the urban zone in 2006 (Table 1). The only index that differed significantly among zones in both comparisons was dominance: it was highest in the urban zone, intermediate in the transition zone and lowest in the rural zone in 2007–2008, with a similar difference between the urban and transition zones in 2006 (Table 1).
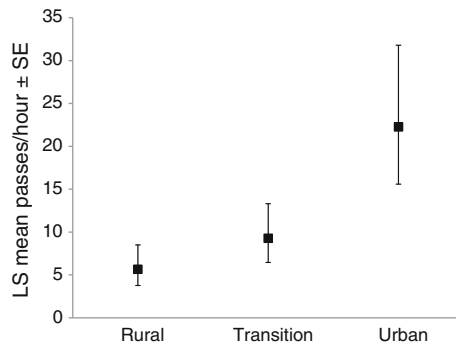

Fig. 2 Variation in mean bat activity among rural, transition and urban zones in 2007 and 2008 near Calgary, Alberta. Points represent back-transformed least squares means and bars represent back-transformed standard errors

Table 1 Bat captures and activity, and measures of bat-assemblage diversity calculated separately for 2006 (transition and urban) and 2007–2008 (rural, urban and transition) in and near Calgary, Alberta. Standard errors are jackknifed values for all estimates except species richness, and different superscript letters indicate significant differences among zones (within either 2006 or 2007–2008) based on randomisation tests. Also shown are total individuals (or passes) of each species (or species-category) captured (or recorded) in each zone

	2006		2007–2008		
	Transition	Urban	Rural	Transition	Urban
Total captures					
Eptesicus fuscus	16	20	20	16	20
Lasiurus borealis	0	1	1	0	2
L. cinereus	16	14	31	18	42
Lasionycteris noctivagans	14	9	66	15	9
Myotis ciliolabrum	0	0	2	0	0
M. evotis	0	0	2	0	0
M. lucifugus	109	172	304	227	719
M. volans	0	0	1	1	1
Total passes					
E. fuscus/L. noctivagans	404	534	2336	1895	4529
L. cinereus	70	239	628	706	790
Myotis spp.	2528	3785	8236	5401	17386
L. borealis	1	2	33	34	94
Diversity indices (dataset)					
Species richness ± SE (captures)	2.60 ± 0.51^a	2.38 ± 0.42^a	3.50 ± 0.89^a	3.13 ± 0.35^a	2.82 ± 0.42^a
Fisher's α ± SE (captures)	0.75 ± 0.14^a	0.92 ± 0.14^a	1.40 ± 0.40^a	0.87 ± 0.20^a	0.88 ± 0.18^a
Fisher's α ± SE (acoustic)			0.57 ± 0.08^a	0.52 ± 0.02^a	0.05 ± 0.02^b
Simpson's E ± SE (captures)	0.48 ± 0.06^a	0.30 ± 0.17^b	0.23 ± 0.08^a	0.29 ± 0.09^a	0.20 ± 0.03^a
Simpson's E ± SE (acoustic)			0.43 ± 0.07^a	0.49 ± 0.05^b	0.40 ± 0.02^c
Berger-Parker ± SE (captures)	0.70 ± 0.05^a	0.80 ± 0.12^b	0.71 ± 0.18^a	0.82 ± 0.09^b	0.91 ± 0.04^c
Berger-Parker ± SE (acoustic)			0.73 ± 0.09^a	0.67 ± 0.06^b	0.76 ± 0.02^c

Acoustic data revealed greater among-zone differences in diversity indices than those revealed by capture data. We recorded all four bat categories in all zones, but α-diversity was lower in the urban zone than in the other two (between which it was similar) by more than an order of magnitude (Table 1). Evenness was highest in the transition zone, intermediate in the rural zone and lowest in the urban zone, and we observed the exact opposite pattern for dominance among zones.

The loglinear analysis of bat-category diversity produced a final model that retained all effects, as the zone X period X bat category interaction was significant ($\chi^2=392.24$, df=6, $P<0.001$). Thus, the strength of association between any two variables differed among levels of the third. We decomposed the third-order term into two-way tables for each bat category, and the zone X period interaction was significant for all except *L. borealis* (*Myotis* spp.: $\chi^2=942.20$, df=2, $P<0.001$; *E. fuscus/L. noctivagans*: $\chi^2=24.00$, df=2, $P<0.001$; *L. cinereus*: $\chi^2=13.25$, df=2, $P=0.001$; *L. borealis*: $\chi^2=1.71$, df=2, $P>0.05$). Considering periods separately (but without *L. borealis*, for which expected counts were <5 in 25% of cells), distributions of passes among bat categories differed among

zones slightly more before (χ^2=376.60, df=6, P<0.001) than during migration (χ^2= 224.30, df=6, P<0.001).

Next, we examined the interaction between zone and bat category (except *L. borealis*) by comparing the proportions of each category with that of the others combined. Dominance by *Myotis* spp. was highest in the rural zone, intermediate in the urban zone and lowest in the transition zone before migration (χ^2>101, df=1, P<0.001 in each case; Fig. 3). During migration, it was lower in the rural zone than in the other two (χ^2>35, df=1, P<0.001 in both cases; Fig. 3), which did not differ (χ^2=1.21, df=1, P>0.05; Fig. 3). Before migration, the proportion of *E. fuscus/L. noctivagans* was highest in the transition zone, intermediate in the urban zone and lowest in the rural zone (χ^2>107, df=1, P<0.001 in each case; Fig. 3). During migration, it was lower in the transition zone than in the other two (χ^2>68, df=1, P< 0.001 in both cases; Fig. 4), which did not differ (χ^2=1.97, df=1, P>0.05; Fig. 3). The proportion of *L. cinereus* was consistently highest in the transition zone and lowest in the urban zone, but only differed between the urban and rural zones during migration (before: χ^2>11, df=1, P<0.01 for comparisons involving the transition zone and χ^2= 2.54, df=1, P>0.05 for rural vs. urban; during: χ^2>82, df=1, P<0.001 for comparisons involving the urban zone and χ^2=6.45, df=1, P=0.01 for rural vs. transition; Fig. 3).

Discussion

This is not the first study to compare the abundance and diversity of urban and non-urban bats, but we believe we avoided five shortcomings of prior investigations. First, only two

Fig. 3 Among-zone differences in the distribution of all bat passes among the three most abundant bat categories, before **a** and during **b** the bat migration period in 2007 and 2008 near Calgary, Alberta. Letters above columns represent significant differences among zones (within a bat category), and numbers are total passes in each zone. Note that proportions may not sum to one *L. borealis* was omitted from the analysis, and that Epfu/Lano refers to the combined *E. fuscus/L. noctivagans* bat category
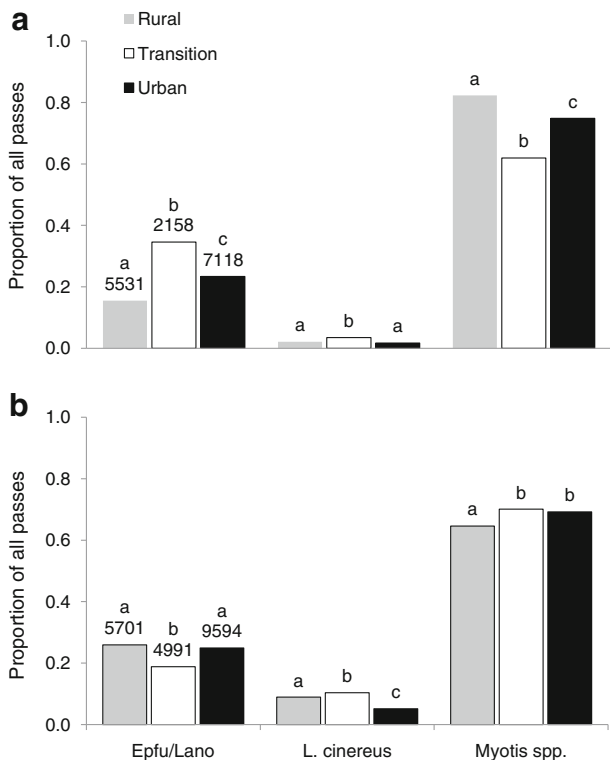
recent studies (Johnson et al. 2008; Loeb et al. 2009) combined acoustic and capture data, as recommended because of the different biases of each technique (Kunz et al. 2009). Other studies (e.g., Gaisler et al. 1998; Gehrt and Chelsvig 2003; Duchamp and Swihart 2008) used only one data source. Second, many studies (e.g., Geggie and Fenton 1985; Walsh and Harris 1996b; Avila-Flores and Fenton 2005) did not survey bats for long enough each night. Sampling for at least four hours, but preferably all night, is recommended for proper bat surveys (e.g., Richards 2001) because timing of bat activity differs among nights, sites (Hayes 1997) and species (Kunz 1973). Third, given potentially significant yearly variation in bat activity (Hayes 1997), surveys limited to a single season (e.g., Vaughan et al. 1997; Avila-Flores and Fenton 2005) seem ill-suited to extrapolating results to years other than the one sampled. Fourth, bat surveys should control for the effect of weather, especially temperature (Kunz et al. 2009), but many studies (e.g., Gehrt and Chelsvig 2004; Rainho 2007; Loeb et al. 2009) did not. Finally, some studies drew inappropriate conclusions by comparing urban data from one year to rural data from other years (Kurta and Teramino 1992) or dedicating unequal sampling effort to urban and non-urban surveys (Sparks et al. 1998).

If the abundance and distribution of temperate-zone bats is mainly limited by roost availability (Humphrey 1975), then the abundance of trees and buildings in Calgary should attract individuals of all species in our study area (except *M. ciliolabrum*, which rarely uses either type of roost), resulting in increased urban bat-abundance. Our finding that activity was higher in the urban than in the rural zone supports this prediction. Increased urban bat-activity has been documented in only two other locales. In the UK, bats used urban habitats more than expected based on availability, but only in areas of intensive agriculture (Walsh and Harris 1996a, b). Most of those urban habitats were residential sectors of small municipalities, unlike the heavily built-up areas surrounding our urban sites. In Chicago, Illinois, bat activity was positively correlated with an index of urban development (Gehrt and Chelsvig 2003). As Chicago's human population was roughly eight times larger than and twice as dense as that of Calgary, we assume that the impact of urbanization on bats there was even greater than in our study. Woodlands were by far the most important bat habitats in both locales (Walsh and Harris 1996a, b; Gehrt and Chelsvig 2003). Our aim was to assess not the effect of habitat type on bat assemblages, but instead the effects of urbanization, which were positive according to our abundance results.

Assuming that bat diversity is largely determined by the diversity of available roosts (Humphrey 1975), we expected the proliferation of trees and buildings in Calgary to be associated with increased bat diversity. Instead, we found the opposite. The only index consistently maximized in any one zone (urban) was dominance, which is the antithesis of diversity (Magurran 2004). All others, i.e., species richness, α-diversity and evenness, were highest outside Calgary. This reflects the increased dominance by *Myotis* spp., namely *M. lucifugus*, in the city. The loglinear analysis suggests a slightly different pattern of representation by *Myotis* spp., but there is a plausible explanation. Unidentified proportions of passes, although universally small, were smallest in the urban zone and largest in the transition zone (Coleman 2010). In all zones, most of those unknown passes were LF bats, i.e., definitely not *Myotis* spp., but that LF proportion was much lower in the urban zone than in the other two. Thus, while our acoustic analysis tends to generally overestimate representation by *Myotis* spp., it does so least of all in the urban zone.

Our data support our prediction that Prairie bats are more abundant in the city, but not our prediction that they are more diverse. Thus, urbanization, rather than benefitting Prairie bats in general, seems to create attractive habitat for one species (*M. lucifugus*), which drives increased urban bat-abundance. Although most other North American urban-bat

studies also found maximal dominance and minimal evenness in urban areas, they invariably identified *E. fuscus* as the dominant species (e.g., Kurta and Teramino 1992; Gehrt and Chelsvig 2004; Kalcounis-Rueppell et al. 2007; Loeb et al. 2009), and ours is the first report of a different bat dominating an urban assemblage.

Myotis lucifugus, like *E. fuscus*, is synanthropic, i.e., the type of animal most likely to prosper in an urban area (McKinney 2002), but the fact that *E. fuscus* was not dominant is noteworthy for at least two reasons. First, this finding may reflect the geographic bias in urban bat-diversity research, which has rarely considered cities west of the Great Lakes (but see Everette et al. 2001). Second, increased availability of buildings may not be the only driver of high urban abundance of *E. fuscus*. Given that *E. fuscus* and *M. lucifugus* roost in trees and buildings (Davis and Hitchcock 1965; Agosta 2002), urbanization in the Prairies should enhance roost availability for both species. However, compared to *Myotis* spp., *E. fuscus* is better-suited to fast, long-distance flight in uncluttered habitat (Duchamp and Swihart 2008). Similarly, *Tadarida brasiliensis*, which epitomizes this flight style (Norberg and Rayner 1987), was the dominant bat in Distrito Federal, Brazil and in Mexico City (Bredt and Uieda 1996; Avila-Flores and Fenton 2005; respectively). Reduced urban abundance of *Myotis* spp. has been attributed to the fact that they are not as well-adapted as *T. brasiliensis* or *E. fuscus* to cover long distances to access prey in widely spaced urban habitat-fragments (Avila-Flores and Fenton 2005; Duchamp and Swihart 2008). Because the Bow River, Elbow River and Fish Creek flow through Calgary with a fairly continuous riparian buffer, resources for bats may be less patchily distributed in Calgary than in other cities. In other words, perhaps where urbanization is not associated with increased habitat fragmentation, *M. lucifugus* can exploit roosting opportunities as easily as *E. fuscus* does.

Reduced numbers of *E. fuscus* in Calgary could be directly related to abundance of *M. lucifugus*, if *M. lucifugus* occupies most of the available roosts and excludes *E. fuscus*. We reject this scenario. Competition for roost space between two bats that often roost in buildings should be virtually non-existent in a city where such roosts are abundant. Also, where such competition does exist, *E. fuscus*, about twice the mass of *M. lucifugus*, usually wins (Agosta 2002). Finally, we found both species roosting together in two buildings (unpublished data).

Although urbanization affects roost availability for bats, it could also affect prey, and in turn, bat assemblages. For example, variation in species richness of bats among urban parks may reflect variation in insect abundance (Avila-Flores and Fenton 2005). There is also evidence that insect abundance and/or diversity are negatively correlated with urbanization. In particular, urbanization may be associated with increases in small dipterans and declines in larger insects (Jones and Clark 1987). This would effectively increase the preferred prey of *Myotis* spp. and reduce that of larger bats, such as *E. fuscus* (Ober and Hayes 2008). Perhaps this is why foraging activity by *E. fuscus* was greater in rural than in urban habitats (Geggie and Fenton 1985), and upstream than downstream from an urban wastewater treatment plant (Kalcounis-Rueppell et al. 2007).

Four species, *L. borealis*, *M. ciliolabrum*, *M. evotis* and *M. volans*, were rare in our study area, but *M. evotis* is noteworthy because we only captured it at two rural sites on opposite sides of Calgary. One site was the one closest to the Red Deer River valley, and the other, nearly 150 km away, was the one closest to the Rocky Mountain foothills. We are confident that had this bat been present elsewhere, we would have caught it because it is quite easy to capture. *Myotis evotis* is the most common bat in the southern Alberta Rockies and the second most common one along the Red Deer River (Solick and Barclay 2006), so its absence in Calgary may reflect the effect of geography more than that of urbanization. However, it is also conceivable that urbanization is more detrimental to *M. evotis* than to

other bats. It is the only bat in our study area that hunts mainly by gleaning, which involves listening for insect-generated sounds, as opposed to detecting prey using echolocation (Faure and Barclay 1994). We suggest that while urbanization in the Prairies, by increasing total foliage cover, i.e., potential gleaning substrate, could benefit gleaners, urban noise may be more likely to interfere with their foraging than with that of other bats (Schaub et al. 2008).

If we discount rare species, all three zones had equal total species richness, but the transition zone still had the most even bat assemblage, with higher representation by *L. cinereus*. This is surprising because the transition zone was an artificial construct, with a mixture of sites on the edges of and well outside the city. If urbanization is detrimental to bat diversity, then species evenness should be highest in the rural, not the transition zone. At first glance this result may appear similar to findings of maximum diversity at suburban levels of development, which are often attributed to the intermediate disturbance hypothesis (McKinney 2002). However, not only is the correlation between intermediate disturbance and diversity equivocal (Mackey and Currie 2001), but also, our transition sites were not in the suburbs and most were surrounded by similar levels of development as those surrounding rural sites. Representation by bat species or categories was more variable among rural than among urban or transition sites, and finding suitable study sites was much more difficult in the rural zone than in the other two. Thus, we suggest that relatively high evenness in the transition zone was due to a combination of urbanization advantaging *M. lucifugus* over other bats, and to the fact that adequate bat habitat seemed most patchily distributed in the rural zone.

Our study is the most comprehensive assessment of urbanization and bat-assemblage structure to date, incorporating two large datasets. Although it is not the first study to document increased abundance and reduced diversity of urban bats, it is the first to do so in a grassland biome. If urbanization enhances bat diversity anywhere, we argue it is especially likely to do so in grasslands, a landscape where urbanization increases habitat heterogeneity. That we found no evidence of such a positive effect in the largest Canadian Prairie city suggests that urbanization, while advantageous to one or a few synanthropes, is universally detrimental to bat diversity. To confirm this, similar studies in other grassland cities would be worthwhile. It would also be useful to examine urban bat-diversity in deserts, which has not yet been done. In such arid environments, urban irrigation is associated with increased productivity (Shochat et al. 2006) and increased abundance and diversity of ground arthropods (Cook and Faeth 2006). Perhaps it has similar effects on nocturnal, aerial insects, and in turn, on their predators. Our finding that urbanization in Calgary only increased abundance of *M. lucifugus* may relate to the differential effects of urbanization on food availability and/or urban resource distribution on various bat species. However, findings of increased urban abundance could also be indicative of the city as a population source for this species (see also Gehrt and Chelsvig 2003). Research should therefore examine the influence of urbanization on insect prey availability and on bat demography in grassland habitats.

References

Agosta SJ (2002) Habitat use, diet and roost selection by the Big Brown Bat (*Eptesicus fuscus*) in North America: a case for conserving an abundant species. Mamm Rev 32:179–198

Alberta Environmental Protection (1997) 1997 Alberta State of the Environment Report: Terrestrial ecosystems. Alberta Environmental Protection, Edmonton, Alberta

Avila-Flores R, Fenton MB (2005) Use of spatial features by foraging insectivorous bats in a large urban landscape. J Mammal 86:1193–1204

Barclay RMR (1989) The effect of reproductive condition on the foraging behavior of female hoary bats, *Lasiurus cinereus*. Behav Ecol Sociobiol 24:31–37

Barclay RMR (1993) The biology of Prairie bats, In The 3rd Prairie Conservation and Endangered Species Workshop. In Holroyd GL, Dickson HL, Regnier M, Smith HC (eds), Provincial Museum of Alberta, Brandon, Manitoba, pp. 353–357

Barclay RMR, Harder LD (2003) Life histories of bats: life in the slow lane. In: Kunz TH, Fenton MB (eds) Bat ecology. The University of Chicago Press, Chicago, Illinois, pp 209–253

Bate LJ, Wisdom MJ, Wales BC (2007) Snag densities in relation to human access and associated management factors in forests of Northeastern Oregon, USA. Landsc Urban Plann 80:278–291

Bredt A, Uieda W (1996) Bats from urban and rural environments of the Distrito Federal, mid-western Brazil. Chiroptera Neotropical 2:54–57

Chace JF, Walsh JJ (2006) Urban effects on native avifauna: a review. Landsc Urban Plann 74:46–69

Coleman J (2010) The Effects of urbanization on Prairie Bats, In Department of Biological Sciences. p. 206. University of Calgary, Calgary, Alberta.

Cook WM, Faeth SH (2006) Irrigation and land use drive ground arthropod community patterns in an urban desert. Environ Entomol 35:1532–1540

Corben C (2000) Anamusic WAV File Generation Utility

Corben C (2004) Analook bat call analysis system

Cromartie JB (1998) Net migration in the Great Plains increasingly linked to natural amenities and suburbanization. Rural Dev Perspect 13:27–34

Crooks KR, Soulé ME (1999) Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400:563–566

Czech B, Krausman PR, Devers PK (2000) Economic associations among causes of species endangerment in the United States. Bioscience 50:593–601

Davis WH, Hitchcock HB (1965) Biology and migration of the bat, *Myotis lucifugus*, in New England. J Mammal 46:296–313

Duchamp JE, Swihart RK (2008) Shifts in bat community structure related to evolved traits and features of human-altered landscapes. Landscape Ecol 23:849–860

Ecological Stratification Working Group (1995) Terrestrial ecozones, ecoregions, and ecodistricts of Canada: Provinces of Alberta, Saskatchewan, and Manitoba. A national ecological framework for Canada. Agriculture and Agri-Foods Canada, Research Branch Centre for Land and Biological Resources Research and Environment Canada, State of the Environment Directorate, Ecozone Analysis Branch, Ottawa–Hull, Canada

Engqvist L (2005) The mistreatment of covariate interaction terms in linear model analyses of behavioural and evolutionary ecology studies. Anim Behav 70:967–971

Evelyn MJ, Stiles DA, Young RA (2004) Conservation of bats in suburban landscapes: roost selection by *Myotis yumanensis* in a residential area in California. Biol Conserv 115:463–473

Everette AL, O'Shea TJ, Ellison LE, Stone LA, McCance JL (2001) Bat use of a high-plains urban wildlife refuge. Wildl Soc Bull 29:967–973

Faure PA, Barclay RMR (1994) Substrate-gleaning versus aerial-hawking: plasticity in the foraging and echolocation behaviour of the long-eared bat, *Myotis evotis*. J Comp Physiol A Neuroethol Sens Neural Behav Physiol 174:651–660

Fenton MB (2003) Science and the conservation of bats: where to next? Wildl Soc Bull 31:6–15

Fenton MB, Fleming TH (1976) Ecological interactions between bats and nocturnal birds. Biotropica 8:104–110

Fischer J, Stott J, Law BS, Adams MD, Forrester RI (2009) Designing effective habitat studies: quantifying multiple sources of variability in bat activity. Acta Chiropterologica 11:127–137

Forman RTT, Alexander LE (1998) Roads and their major ecological effects. Annu Rev Ecol Syst 29:207–231

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

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

Gauthier DA, Wiken EB (2003) Monitoring the conservation of grassland habitats, prairie ecozone, Canada. Environ Monit Assess 88:343–364

Geggie JF, Fenton MB (1985) A comparison of foraging by *Eptesicus fuscus* (Chiroptera: Vespertilionidae) in urban and rural environments. Can J Zool 63:263–266

Gehrt SD, Chelsvig JE (2003) Bat activity in an urban landscape: patterns at the landscape and microhabitat scale. Ecol Appl 13:939–950

Gehrt SD, Chelsvig JE (2004) Species-specific patterns of bat activity in an urban landscape. Ecol Appl 14:625–635

Ghitter G, Smart A (2009) Mad cows, regional governance, and urban sprawl: path dependence and unintended consequences in the Calgary Region. Urban Aff Rev 44:617–644

Hayes JP (1997) Temporal variation in activity of bats and the design of echolocation-monitoring studies. J Mammal 78:514–524

Holloway GL, Barclay RMR (2000) Importance of prairie riparian zones to bats in southeastern Alberta. Ecoscience 7:115–122

Holloway GL, Barclay RMR (2001) Myotis ciliolabrum. Mammalian Species 670:1–5

Hourigan CL, Johnson C, Robson SKA (2006) The structure of a micro-bat community in relation to gradients of environmental variation in a tropical urban area. Urban Ecosyst 9:67–82

Humphrey SR (1975) Nursery roosts and community diversity of Nearctic bats. J Mammal 56:321–346

Johnson JB, Gates JE, Ford WM (2008) Distribution and activity of bats at local and landscape scales within a rural–urban gradient. Urban Ecosyst 11:227–242

Jones RC, Clark CC (1987) Impact of watershed urbanization on stream insect communities. J Am Water Resour Assoc 23:1047–1055

Kalcounis-Rueppell MC, Payne VH, Huff SR, Boyko AL (2007) Effects of wastewater treatment plant effluent on bat foraging ecology in an urban stream system. Biol Conserv 138:120–130

Kirsten I, Klomp NI (1998) Microchiroptera in urban, rural and forest areas of southern NSW. Australas Bat Soc Newsl 11:28–31

Kunz TH (1973) Resource utilization: temporal and spatial components of bat activity in central Iowa. J Mammal 54:14–32

Kunz TH, Fenton MB (2003) Bat ecology. University of Chicago Press, Chicago

Kunz TH, Hodgkison R, Weise CD (2009) Methods of capturing and handling bats. In: Kunz TH, Parsons S (eds) Ecological and behavioral methods for the study of bats, 2nd edn. Johns Hopkins University Press, Baltimore, pp 3–35

Kurta A, Teramino JA (1992) Bat community structure in an urban park. Ecography 15:257–261

Lac S, Colan C (2004) South Saskatchewan river basin biogeography. University of Regina, Regina, SK

Larson DJ, Hayes JP (2000) Variability in sensitivity of Anabat II bat detectors and a method of calibration. Acta Chiropterologica 2:209–213

Lauriault J (1989) Identification guide to the trees of Canada. National Museum of Natural Sciences, Ottawa

Lemmen DS, Vance RE, Wolfe SA, Last WM (1997) Impacts of future climate change on the southern Canadian Prairies: a paleoenvironmental perspective. Geosci Can 24:121–133

Loeb SC, Post CJ, Hall ST (2009) Relationship between urbanization and bat community structure in national parks of the southeastern U.S. Urban Ecosyst 12:197–214

Mackey RL, Currie DJ (2001) The diversity-disturbance relationship: is it generally strong and peaked? Ecology 82:3479–3492

Magurran AE (2004) Measuring biological diversity, 2nd edn. Blackwell Science Ltd., Oxford

Marzluff JM, Ewing K (2001) Restoration of fragmented landscapes for the conservation of birds: a general framework and specific recommendations for urbanizing landscapes. Restor Ecol 9:280–292

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

McKinney ML (2002) Urbanization, biodiversity, and conservation. Bioscience 52:883–890

McKinney ML (2006) Urbanization as a major cause of biotic homogenization. Biol Conserv 127:247–260

Moss EH (1932) The vegetation of Alberta: IV. The poplar association and related vegetation of central Alberta. J Ecol 20:380–415

Niemelä J (1999) Is there a need for a theory of urban ecology? Urban Ecosyst 3:57–65

Norberg UM, Rayner JMV (1987) Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. Phil Trans Roy Soc Lond B Biol Sci 316:335–427

Ober HK, Hayes JP (2008) Prey selection by bats in forests of western Oregon. J Mammal 89:1191–1200

Ormsbee PC, McComb WC (1998) Selection of day roosts by female long-legged Myotis in the central Oregon Cascade Range. J Wildl Manage 62:596–603

Potere D, Schneider A, Angel S, Civco DL (2009) Mapping urban areas on a global scale: which of the eight maps now available is more accurate? Int J Remote Sens 30:6531–6558

Racey PA, Entwistle AC (2003) Conservation Ecology of Bats. In: Kunz TH, Fenton MB (eds) Bat ecology. The University of Chicago Press, Chicago, pp 680–743

Rainho A (2007) Summer foraging habitats of bats in a Mediterranean region of the Iberian Peninsula. Acta Chiropterologica 9:171–181

Richards GC (2001) Towards defining adequate bat survey methodology: why electronic call detection is essential throughout the night. Australas Bat Soc Newsl 16:24–28

Samson F, Knopf F (1994) Prairie conservation in North America. Bioscience 44:418–421

Schaub A, Ostwald J, Siemers BM (2008) Foraging bats avoid noise. J Exp Biol 211:3174–3180

Seaby RM, Henderson PA (2006) Species diversity and richness. Pisces Conservation Ltd., Lymington

Shochat E, Warren PS, Faeth SH, McIntyre NE, Hope D (2006) From patterns to emerging processes in mechanistic urban ecology. Trends Ecol Evol 21:186–191

Solick DI, Barclay RMR (2006) Morphological differences among western long-eared myotis (Myotis evotis) populations in different environments. J Mammal 87:1020–1026

Solick DI, Barclay RMR (2007) Geographic variation in the use of torpor and roosting behaviour of female western long-eared bats. J Zool 272:358–366

Solow AR (1993) A simple test for change in community structure. J Anim Ecol 62:191–193

Sparks DW, Laborda JA Jr, Whitaker JO (1998) Bats of the Indianapolis International Airport as compared to a more rural community of bats at Prairie Creek. Proc Indiana Acad Sci 107:171–179

Statistics Canada (2007) Population and dwelling counts, for census metropolitan areas and census agglomerations, 2006 and 2001 censuses—100% data

Sun H, Forsythe W, Waters N (2007) Modeling urban land use change and urban sprawl: Calgary, Alberta, Canada. Network Spatial Econ 7:353–376

Thomas DW (1988) The distribution of bats in different ages of Douglas-fir forests. J Wildl Manage 52:619–626

Thomas DW, LaVal RK (1988) Survey and census methods. In: Kunz TH (ed) Ecological and behavioral methods for the study of bats. Smithsonian Institution Press, Washington, pp 77–89

Ticer CL, Ockenfels RA, Devos JC, Morrell TE (1998) Habitat use and activity patterns of urban-dwelling javelina. Urban Ecosyst 2:141–151

United Nations (2008) World Urbanization Prospects: The 2007 Revision Highlights. United Nations Dept. of Economic and Social Affairs, Population Division, New York, New York

van der Ree R, McCarthy MA (2005) Inferring persistence of indigenous mammals in response to urbanisation. Anim Conserv 8:309–319

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

Vujnovic K, Wein RW, Dale MRT (2002) Predicting plant species diversity in response to disturbance magnitude in grassland remnants of central Alberta. Can J Bot 80:504–511

Walsh AL, Harris S (1996a) Factors determining the abundance of vespertilionid bats in Britain: geographical, land class and local habitat relationships. J Appl Ecol 33:519–529

Walsh AL, Harris S (1996b) Foraging habitat preferences of vespertilionid bats in Britain. J Appl Ecol 33:508–518

Wickett SM (1900) City government in Canada. Polit Sci Q 15:240–259

Willis CKR, Brigham RM (2005) Physiological and ecological aspects of roost selection by reproductive female hoary bats (Lasiurus cinereus). J Mammal 86:85–94