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Distribution and activity of bats at local and landscape scales within a rural–urban gradient

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Abstract We examined the relationship between bat species activity and composition and the extent of forest cover and urbanization in and adjacent to 11 U.S. National Park Service, National Capital Region Parks in Maryland, Virginia, West Virginia, and Washington, D.C., from 2003–2004, using mist nets, harp traps, acoustical detectors, and visual observations in a variety of habitats. Our efforts included 363 trap nights across 74 sites along with acoustical sampling at 362 sites. We captured 383 bats and identified 6,380 echolocation passes of 6 species. Both overall and species-specific activities were affected more by forest fragmentation within parks than by urbanization adjacent to parks. With an ability to exploit anthropogenic structures for day-roosts, big brown bats (*Eptesicus fuscus*) were the most ubiquitous and probably the most abundant species in NCR Parks, particularly in forested, urban parks. Northern myotis (*Myotis septentrionalis*), and to a lesser extent, little brown myotis (*Myotis lucifugus*) were more prevalent in forested, rural parks of the Ridge and Valley and Blue Ridge than in eastern, less forested urban parks of the Piedmont and Coastal Plain physiographic provinces. Retention of larger, residual forest tracts and day-roosting habitat (i.e., trees and snags) would be beneficial to most species, as urban expansion continues throughout the region.

Keywords Bats · Forest fragmentation · Landscape · National capital region · Urbanization

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Introduction

Bat conservation and management have received considerable recent attention due to both real and perceived population declines that have been attributed to numerous human-induced environmental changes and degradation (Fenton 1997; Pierson 1998; O'Shea et al. 2003). Although human population growth with concomitant land use changes such as urbanization undoubtedly have had an impact on bat populations, community compositions, and habitat use of bats through modification or loss of roosting substrates, foraging habitats, and insect prey availability (Kurta and Teramino 1992; Pierson 1998; Ghert and Chelsvig 2003, 2004; Avila-Flores and Fenton 2005), these changes that may be directly attributed to urbanization often are difficult to quantify *post hoc*. Recent research indicates different bat species vary in their response to urbanization (Kurta and Teramino 1992; Ghert and Chelsvig 2004). Although some species such as big brown bats (*Eptesicus fuscus*) exploit urban areas as roosting and foraging habitats (Everette et al. 2001; Menzel et al. 2001), other species such as Indiana myotis (*Myotis sodalis*) are more sensitive to urbanization (Duchamp et al. 2004; Sparks et al. 2005). Within urbanized landscapes, many bat species use remnant forest patches, as their high mobility allows them to utilize patches in otherwise unsuitable surroundings (Clergeau et al. 2001; Ghert and Chelsvig 2003). However, the importance of forest patch size and connectivity in influencing bat distributions and population viability is poorly understood (Fenton 1997).

Bat habitat selection may occur as a hierachical series of decisions, beginning at the geographic or landscape scale and ending at the local or home-range scale (Johnson 1980; Ford et al. 2006; Loeb and O'Keefe 2006). Differences in bat community composition at the distributional and landscape scales have been attributed to natural influences, including summer roost diversity, proximity to winter hibernacula, topography, latitude, and climate conditions (Humphrey 1975; Graham 1983; Furlonger et al. 1987; Patten 2004) as well as human-induced land use changes, such as urbanization and deforestation (Ghert and Chelsvig 2003, 2004; Duchamp et al. 2004; Owen et al. 2004; Sparks et al. 2005). At the local scale, habitat use likely is a consequence of day-roost preferences and availability, presence of water sources, and foraging preferences, which are largely dictated by morphological and echolocation adaptations (Barclay 1986; Aldridge and Rautenbach 1987; Kalcounis and Brigham 1995; Ford et al. 2005, 2006).

Our objective was to determine if bat species distributions and activity levels were affected by local and/or landscape scale attributes along the urban–rural gradient in the National Capital Region (NCR), extending northwest of and including Washington, D.C. Specifically, we examined species-specific and overall bat activity throughout the NCR at parklands, with representative parks occurring in both rural and urban areas, and containing varying degrees of forest fragmentation. This area encompasses both karst and non-karst geology and is entirely within known migrating distances of several cavernicolous bat species (Griffin 1940; Barbour and Davis 1969; Franz and Slifer 1976). We examined differences among bat species distributions and activity levels, which may be dictated according to local- (e.g., amount of forest cover, proximity to water sources) or landscape-scale attributes (distance to hibernacula, degree of urbanization), or some combination thereof (Humphrey 1975).

Based on previous research on bat foraging preferences and sensitivity to forest structure and urbanization, we developed *a priori* predictions of species-specific and overall bat activity among the NCR parks. Big brown bats should occur more frequently in urban parks because of greater availability of anthropogenic structures (e.g., buildings), and would more frequently be detected in fragmented (i.e., less forest cover and more open area) parks

regardless of urban or rural setting due to its preference for foraging in open, uncluttered habitats (Geggie and Fenton 1985; Barclay 1986; Duchamp et al. 2004; Ford et al. 2005). Similarly, the foliage roosting hoary bat (*Lasiurus cinereus*) and eastern red bat (*Lasiurus borealis*), adapted for foraging in fully open conditions and less cluttered conditions, respectively, should more frequently be detected in fragmented parks without regard to condition of urbanization (Furlonger et al. 1987; Ghert and Chelsvig 2004, Ford et al. 2005, 2006, Yates and Muzika 2006, Walters et al. 2007). Eastern pipistrelles (*Pipistrellus subflavus*) should be detected similarly between forested and fragmented parks, and more frequently at rural parks, which were closer to hibernacula (Menzel et al. 2002a, Ghert and Chelsvig 2004, Ford et al. 2005). We expected that northern myotis (*Myotis septentrionalis*) and eastern small-footed myotis (*Myotis leibii*), a Maryland state-endangered species, would be encountered more frequently in rural, forested parks (Caceres and Barclay 2000; Owen et al. 2003; Patriquin and Barclay 2003; Ghert and Chelsvig 2004; Ford et al. 2005; Wund 2006). Although Indiana myotis, a federally-listed endangered species, also most likely would be detected in forested parks (Clawson 2002; Ford et al. 2005), they could occur throughout the landscape regardless of distance to hibernacula because of their ability to migrate >500 km (Kurta and Murray 2002). Unlike the other myotine bats, little brown myotis (*Myotis lucifugus*) is more likely to be detected in fragmented parks throughout the NCR because they are known to forage in various cover types, roost in buildings, and migrate >200 km, well within range of all NCR Parks (Griffin 1940; Ghert and Chelsvig 2004; Ford et al. 2005). We predicted overall bat activity would be higher at water sources and in fragmented parks than in forested parks, and similarly between rural and urban parks throughout the landscape (Johnson et al. 2002; Broders et al. 2003; Ghert and Chelsvig 2003; Russo and Jones 2003; Owen et al. 2004; Ford et al. 2005). The remaining two extant species, i.e., silver-haired bats (*Lasionycteris noctivagans*) and evening bats (*Nycticeius humeralis*), which occur in the region, may use both fragmented and forested parks (Hutchinson and Lacki 1999; Carter et al. 2004). However, evening bat distribution is restricted to the Coastal Plain, whereas silver-haired bats, at least during summer, are more frequently detected in the mountainous provinces (Paradiso 1969).

Study areas

We inventoried bat communities of the following U.S. National Park Service, NCR Parks: Antietam National Battlefield (ANTI), Catoctin Mountain Park (CATO), Chesapeake and Ohio Canal National Historical Park (CHOH), George Washington Memorial Parkway (GWMP), Harpers Ferry National Historical Park (HAFE), Manassas National Battlefield Park (MANA), Monocacy National Battlefield (MONO), National Capital Parks-Central (NACC), National Capital Parks-East (NACE), Rock Creek Park (ROCR), and Wolf Trap National Park for the Performing Arts (WOTR). The parks were located in Maryland, northern Virginia, Washington, D.C., and West Virginia, and ranged in area from 53 ha at WOTR to 7,788 ha at CHOH, encompassing a total of 26,203 ha (Appendix A). Land uses and habitats surrounding and within the NCR Parks were a mosaic of urban development, agricultural fields, upland and riparian forests, lentic and lotic waterways, and wetlands. Parks near the Washington D.C., metropolitan area had relatively high percentages of residential/urban area adjacent to them compared to parks distant from Washington, D.C. In both urban and rural settings, NCR Parks varied in percentages of cover types within their boundaries (Appendix A).

The NCR Parks were located across four physiographic provinces including, from east to west, Coastal Plain (CHOH, GWMP, NACC, NACE), Piedmont (CHOH, GWMP, MANA, MONO, ROCR, WOTR), and the mountainous Blue Ridge (CATO, CHOH, HAFE) and Ridge and Valley (ANTI, CHOH, HAFE). Elevations ranged from sea level in the Washington, D.C., area, to >500 m in the Blue Ridge Province (Schmidt 1993). Washington, D.C. had an average annual rainfall of 104.5 cm and an average summer (June–August) temperature of 23.2°C. In the Ridge and Valley, Cumberland, Maryland, the western terminus of CHOH, had an average annual rainfall of 95.5 cm and an average summer temperature of 22.5°C. In the Blue Ridge, CATO had an average annual rainfall of 112.8 cm and an average summer temperature of 21.8°C (NOAA 2005).

At the time of our study, virtually no quantitative research had been conducted on bat communities in the NCR Parks. The majority of previous efforts had focused on hibernacula monitoring in rural western Maryland and along CHOH (Gates et al. 1984; Fisher and Fisher 1997). A limited amount of descriptive bat inventory work had been conducted in CATO, MANA, and GEWA (Cherry 1985; Hobson 2001; W. Bulmer, Northern Virginia Community College, personal communication).

Materials and methods

To inventory bats, we used a combination of capture and acoustic methods during summer (May–August) 2003–2004. Differences in bat species detectability when using acoustic and capture methods are well documented and necessitate using a complementary combination of acoustic and capture methods to yield a more complete inventory of bat species (Kunz and Brock 1975; Murray et al. 1999; O'Farrell and Gannon 1999; Flaquer et al. 2007).

To capture bats, we erected mist nets (Avinet, Inc., Dryden, New York) over stream corridors, small pools, hiking trails, and service roads. We placed harp traps (1 × 1 m; Bat Conservation and Management, Carlisle, Pennsylvania) in or adjacent to cave entrances to capture bats entering or exiting caves. We completely surrounded harp traps with tarpaulin to prevent bats from bypassing the trap. Typically, we mist netted and harp trapped for 5-h sessions following sunset. We attempted no bat inventories during periods of rain, wind ≥20 km/h, or temperatures <10°C because these conditions can influence bat activity levels. We followed Menzel et al. (2002b) to determine species, sex, age, weight, forearm length, and reproductive condition of captured bats prior to release. Bats were not marked to identify recaptures. However, recaptures of individuals within a night when mist netting in forested (i.e., non-hibernacula) settings is quite uncommon (LaVal and LaVal 1980).

We used Anabat II (Titley Electronics, Ballina, Australia) broadband, frequency-division, bat detectors to acoustically monitor for and record bat echolocation passes within the parks. Bat echolocation passes are a series of echolocation pulses or calls emitted by bats as they navigate and search for food (Thomas 1988; Broders 2003). We acoustically monitored at multiple sites within various land covers (e.g., forests, fields, and water sources) at each park to exploit the various foraging strategies exhibited by bat species that potentially occur in the parks and across the region (Menzel 2003; Ford et al. 2005). All sites were separated by >30 m, the approximate zone of reception of the Anabat II bat detector (Livengood 2003). Unlike mist netting sites, which typically are restricted to forested riparian corridors to be most effective, we positioned our acoustic monitoring sites throughout each park, including at mist net sites on nights when those sites were not being mist netted. We conducted acoustic monitoring for a single, 20-min period at each site between sunset and 0200 h, i.e., concurrent with mist netting. Our echolocation passes were

recorded to an Anabat CompactFlash storage Zero-Crossing Analysis Interface Module (ZCAIM) and downloaded to a computer for analysis using Analook 4.8p software (Corben 2001). We identified echolocation passes by comparing the structure, e.g., frequency-modulated and quasi-constant frequency, frequency, and change in octaves per second, of our unknowns to a library comprised of echolocation passes collected from hand-released bats marked with chemiluminescent tags collected throughout the southeastern and mid-Atlantic United States (Fenton and Bell 1981; O'Farrell et al. 1999; Murray et al. 2001; Menzel et al. 2002a). We only attempted identification of echolocation passes containing ≥3 pulses (Johnson et al. 2002). However, echolocation passes containing ≥1 echolocation pulse, identified or not, counted towards total bat activity. All echolocation passes were identified by the senior author to reduce bias and increase identification precision (O'Farrell et al. 1999; Johnson et al. 2002). Our identifications were limited to species as no techniques exist to reliably distinguish male/female or adult/juvenile bat echolocation calls. We used Horn's Index of Similarity to compare relative frequencies of species detected using acoustic monitoring and capture techniques. The index ranges from 0–1 with values nearer to 1 indicating similar relative frequencies detected among methods (Krebs 1999).

We used ArcView (Version 3.2, Environmental Systems Research Institute, Redlands, California) and the 2001 National Land Cover Dataset (NLCD) to analyze land cover types within each of the NCR Parks and adjacent surrounding areas (Homer et al. 2004). Percentage of each land cover type was calculated within the political boundary of each park. Obviously, bats do not recognize political boundaries of parks; however they are affected by surrounding land uses. Therefore, we calculated the percentage of each land cover type in a 2-km buffer surrounding each park (Ghert and Chelsvig 2003). All extant bat species in the region are known to forage up to 2 km or more from their roost sites (Menzel et al. 2001; Owen et al. 2003; Elmore et al. 2005; Broders et al. 2006). We consolidated the original 19 land cover types in the NLCD into six land cover types: water, developed (low and high intensity residential, commercial, industrial, and transportation), barren (emergent rock, sand, quarries, and mines), forested, open (pastures, row crops, and urban grasses), and wetlands (woody and emergent herbaceous wetlands). We classified parks with ≥57.3% (median among all parks) forest cover as forested parks and all others as fragmented parks regardless of extant forest complexity or connectivity. To further differentiate park classes, we measured the distance from each park to the center of the Washington, D.C., metropolitan area. We considered those parks ≤50 km of Washington, D.C., and surrounded by ≥30.5% (median among all parks) development as urban parks, whereas the remaining parks were considered rural. The portion of CHOH that was ≤50 km of Washington, D.C., was considered urban and forested according to our criteria. Accordingly, all sample sites within the parks were in one of four landscape type categories: forested/rural, forested/urban, fragmented/rural, and fragmented/urban. Because bat activity typically is higher near water sources than in upland areas, we also classified each sampling site as a water or non-water site (Grindal et al. 1999; Owen et al. 2004). Furthermore, to account for the possible influence of distance from sampling sites to hibernacula located from the Blue Ridge physiographic province west (Franz and Slifer 1976), we assigned sampling sites to one of three landform/physiographic province types: mountain (Blue Ridge and Ridge and Valley), Piedmont, or Coastal Plain (Schmidt 1993). To determine if local site, landscape, or province affected bat activity, we used generalized linear models to examine species-specific and combined species (i.e., all species combined) activity in the various landscape types, provinces, and water/non-water sites (PROC GENMOD; Nelder and Wedderburn 1972; SAS Institute, Inc. 2004). Using *a priori* contrasts, we examined differences in bat activity between the following categorical combinations: urban and rural

areas (regardless of forested/fragmented), forested and fragmented areas (regardless of urban/rural), forested/rural and fragmented/rural, forested/urban and fragmented/urban, forested/rural and forested/urban, and fragmented/rural and fragmented/urban.

Results

We mist netted at 74 sites among the 11 NCR Parks, accounting for 363 mist-net nights (number of mist nets×number of nights) and 42647.45 mist net hours [mist net area (m^2)× hours open]. We captured 383 bats representing six species: big brown bats, eastern red bats, hoary bats, little brown myotis, northern myotis, and eastern pipistrelles (Appendix B). We captured bats in all parks and at 75.7% of mist-net sites. We acoustically monitored 362 sites among NCR Parks, therein recording 6,380 echolocation passes. We were able to identify 4,287 echolocation passes to species or species group. We detected the same six species as identified from mist netting. Big brown bats were the most frequently detected species, comprising 53.5% of identifiable passes at 53.9% of all acoustic monitoring sites (Appendix C).

Captured species richness ranged from one at NACC to six at CHOH and ROCR; acoustic species richness ranged from three at MANA to six at ANTI, CATO, CHOH, HAFE, MONO, and ROCR, which was the same when considering both acoustic and capture data. Generally, bat species richness was higher in rural parks and in forested parks. Horn's Index of Similarity was 0.85 between acoustic and capture techniques overall and >0.69 within each landscape type, indicating similar relative frequencies of each species were recorded between the two methods.

Bat activity varied among physiographic provinces. Hoary bat (χ^2=6.77, P=0.034) and northern myotis (χ^2=6.00, P=0.050) activity decreased from the mountains (i.e., Blue Ridge and west) to the Coastal Plain (Table 1). Little brown myotis (χ^2=8.12, P=0.017) activity was greatest in the mountains, next highest in the Coastal Plain, and lowest in the Piedmont (Table 1). Eastern pipistrelle (χ^2=10.10, P=0.006) activity was greatest in the Piedmont, next highest in the mountains, and lowest in the Coastal Plain (Table 1). Big brown bats (χ^2=1.31, P=0.519), eastern red bats (χ^2=0.13, P=0.935), and overall bat activity (χ^2=1.22, P=0.544) did not vary significantly among provinces (Table 1). Eastern red bat (χ^2=13.99, P<0.001), eastern pipistrelle (χ^2=23.45, P<0.001), and overall bat

Table 1 Mean (±SE) bat echolocation passes recorded among physiographic provinces in the National Capital Region Parks, 2003–2004

Species	Physiographic province		
	Mountain (n=127)	Piedmont (n=116)	Coastal plain (n=119)
Eptesicus fuscus	2.47 (0.79)	7.25 (1.44)	9.56 (1.94)
Lasiurus borealis	4.76 (1.38)	1.58 (0.47)	1.34 (0.45)
Lasiurus cinereus	0.30 (0.07)	0.04 (0.03)	0.03 (0.02)
Myotis lucifugus	0.30 (0.08)	0.02 (0.01)	0.18 (0.07)
Myotis septentrionalis	0.61 (0.22)	0.15 (0.07)	0.02 (0.01)
Pipistrellus subflavus	1.69 (0.88)	3.20 (0.88)	0.79 (0.20)
All species combined	16.17 (2.87)	18.34 (2.75)	18.47 (2.76)

Sampling occurred over single 20-min sessions at each site

Mountain Blue Ridge and Ridge and Valley physiographic provinces combined

activity (χ^2=9.24, P=0.002) was higher at water sources. The presence of or proximity to water had no significant effect on big brown bat (χ^2=0.36, P=0.546), hoary bat (χ^2=0.29, P=0.587), little brown myotis (χ^2=0.02, P=0.876), or northern myotis (χ^2=0.91, P=0.341) activity. Forest fragmentation, urbanization, or some combination thereof had a significant effect on overall (i.e., all species combined) bat activity and every recorded species (Table 2). Urbanization alone did not have an effect on bat activity, but fragmentation had an effect on all but hoary bats and eastern pipistrelles (Table 2). Overall bat activity, eastern red bat activity, and little brown myotis activity were higher in forested parks than fragmented parks, regardless of urbanization (Table 2). Big brown bat activity was highest in forested, urban parks (Table 2). Hoary bat activity was highest in fragmented, rural parks (Table 2). Northern myotis activity was highest in forested, rural parks, similar in forested, urban parks and fragmented, rural parks, and lowest in fragmented, urban parks (Table 2). Eastern pipistrelle activity was not affected by fragmentation or urbanization alone, but was higher in fragmented, urban parks than in fragmented, rural parks (Table 2).

Discussion

We positively identified six of the ten bat species that could potentially occur within the NCR Parks. All six are considered common in the mid-Atlantic region (Paradiso 1969, Harvey et al. 1999). Most urban NCR Parks had lower species richness than most rural parks, similar to the Detroit, Michigan metropolitan area where bat species diversity and evenness were lower in urban areas compared to rural areas (Kurta and Teramino 1992). Conversely, in the Chicago, Illinois region, higher overall and species-specific bat activity levels were documented in urban parks than in rural parks dominated by agricultural use (Ghert and Chelsvig 2003). In northern, temperate France, up to 53% of potential bat species occurred in urban parks (DeCornulier and Clergeau 2001). At ROCR, a largely forested park surrounded by downtown Washington, D.C., bat species richness equaled that of the sampled rural parks. Rock Creek Park appears to provide an outlier of habitat or refugia for many bat species in an otherwise urban setting. Throughout the NCR, forested parks had higher bat activity than fragmented parks, emphasizing the importance of retaining forest structure regardless of rural or urban setting.

Some species-specific trends were apparent among NCR Parks. Big brown bats, eastern red bats, and eastern pipistrelles were the most ubiquitous bat species throughout the landscape, occurring at all parks. This distribution may be attributed to their broad niche and generalist foraging behaviors and ability to migrate to all NCR Parks (Hutchinson and Lacki 1999; Ford et al. 2005; Menzel et al. 2005). Still, some variation in big brown bat activity did occur among parks. Big brown bat activity was highest in forested, urban parks and was relatively low in fragmented and rural parks, similar, in part, to our prediction. Assuming that some minimum threshold of less developed or riparian areas exist, urban areas typically have higher big brown bat activity than nearby rural areas (Kurta and Teramino 1992; Everette et al. 2001; Ghert and Chelsvig 2004). Undoubtedly, urban parks and surrounding development can and do provide an abundance of potential big brown bat roosting sites, natural and anthropogenic, but it is difficult to establish if they provide more roosting sites than rural areas. Big brown bats roosting in urban areas readily use surrounding parks or natural areas when foraging (Everette et al. 2001; Menzel et al. 2001). Within NCR Parks, ROCR is a quintessential example of a park surrounded by urbanization, i.e., abundant anthropogenic roosts, while containing a substantial corridor

Table 2 Mean (±SE) bat echolocation passes and preplanned contrasts between forested, fragmented, urban, and rural National Capital Region Parks, 2003–2004

	Contrast											
	Rural vs urban				Forested vs fragmented				Rural forested vs rural fragmented			
	Mean (±SE)		χ^2	P	Mean (±SE)		χ^2	P	Mean (±SE)		χ^2	P
	Rural	Urban			Forested	Fragmented			Rural forested	Rural fragmented		
Eptesicus fuscus	2.67 (0.71)	9.01 (1.34)	1.30	0.254	7.23 (1.07)	3.30 (0.74)	4.59	0.032	2.71 (0.85)	2.53 (1.22)	0.27	0.605
Lasiurus borealis	4.42 (1.18)	1.30 (0.30)	0.47	0.492	3.15 (0.68)	0.81 (0.27)	10.88	0.001	5.40 (1.50)	0.97 (0.52)	7.87	0.005
Lasiurus cinereus	0.25 (0.06)	0.03 (0.02)	0.18	0.672	0.09 (0.03)	0.25 (0.09)	1.90	0.168	0.17 (0.05)	0.56 (0.20)	6.46	0.011
Myotis lucifugus	0.25 (0.07)	0.11 (0.04)	2.14	0.143	0.21 (0.05)	0.02 (0.02)	5.64	0.018	0.31 (0.09)	0.06 (0.04)	1.54	0.215
Myotis septentrionalis	0.56 (0.19)	0.05 (0.02)	3.76	0.053	0.34 (0.11)	0.02 (0.02)	13.56	<0.001	0.71 (0.24)	0.06 (0.06)	8.43	0.004
Pipistrellus subflavus	1.71 (0.78)	2.00 (0.46)	2.91	0.088	1.62 (0.44)	2.75 (1.10)	0.43	0.510	1.80 (0.94)	1.39 (1.26)	0.66	0.418
All species combined	15.81 (2.61)	18.95 (2.04)	1.80	0.179	19.52 (1.98)	11.24 (2.19)	11.47	<0.001	17.76 (3.18)	9.00 (3.58)	4.91	0.027

	Contrast											
	Urban forested vs urban fragmented				Rural forested vs urban forested				Rural fragmented vs urban fragmented			
	Mean (±SE)		χ^2	P	Mean (±SE)		χ^2	P	Mean (±SE)		χ^2	P
	Urban forested	Urban fragmented			Rural forested	Urban forested			Rural fragmented	Urban fragmented		
Eptesicus fuscus	10.59 (1.72)	3.84 (0.92)	7.14	0.008	2.71 (0.85)	10.59 (1.72)	2.81	0.093	2.53 (1.22)	3.84 (0.92)	0.08	0.783
Lasiurus borealis	1.48 (0.38)	0.69 (0.28)	3.25	0.071	5.40 (1.50)	1.48 (0.38)	1.42	0.234	0.97 (0.52)	0.69 (0.28)	0.00	0.977
Lasiurus cinereus	0.03 (0.02)	0.04 (0.03)	0.00	0.945	0.17 (0.05)	0.03 (0.02)	0.89	0.344	0.56 (0.20)	0.04 (0.03)	0.02	0.875
Myotis lucifugus	0.14 (0.06)	0.00 (0.00)	4.24	0.040	0.31 (0.09)	0.14 (0.06)	0.71	0.400	0.06 (0.04)	0.00 (0.00)	2.45	0.118
Myotis septentrionalis	0.06 (0.02)	0.00 (0.00)	5.96	0.015	0.71 (0.24)	0.06 (0.02)	3.23	0.073	0.06 (0.06)	0.00 (0.00)	2.21	0.137
Pipistrellus subflavus	1.49 (0.33)	3.69 (1.65)	0.00	0.948	1.80 (0.94)	1.49 (0.33)	0.84	0.359	1.39 (1.26)	3.69 (1.65)	5.02	0.025
All species combined	20.84 (2.51)	12.80 (2.78)	7.00	0.008	17.76 (3.18)	20.84 (2.51)	1.30	0.254	9.00 (3.58)	12.80 (2.78)	1.39	0.238

Sampling occurred over single 20-min sessions at each site

of large, mature, deciduous forests that provide enough uncluttered subcanopy space, road networks, and riparian zones to enable big brown bats to forage efficiently.

Among urban and rural NCR Parks, there were no apparent trends in foliage-roosting bat (i.e., eastern red bats, hoary bats, and eastern pipistrelles) activity. Local scale attributes, and distance to hibernacula for eastern pipistrelles, seemed to override effects of urbanization or forest fragmentation. These bats likely are very cosmopolitan in their roosting and foraging habitat requirements, allowing them to exploit urban and rural parks throughout the landscape, regardless of the amount of forest cover (Hutchinson and Lacki 1999; Ford et al. 2005; Menzel et al. 2005). Consistent with earlier findings, both eastern red bat and eastern pipistrelle activity were higher at water sources than non-water sources (Owen et al. 2004; Ford et al. 2005, 2006). Although it is not wholly clear why eastern pipistrelle activity was highest in the Piedmont, the reasonable proximity to hibernacula in conjunction with the presence of larger waterways east of the Blue Ridge, or some combination thereof, probably account for their higher occurrence there. Little is known about the factors affecting the distribution of eastern pipistrelles at both landscape and home range scales (Fujita and Kunz 1984). Similarly, even less is known about correlates of hoary bat distributions at the landscape scale, particularly in the eastern United States. In the NCR Parks, hoary bat activity was higher in the rural, mountainous parks to the west than in the Piedmont and hence eastward. As predicted, hoary bats were more frequently detected in fragmented parks, at least within rural settings (Ford et al. 2005).

We suggest that myotine bat species distributions in the NCR Parks are dictated hierarchically, first by proximity of parks to hibernacula, then by amount of forest cover within the parks, and then by urbanization surrounding the parks. We found relatively high little brown myotis and northern myotis activity in the western-most of the NCR Parks, which were closest to available hibernacula in the region. Furlonger et al. (1987) suggested myotine bat activity in Ontario, Canada, decreased with increasing distance from hibernacula. Although little brown myotis and northern myotis are capable of migrating to all NCR Parks, it is unknown if, in summer, their densities decline with increasing distance from hibernacula in the mid-Atlantic region (Griffin 1940, Franz and Slifer 1976; Gates et al. 1984; Dalton 1987). Our data clearly show that northern myotis and little brown myotis activity were higher in forested parks from the Blue Ridge and west, possibly as a result of proximity to hibernacula. Although ANTI, MONO, MANA, and WOTR were similar in cover types and water resources, we detected little brown myotis and northern myotis only at ANTI and MONO, both of which are closer to hibernacula than MANA or WOTR. The absence of myotine bats at MANA and WOTR may be a landscape trend, more prominently expressed at the local level. Manassas National Battlefield Park lacked suitable foraging and roosting habitat for myotine bats and possibly is located in an area of low myotine population density because of its relatively long distance from hibernacula. Rock Creek Park, where we recorded little brown myotis and northern myotis, is equally as far from hibernacula as MANA, but contains more forest cover, suitable for myotine bat foraging and roosting. Additionally, eastern pipistrelles would have to migrate as far as myotine bats do to reach MANA and other sparsely forested urban parks (assuming their winter distributions are similar), but are able to exploit these fragmented, urban parks because their foraging behavior is more plastic than that of myotine bats (Fujita and Kunz 1984; Ford et al. 2005). At NACE, little brown myotis and northern myotis activity was relatively low, and was restricted to areas with contiguous forest tracts. In the western portion of the NCR, northern myotis densities and intra-specific competition may be higher closer to hibernacula, causing some degree of niche shift resulting in bats using suboptimal habitats, i.e., fragmented rural parks. In the urban parks in and adjacent to Washington

D.C., northern myotis densities and competition may be less, allowing them to forage in their preferred habitat, i.e., forests. This is similar to what has been observed in many bird species (Hutto 1985). Minimum forest patch size and connectivity within an urban setting that is suitable for northern myotis, as well as the influence of distance to hibernacula, remains unknown. We more frequently detected little brown myotis activity than northern myotis closer to Washington, D.C., possibly because they are more inclined to take advantage of anthropogenic structures for roost sites, are more plastic in their foraging behavior, and are known to migrate longer distances (Barbour and Davis 1969).

Although it is impossible to know what bat species distributions and abundances historically were in what is now the Washington, D.C., area prior to European settlement, land use transformations since then surely have had an impact, at least at the local scale and probably at the landscape scale. At the local scale, a mosaic of cover types may favor a wide range of species, particularly those with generalist roosting and foraging behaviors. As urbanization expands, retention of larger forest tracts may allow specialists to marginally succeed in otherwise unsuitable surroundings. Certainly, some minimum forest patch size and connectivity affects bat communities within urban settings, but the parameters remain unclear, requiring further investigation. Over time, bats with specific habitat requirements may not be able to adapt and persist in areas of land use transformation and forest fragmentation, resulting in restriction of distributions on the landscape, and perhaps at the geographic scale. Generalist bat species that currently have vast geographic ranges may be better able to adapt to land use changes.

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Appendix A

Table 3 Percentage of land cover types within National Capital Region Parks and within a 2-km buffer surrounding each park

Landscape type and park	Park area (ha)	Distance[a]	Analysis area	Land cover					
				Water	Developed	Barren	Forested	Open	Wetlands
Urban, fragmented									
NACC	406	0	Within park	10.9	84.4	0.1	0.4	2.9	1.4
			Buffer	13.5	80.7	0.4	3.2	1.2	0.9
MANA	2,064	40	Within park	0.0	5.4	2.7	45.4	45.7	0.6
			Buffer	0.2	30.5	1.5	41.9	25.0	1.0
WOTR	53	19	Within park	0.0	33.7	1.2	55.1	9.3	0.7
			Buffer	0.1	43.2	0.7	30.0	25.1	0.9

Table 3 (continued)

Landscape type and park	Park area (ha)	Distance[a]	Analysis area	Land cover					
				Water	Developed	Barren	Forested	Open	Wetlands
Urban, forested									
GWMP	3,198	<1–23	Within park	10.1	15.7	0.6	57.3	8.8	7.5
			Buffer	16.9	43.8	0.9	25.1	11.0	2.4
NACE	3,237	3–37	Within park	2.9	23.7	1.5	57.9	10.6	3.4
			Buffer	11.9	55.8	0.7	23.6	6.8	1.2
ROCR	710	2	Within park	<0.1	22.8	0.4	65.5	7.3	3.9
			Buffer	2.4	81.6	0.7	10.0	3.0	2.3
Rural, fragmented									
ANTI	1,318	85	Within park	2.0	7.9	0.0	13.7	75.9	0.6
			Buffer	2.6	8.5	0.0	27.0	60.8	1.1
MONO	667	58	Within park	1.5	11.9	3.4	13.4	64.0	5.8
			Buffer	0.6	26.5	1.7	16.7	50.5	4.0
Rural, forested									
CHOH[b]	7,788	2–171	Within park	6.3	5.1	0.3	69.1	12.4	6.7
			Buffer	6.2	13.1	0.4	49.6	29.4	1.4
HAFE	926	73	Within park	3.5	16.2	0.0	72.1	7.2	1.0
			Buffer	9.4	15.2	<0.1	51.0	22.7	1.6
CATO	2,336	87	Within park	0.0	5.1	0.0	94.0	0.7	0.2
			Buffer	0.4	12.4	0.0	71.1	15.4	0.7

ANTI Antietam National Battlefield, *CATO* Catoctin Mountain Park, *CHOH* Chesapeake and Ohio Canal National Historical Park, *GWMP* George Washington Memorial Parkway, *HAFE* Harpers Ferry National Historical Park, *MANA* Manassas National Battlefield Park, *MONO* Monocacy National Battlefield, *NACC* National Capital Parks-Central, *NACE* National Capital Parks-East, *ROCR* Rock Creek Park, *WOTR* Wolf Trap National Park for the Performing Arts, *Within park* analysis of cover types within each park, *Buffer* analysis of cover types within a 2-km buffer surrounding each park, *Water* open water, *Developed* residential, commercial, industrial, transportation, *Barren* bare rock, quarry, transitional, *Forested* deciduous, coniferous, mixed forest, *Open* pasture, row crops, urban grasses, *Wetlands* woody or emergent wetlands

[a] Distance (km) from park to center of Washington, D.C. There were a wide range of distances of linear parks (i.e., CHOH and GWMP) and park conglomerates (i.e., NACE) to Washington, D.C.

[b] The portion of CHOH that was within 50 km of Washington, D.C. was considered urban and forested

Appendix B

Table 4 Bat captures at National Capital Region Parks, 2003–2004

Landscape type and park	No. sites[a]	Species	No. capture sites[b]	No. captures[c]	Male		Female	
					Adult	Juvenile	Adult	Juvenile
Urban, fragmented								
NACC	1	LABO	1	1	0	0	0	1
MANA	8	EPFU	1	7	2	0	2	0
		LABO	2	3	0	0	1	1
		PISU	1	2	0	1	1	0
WOTR	2	EPFU	1	4	1	0	2	0
		LABO	2	3	2	0	0	0
Urban, forested								
GWMP	7	EPFU	3	19	6	1	12	0
		LABO	2	2	0	0	1	1
NACE	7	EPFU	5	40	13	0	23	1
		LABO	2	3	2	0	1	0
		MYLU	2	9	0	0	7	2
		PISU	3	10	1	0	9	0
Urban, forested								
ROCR	8	EPFU	6	28	14	2	11	0
		LABO	2	4	1	0	1	1
		LACI	1	1	1	0	0	0
		MYLU	1	2	1	0	0	0
		MYSE	2	2	0	1	0	1
		PISU	3	12	1	4	4	3
Rural, fragmented								
ANTI	5	EPFU	2	4	2	1	1	0
		LABO	3	11	2	0	4	5
		MYLU	2	15	4	0	9	2
MONO	5	EPFU	3	6	0	0	5	0
		LABO	3	6	1	0	4	1
		MYLU	2	3	0	0	3	0
		PISU	2	3	0	0	2	1
Rural, forested								
CHOH[d]	19	EPFU	10	27	12	1	12	1
		LABO	9	20	5	2	3	5
		LACI	1	2	1	0	1	0
		MYLU	12	60	11	2	39	8
		MYSE	1	1	0	0	1	0
		PISU	4	6	2	3	1	0
HAFE	6	EPFU	2	4	3	0	1	0
		LABO	3	3	2	0	0	0
		MYSE	3	9	3	0	6	0
CATO	6	EPFU	3	10	5	0	3	1
		LABO	2	7	5	0	1	0
		MYLU	5	20	7	2	10	1
		MYSE	5	14	7	0	6	1
All parks	74	EPFU	36	149	58	5	72	3
		LABO	31	63	20	2	16	15
		LACI	2	3	2	0	1	0

Table 4 (continued)

Landscape type and park	No. sites[a]	Species	No. capture sites[b]	No. captures[c]	Male		Female	
					Adult	Juvenile	Adult	Juvenile
		MYLU	24	109	23	4	68	13
		MYSE	11	26	10	1	13	2
		PISU	13	33	4	8	17	4

ANTI Antietam National Battlefield, *CATO* Catoctin Mountain Park, *CHOH* Chesapeake and Ohio Canal National Historical Park, *GWMP* George Washington Memorial Parkway, *HAFE* Harpers Ferry National Historical Park, *MANA* Manassas National Battlefield Park, *MONO* Monocacy National Battlefield, *NACC* National Capital Parks-Central, *NACE* National Capital Parks-East, *ROCR* Rock Creek Park, *WOTR* Wolf Trap National Park for the Performing Arts, *EPFU Eptesicus fuscus*, *LABO Lasiurus borealis*, *LACI Lasiurus cinereus*, *MYLU Myotis lucifugus*, *MYSE Myotis septentrionalis*, *PISU Pipistrellus subflavus*

[a] Number of mist net sites within each park

[b] Number of mist net sites at which each bat species was captured

[c] Discrepancies in total number of bats captured and sum of males and females are because bats escaped before sex was determined

[d] The portion of CHOH that was within 50 km of Washington, D.C. was considered urban and forested

Appendix C

Table 5 Bat echolocation passes recorded at National Capital Region Parks, 2003–2004

Landscape type and park	No. sites	Total[a]	Bat species							
			NOID	EPFU	LABO	LACI	MYLU	MYSE	MYsp	PISU
Urban, fragmented										
NACC	14	72	24	43 (42.9)	2 (14.3)	1 (7.1)	0	0	0	2 (14.3)
MANA	27	441	158	100 (66.7)	25 (25.9)	0	0	0	0	158 (25.9)
WOTR	8	114	40	45 (87.5)	7 (25.0)	1 (12.5)	0	0	0	21 (37.5)
Urban, forested										
GWMP	38	588	172	308 (71.7)	46 (18.4)	0	8 (2.6)	1 (2.6)	9 (2.6)	42 (36.8)
NACE	86	1,767	648	905 (64.0)	142 (26.7)	0	13 (12.8)	2 (2.3)	6 (3.5)	51 (20.9)
ROCR	19	743	201	422 (89.5)	31 (26.3)	3 (5.3)	1 (5.3)	4 (15.8)	3 (15.8)	78 (52.6)
Rural, fragmented										
ANTI	21	144	51	42 (38.1)	19 (19.0)	18 (33.3)	1 (4.8)	1 (4.8)	1 (4.8)	3 (9.5)
MONO	13	162	49	44 (30.8)	14 (23.1)	1 (7.7)	1 (7.7)	1 (7.7)	0	44 (15.4)
Rural, forested										
CHOH[b]	93	1,801	563	377 (51.6)	483 (54.8)	5 (4.3)	24 (11.8)	42 (24.7)	70 (26.9)	225 (32.3)
HAFE	18	214	67	5 (22.2)	115 (33.3)	13 (38.9)	6 (16.7)	3 (11.1)	1 (5.6)	3 (11.1)
CATO	25	334	120	1 (4.0)	63 (24.0)	4 (12.0)	7 (12.0)	42 (20.0)	42 (36.0)	53 (8.0)
Total	362	6,380	2,093	2,292 (53.9)	947 (32.0)	46 (6.9)	61 (8.8)	96 (10.5)	132 (11.9)	680 (25.4)

Sampling occurred over single 20-min sessions at each site

ANTI Antietam National Battlefield, *CATO* Catoctin Mountain Park, *CHOH* Chesapeake and Ohio Canal National Historical Park, *GWMP* George Washington Memorial Parkway, *HAFE* Harpers Ferry National Historical Park, *MANA* Manassas National Battlefield Park, *MONO* Monocacy National Battlefield, *NACC* National Capital Parks-Central, *NACE* National Capital Parks-East, *ROCR* Rock Creek Park, *WOTR* Wolf Trap National Park for the Performing Arts, *NOID* Unidentifiable bat pass, *EPFU Eptesicus fuscus*, *LABO Lasiurus borealis*, *LACI Lasiurus cinereus*, *MYLU Myotis lucifugus*, *MYSE Myotis septentrionalis*, *MYsp Myotis* spp., *PISU Pipistrellus subflavus*

[a] Ambiguous *Eptesicus fuscus*/*Lasionycteris noctivagans* calls and *E. fuscus/Lasiurus cinereus* passes included in totals

[b] The portion of CHOH that was within 50 km of Washington, D.C. was considered urban and forested

Percentage of acoustic monitoring sites at which each bat species was detected is in parenthesis

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