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Bat ecology and public health surveillance for rabies in an urbanizing region of Colorado

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Abstract We describe use of Fort Collins, Colorado, and nearby areas by bats in 2001–2005, and link patterns in bat ecology with concurrent public health surveillance for rabies. Our analyses are based on evaluation of summary statistics, and information-theoretic support for results of simple logistic regression. Based on captures in mist nets, the city bat fauna differed from that of the adjacent mountains, and was dominated by big brown bats (*Eptesicus fuscus*). Species, age, and sex composition of bats submitted for rabies testing locally and along the urbanizing Front Range Corridor were similar to those of the mist-net captures and reflected the annual cycle of reproduction and activity of big brown bats. Few submissions occurred November- March, when these bats hibernated elsewhere. In summer females roosted in buildings in colonies and dominated health samples; fledging of young corresponded to a summer peak in health submissions with no increase in rabies prevalence. Roosting ecology of big brown bats in buildings was similar to that reported for natural sites, including colony size, roost-switching behavior, fidelity to roosts in a small area, and attributes important for roost selection. Attrition in roosts occurred from structural modifications of buildings to exclude colonies by citizens, but without major effects on long-term bat reproduction or survival. Bats foraged in areas set aside for nature conservation. A pattern of lower diversity

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in urban bat communities with dominance by big brown bats may occur widely in the USA, and is consistent with national public health records for rabies surveillance.

Keywords Bats · Chiroptera · Disease · Public health · Rabies · Big brown bats

Introduction

Management of wildlife disease threats in urban areas requires research at the interface of urban ecosystem studies and infectious disease ecology (Bradley and Altizer 2007). Most bat research involving urban ecosystems of the United States has been the subject of two areas of attention, which seldom overlap: bat ecology and public health surveillance of bats for rabies. Research on the urban ecology of bats in the USA has centered on species composition of urban bat faunas (Johnson et al. 2008; Kurta and Teramino 1992; Loeb et al. 2009), characterizing areas where bats forage (Duchamp et al. 2004; Everette et al. 2001; Gehrt and Chelsvig 2004), and describing features of roosting places used by bats (Evelyn et al. 2004; Neubaum et al. 2007; Williams and Brittingham 1997). Separate research involves reporting results of public health surveillance of bats for human or domestic animal exposure to rabies (Blanton et al. 2007; Mondul et al. 2003; Whitaker and Douglas 2006), with exposure typically occurring around buildings in cities and towns (Pape et al. 1999). Little effort has been dedicated to understanding how patterns in the species, sex, and age composition of bats sampled for public health surveillance relate to the structure of urban bat faunas or to the roosting ecology of bats in cities. Indeed, many public health agencies do not identify all bats examined to species (Mondul et al. 2003), and few details on routine circumstances of exposure appear in the literature. Similarly, many analyses of bat behavior and ecology in relation to their use of natural roosts have been conducted (e.g. Lacki et al. 2007), but it is unknown if findings from more natural habitats apply to the roosting ecology of bats in cities. This is because most research on bats in urban areas of the USA has not emphasized roosting ecology or the annual cycle in the life history of even the most common urban bats.

Questions surrounding the ecology of bats in cities in relation to rabies surveillance are important because rabies and other emerging diseases from bats are of increasing public health concern. Rabies is a disease of the nervous system caused by a rapidly evolving RNA virus that is transmitted through saliva by the bites of infected mammals (Jackson and Wunner 2007). Rabies is fatal, and causes a gruesome and painful death; about 55,000 human cases occur worldwide every year, most transmitted by bites from dogs (World Health Organization 2009). In the USA human deaths from rabies are very rare because of stringent anti-rabies public health efforts. With the success of vaccination against rabies in dogs and cats, rabies instead has become a disease of wildlife. In many states bats are the main wildlife source of exposure to rabies virus, and numbers of case reports of rabies in bats appear to be increasing (Blanton et al. 2007; Kuzmin and Rupprecht 2007). Most deaths due to rabies in humans in the USA over the past 50 years have been of bat origin (De Serres et al. 2008). In particular, human deaths due to rabies from bats often involve people unaware that they have been bitten, and virus variants from species (such as silver-haired bats, *Lasionycteris noctivagans*) not associated with colonies in buildings (Messenger et al. 2002; Mondul et al. 2003). Limited information about urban bat ecology is available to help inform these public health statistics, and most of the bat research has operated with an underlying premise that bat diversity and abundance in urban settings are positive goals. However, it is also becoming increasingly recognized that urbanization results in altered wildlife communities and populations that may be ecologically more vulnerable to pathogens, resulting in increased risks of disease for both wildlife and humans (Bradley and Altizer 2007). Additional serious pathogens have recently been determined to have emerged from bats elsewhere in the world, including viruses that were the source of Sudden Acute Respiratory Syndrome, Ebola, Nipah, and other diseases (Calisher et al. 2008; Wong et al. 2007). Bats as sources of rabies or other zoonotic pathogens can cause confusion and creates tension between public health interests and the desire for bat conservation. We undertook our study with the goal of clarifying the poorly understood ecological backdrop against which public health efforts operate in response to rabies exposure from bats in USA cities.

The four objectives of our research were: (1) to determine the composition of the bat faunas of the city of Fort Collins, Colorado and adjacent areas of the Rocky Mountains; (2) to describe the roosting ecology and (3) movements of the dominant species in the city; and (4) to relate these findings to public health efforts for rabies surveillance. Previous reports on public health aspects of rabies in bats fail to consider the relationships between bat ecology and patterns in disease surveillance. We use our findings to discuss the urbanization of regional and USA bat faunas, to compare patterns in the urban roosting ecology of the dominant species with literature relevant to more natural habitats, and to discuss the public health implications of the ecology of bats in an urbanizing area. We hypothesized that the city bat fauna would share similarities with the bat fauna of the adjacent Rocky Mountains but would be less diverse and characterized by a disproportionate abundance of one or a few species. This hypothesis was based on general findings about the nature of other plant and animal communities along natural-urban habitat gradients. We also hypothesized that patterns in the species, sex, and age composition of bats submitted for rabies diagnosis locally would closely correspond with the composition of the city bat fauna; that the composition of local public health samples would be representative of larger regional samples; and that the most urbanized area within the region (Denver) would have the least diversity in public health samples submitted for rabies diagnosis, also following a natural-urban gradient (McKinney 2006). Results from tests of such hypotheses should be useful for future interpretations of data resulting from public health surveillance records of bats throughout the USA.

In addition to faunal composition, we investigated roosting ecology and the annual cycle of reproduction and activity of the dominant species (the big brown bat, *Eptesicus fuscus*) in Fort Collins. We determined where these bats roosted, the proportion of potential roosting structures that were occupied, the sizes, sex, and age composition of colonies, and seasonality in use of roosts. We hypothesized that the samples submitted for rabies diagnoses would be dominated by the species roosting in closest association with human activities (particularly those using buildings), and that the annual cycle in big brown bat roosting ecology in the city would explain patterns in the seasonality, sex, and age composition of public health samples. We describe movements of bats among summer roosts and movements from these roosts to feeding areas and winter hibernacula. We hypothesized that characteristics of movements and roosting ecology of bats as reported in the literature for more natural areas also would be observed in the urban bat population. These characteristics include colony sizes, seasonal use of roosts, switching among roosts in local areas but little switching over larger areas, use of roosts based on attributes similar to those selected in natural habitats, and similarities in distances between roosts and foraging places. The retention of patterns in roosting ecology and movements from more natural habitats in urban areas might help explain seasonal patterns in specimens submitted for rabies diagnoses, and why and when bats become obvious to the public. We also document the attrition of available roosts due to exclusion by people, the fates of bats following exclusion, observations of mortality and predation at roosts, and circumstances surrounding potential exposures of humans and domestic animals to bat rabies.

Methods

Study area

Field sampling took place during 2001–2005 in and near Fort Collins, Larimer County, Colorado, USA. Fort Collins is at the north end of the rapidly urbanizing corridor where the Great Plains meet the Front Range of the Rocky Mountains. Elevation at Fort Collins is 1,525 m. Climate is temperate and semi-arid, with a mean annual precipitation of 36.8 cm and mean monthly temperatures of −2°C in January and 22°C in July (Colorado State University 2006). The area was settled by European-Americans beginning about 1860, with the first permanent building erected in 1870, and completion of a railroad link in 1877 (Noel and Sladek 2002; Watrous 1911). In 2005 Fort Collins occupied 134 km^2 with a population of about 140,000 people, increasing from 25,000 in 1960 (City of Fort Collins 2006a). Fort Collins took conservation measures in response to urbanization by establishing a city-owned Natural Areas program in the late 1980s, focusing on floodplains of the Poudre River and Spring Creek, the only permanent watercourses through the city. This program has been described as an excellent model for a "nature-friendly" city (Duerksen and Snyder 2005). About 4,900 ha are preserved as Natural Areas within or near the city limits (Fig. 1a; City of Fort Collins 2006b). These areas remain undeveloped and are managed for nature conservation. The 48 city parks, in contrast, are used more heavily for recreation and include developed facilities.

Areas to the east of Fort Collins are rural prairies devoted primarily to farming and ranching. These rural habitats are sparsely developed (but with increasing housing subdivisions), and lack significant natural roosts for bats other than planted trees. The area to the west of Fort Collins is mountainous, with coniferous forest and numerous rock outcrops and cliffs, providing considerable potential roosting habitat for bats (Humphrey 1975). Much of the mountainous area is managed as the Roosevelt-Arapaho National Forest. Elevations where we sampled bats in the mountains (Fig. 1b) ranged from 1,585 to 2,630 m, with ponderosa pine (*Pinus ponderosa*) forest at lower elevations and spruce-fir forests (*Picea engelmannii, Picea pungens, Pseudotsuga menziesii, Abies lasiocarpa*) at the highest elevations (Neubaum et al. 2006).

Methods of capture, marking and tagging big brown bats

Big brown bats were captured in mist nets set over water in Fort Collins and adjacent mountains. In Fort Collins they were individually tagged by subdermal insertion of passive integrated transponders (PIT tags; Wimsatt et al. 2005; O'Shea et al. 2004). Bats were captured at roosts using standard techniques that varied with logistics, including mist nets, harp traps, hand held nets, and funnel traps (Kunz et al. 1996). We captured bats at selected roosts from 1 to 8 times each summer (from the fourth week in May to the second week in August each year). We maintained a mean interval of 20.5 (*CI* 20.0–23.0) days between captures (mode 21 days, $n=181$ intervals) to reduce potential effects of captures on roost occupancy by bats. Numbers and locations of roosts sampled changed each summer because of factors beyond our control (e.g., exclusion of bats by owners, occupant changes in willingness to cooperate), but some were sampled in each of the 5 years.

We also employed radio telemetry. Miniature (0.5–1.0 g) radio transmitters (Holohil Ltd, Carp, Ontario, Canada) were attached temporarily to trimmed fur in the interscapular region with Skin Bond (Pfizer Hospital Products Group, Inc., Largo, Florida). We matched transmitter mass to 5% of body mass (Aldridge and Brigham 1988; Neubaum et al. 2005).

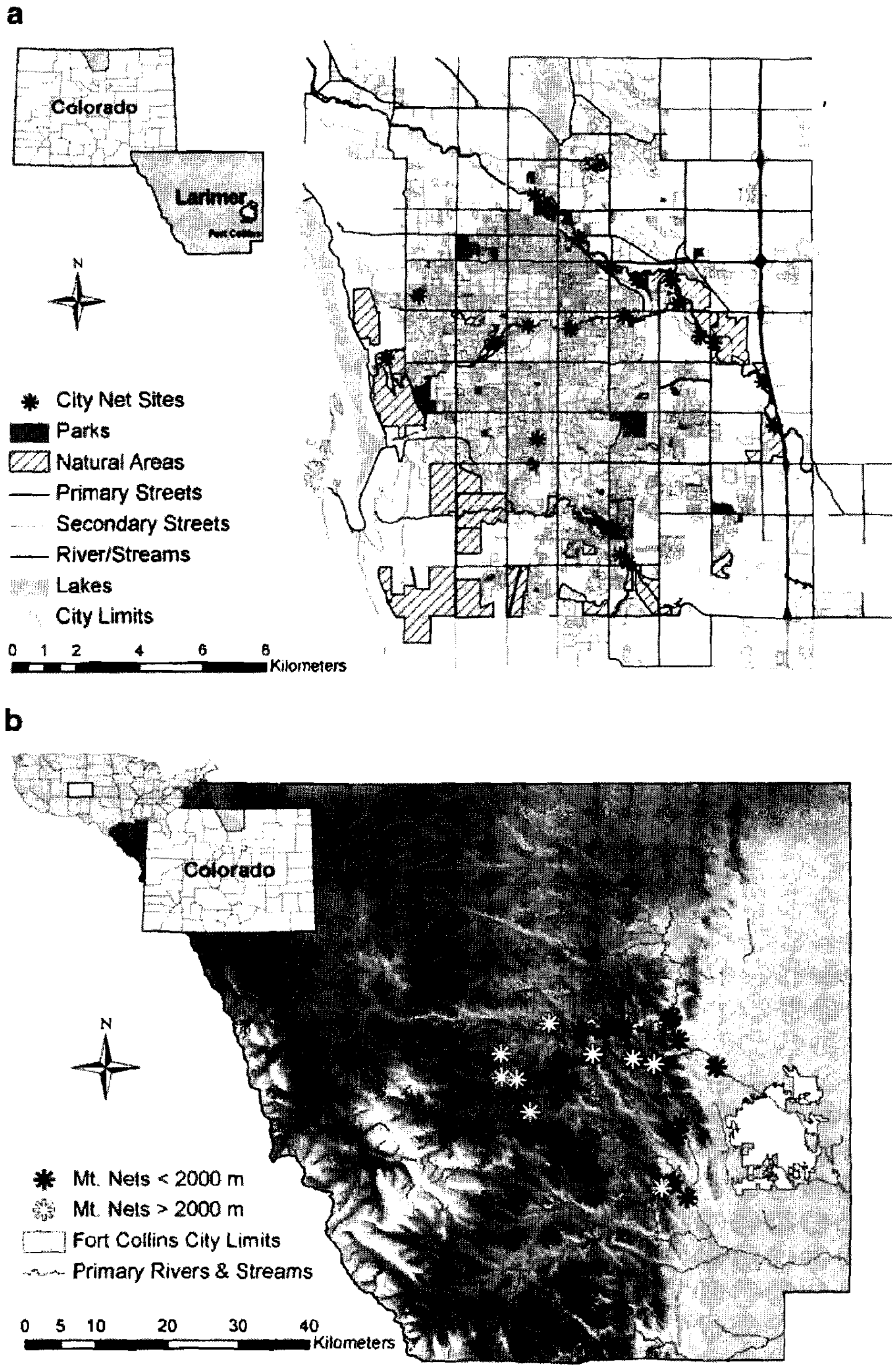


Fig. 1 Locations of sites where bats were sampled using mist nets over water in **a**) the city of Fort Collins, Colorado, USA and **b**) adjacent forested areas in the Rocky Mountains

Transmitters typically expended battery life (2–3 weeks) or detached prematurely. We located signals using scanning radio telemetry receivers (model R2000, Advanced Telemetry Systems, Isanti, Minnesota, USA). Details on our radio tagging and tracking methods are available elsewhere (Neubaum et al. 2005, 2006; O'Shea et al. 2004). Bat capture, marking, and sampling procedures were approved by the Institutional Animal Care and Use Committees of Colorado State University and the US Geological Survey. Bats were captured under authority of a scientific collecting license issued by the Colorado Division of Wildlife. All staff who handled bats were administered pre-exposure rabies prophylaxis, had anti-rabies antibody titer checks annually, wore gloves while handling bats, and followed guidelines of the Advisory Committee on Immunization Practices regarding possible post-exposure prophylaxis (Centers for Disease Control and Prevention 1999).

Composition of the bat faunas of Fort Collins and adjacent mountains

We determined species composition of bat faunas in Fort Collins and adjacent areas of the Rocky Mountains by identifying bats captured in mist nets set over water sources (Kunz et al. 1996). We captured bats in the city during summers 2001–2005 over water in Natural Areas and parks (Fig. 1a). Bats were captured at mountain sites in 2003–2005 in mist nets over ponds, watering tanks, streams, and the Poudre River. Capture sites in the mountains were a mean distance of 16.7 km from the city (± 8.8 *SD*, range 6–33 km, n=23 sites) at a mean elevation of 1,983 m (± 312 *SD*, range 1,585–2,630 m). We identified bats to species based on external characters reported in Fitzgerald et al. (1994), determined sex and reproductive condition of females by external examination (Racey 1988), and assigned age as adult or volant juvenile based on ossification of phalangeal epiphyses (Anthony 1988). Litter size was determined by radiography (O'Shea et al. 2010).

Sites for sampling bats over water were chosen based on logistics (safety, access) and configurations that suggested bat captures were feasible. Bat faunas of the city, the adjacent mountains, and the sample of Larimer County public health specimens were compared with respect to species richness (number of species detected), proportions of the total bats captured that belonged to each species, Simpson's Diversity Index, and an index of evenness of distribution of individuals among species based on Simpson's Index. We calculated Simpson's Index as $1\text{-}D$, where $D=\sum n\,(n\text{-}1)/[N\,(N\text{-}1)]$, n is the number of individuals in each species, and N is the total number of individuals captured (Magurran 1988). The index ranges on a scale from 0 (no diversity) to 1 (infinite diversity). Evenness is expressed by the formula $(1/D)/S$, where S is the number of species in the bat fauna. Evenness ranges on a scale from 0 to 1, where one is complete evenness (Magurran 1988). We relied on these simple measures of diversity and evenness for comparative purposes. They were not intended as an in-depth analysis of bat species diversity, but as a simple means to contrast faunas using identical sampling methods. Capturing bats in mist nets over water can have biases, such as favoring less maneuverable and low-flying species, but these biases did not change between compared areas. We captured all species previously known from our area over the past 100 years (Warren 1910; Armstrong 1972; Armstrong et al. 1994).

Roosts of big brown bats in buildings

We found roosts of colonies of big brown bats by radio tagging adult females captured foraging at night, and then searching for signals by driving streets during the day. We also located roosts through local knowledge. Street addresses and GPS were used to denote locations of roosts, ground observers determined building functions and roosting sites within buildings, and ages and values of buildings were determined by accessing local government property databases. Colony sizes were estimated by counting bats as they emerged from roosts at dusk (Kunz 2003) with observers remaining for 15 min after the last bat emerged. Colony size estimates are based on high counts during June, when colonies had formed but most juveniles were not volant (based on captures at roosts), and are assumed to represent adults only. Evening emergence counts can show daily variability because big brown bat colonies may occupy a number of alternate roosts (e.g. Ellison et al. 2007a; Willis and Brigham 2004). We did not make numerous replicate counts at roosts to quantify this variability. Instead we used evening emergence counts to document the approximate magnitude of colony sizes. We determined sex and age composition of colonies at roosts by intensive captures and sampling by hand (see above).

We determined seasonality in use of buildings by fitting circular (15 and 30 cm diameter) PIT tag reader hoops (activating antennas; Avid, Inc., Norco, CA, USA) over openings that bats used to enter and exit roosts. Individual bat identity, date, and time of detection were recorded on a data logger (Avid, Inc., Norco, CA, USA). Data loggers were downloaded to laptop computers three times weekly. Additional details and applications of this system can be found elsewhere (Wimsatt et al. 2005; Ellison et al. 2007a,b; Neubaum et al. 2006, 2007). We used radio-tracking to determine the timing of seasonal migration away from the city, and to determine fates of colonies following exclusions from roosts by building occupants.

During 2004 we estimated the number and proportion of buildings in Fort Collins occupied by maternity colonies of bats. We followed a completely randomized design in selecting buildings from a list maintained by Larimer County that included 65,049 addresses within the city limits. Personnel with field experience in bat natural history visited each randomly selected address, and with permission of the occupants searched the external walls for signs of bat use such as stains around openings, sounds of bats vocalizing, and bat fecal pellets (guano). We searched from June 14 to July 20 when maternity colonies were active. We initially attempted but were unable to estimate detection probability (see Electronic Supplementary Material), and therefore provide unadjusted results from the random survey as gross estimates of rates of building use by bats.

Movements of big brown bats

We used PIT tag reader records to determine potential interchange of bats among roosts. We also tagged big brown bats with radio transmitters to determine nightly foraging movements. Tracking of foraging bats was conducted 25 May to 25 June 2004, with radio signals monitored nightly until about 0200. On most nights three pairs of trackers in different vehicles kept in contact with mobile phones and drove streets in wide search patterns if they lost the signal. When the signal was detected, trackers immediately notified the others and crews took directional bearings at synchronized intervals until the signal was lost. When multiple bearings were not possible, we plotted areas of occurrence as equilateral triangles radiating out 1.5 km from the tracker's position at an angle of 10° in each direction from the bearing azimuth. We estimated locations from ≥ two concurrent (± 60 s) bearings using LOCATE II software and 95% error ellipses were generated using GIS.EXE software (Nams 1990). All location estimates were calculated using a fixed standard deviation of 10°.

Patterns in public health surveillance of bats for rabies

We examined bat carcasses received for rabies diagnoses by the Colorado Department of Public Health and Environment (CDPHE) Laboratory Services Division. We used CDPHE records during 2001–2005 from nine of the ten most populous counties (Colorado Department of Public Health and Environment 2009) along the Front Range Corridor, excluding Larimer County (the other nine most populous counties were Adams, Arapahoe, Boulder, Denver, Douglas, El Paso, Jefferson, Pueblo, and Weld). We summarized attributes of the specimens submitted from Denver County (the most highly urbanized county in Colorado) separately. We used CDPHE records from 2000 to 2004 for Larimer County (many cases from Larimer County shifted to a different laboratory in 2005 and carcasses were unavailable to us). Most of the carcasses in the Larimer County records were from Fort Collins and the nearby city of Loveland, but because incidents were protected by medical confidentiality laws we could not map precise locations. We examined each carcass after the rabies diagnosis was completed to verify species identifications, and to determine age and sex (rabies positive samples were examined in a Biosafety Level 3 facility at Colorado State University).

We used paper files maintained by the Larimer County Humane Society (a cooperator with the CDPHE) for all case reports of nuisance calls involving possible human or domestic animal exposure to bats in 2001–2005. The local protocol for rabies surveillance was for reports of nuisance bat incidents to be screened by Larimer County Humane Society animal control agents. Agents determined if a person or domestic animal was bitten by the bat or otherwise had a potential exposure to rabies virus (following guidelines of the Centers for Disease Control and Prevention 1999). Agents also documented rabies vaccination records for potentially exposed pets. If the bat was present at the time of the interview and an exposure was likely, the agent transported the bat to the diagnostic laboratory to determine the presence of rabies antigen in brain using fluorescent antibody techniques (Pape et al. 1999). If there was no exposure and the bat was alive, it was released that night. The carcass was discarded if there was no exposure and the bat was dead, although a small number were submitted for surveillance lacking evidence of potential exposure to rabies virus (Pape et al. 1999). We examined nuisance call records for patterns in the occurrence of bat-human incidents, to map the distribution of addresses reporting such incidents for comparison with locations of roosts, and to summarize case histories and associated pertinent information. In mapping locations of calls we excluded multiple records where more than one bat was taken at an address in the same year.

General statistical analysis and mapping

Most of our data are observational and therefore we rely on descriptive summary statistics for comparisons and analyses. We follow suggestions of Johnson (1999) and Anderson et al. (2000, 2001) and provide parameter estimates (means or geometric means, *GM*) and proportions with 95% confidence intervals (*CI*) as informative measures of effect sizes and precision rather than rely on statistical null hypothesis testing. *CIs* on proportions were calculated following Newcombe (1998). For further support in species capture results we also modeled probabilities (proportions captured) as functions of covariates using logistic regression (Proc GENMOD; SAS Institute 2003) and ranked competing models using Akaike's Information Criterion (Burnham and Anderson 2002); details are provided as Electronic Supplementary Material.

We mapped distributions of roosts, foraging areas, and public health incidents using ArcMap applications of ArcGIS (version 8.2) and previously compiled, spatially explicit data on urban structure (City of Fort Collins 1996). Standard distances, used to provide a measure of distribution for roost locations dispersed around a *GM*, were generated using the Standard Distance analysis in the ArcToolbox application of ArcGIS. A circular buffer of 1 standard deviation was used to encompass 68% of the points around the centroid of roost locations.

Results

Composition of the bat faunas of Fort Collins and adjacent mountains

Based on captures over water, the city bat fauna was dominated by big brown bats (Table 1), and 74% (*CI* 69–79%) of adult big brown bats were female. Little brown bats (*Myotis lucifugus*) were second in abundance, with 89% (*CI* 82–94%) adult females (Table 1). Together these two species represented 92% (*CI* 89–94%) of the bats captured in the city. Juvenile and pregnant or lactating female big brown and little brown bats dominated captures, and the proportion of females in the sample differed among city and mountain locations (see below and Electronic Supplementary Material). Other species captured in Fort Collins (in order of abundance, each <5% of the total) were silver-haired bats, hoary bats (*Lasiurus cinereus*, including a lactating female in June and juveniles in July), western small-footed myotis (*M. ciliolabrum*, including two lactating females), long-legged myotis (*M. volans*), and an eastern red bat (*L. borealis*; Table 1). Most (16 of 20) silver-haired bats sampled over water were captured in May during spring migration; all but one was an adult female. The remaining four silver-haired bats (one adult male and three juveniles) were captured in July and August. In addition to the bats caught in mist nets, we also captured three female silver-haired bats based on citizen reports of each roosting on or near buildings (including one in a folding umbrella over a picnic table and one in a door jamb). These were taken in autumn (28 November 2003, 8 September 2004, 30 November 2005). Simpson indices of species diversity and evenness in the city were 0.48 and 0.27, respectively.

Big brown bats accounted for just 22% of captures in the Rocky Mountains west of Fort Collins (Table 2; Electronic Supplementary Material). The bat fauna in the mountain zone included three species not taken in mist nets in Fort Collins (Table 2) but no red bat. Although juveniles and reproductive adult female little brown and big brown bats were captured at these sites, most captures of these two species at sites > 2000 m were adult males (Table 2), unlike findings in the city. The ratios of males to females were also higher at sites > 2000 m in the mountains for hoary bats and long-eared myotis (*Myotis evotis*, Table 2).

Most silver-haired and hoary bats captured in the mountains occurred at sites > 2000 m (Table 2). All but two of the 17 adult female silver-haired bats captured above 2000 m were

Table 1 Numbers, species, sex, and age composition of bats captured in nets set over water at 20 locations at Fort Collins, Colorado, on 73 nights in May to September 2001–2005. Juv = volant juveniles, unk = age and sex not recorded. See Neubaum (2005) for details regarding *L. borealis*

Species	Adult males	Adult females	Juvs	Unk	Total (% of all bats; *CI*)
Eptesicus fuscus	80	233	32	1	346 (68.4%; *CI* 64–72%)
Myotis lucifugus	12	97	9	0	118 (23.3%; *CI* 20–27%)
Lasionycteris noctivagans	2	14	3	1	20 (4.0%; *CI* 3–6%)
Lasiurus cinereus	9	6	2	0	17 (3.4%; *CI* 2–5%)
Myotis ciliolabrum	0	2	0	0	2 (0.4%; *CI* 0.1–1.4%)
Myotis volans	0	2	0	0	2 (0.4%; *CI* 0.1–1.4%)
Lasiurus borealis	0	1	0	0	1 (0.2%; *CI* 0.04–1.1%)
Total					506

Table 2 Numbers, species, sex, and age composition of bats captured in nets set over water at 23 locations in the mountains 10–33 km from the City of Fort Collins. Nets were set on 42 nights during summers 2003–2005. Juvs = volant juveniles, unk = age and sex unrecorded. Numbers captured at higher sites (> 2000 m) are given in parentheses (11 sites at >2000 m were sampled on 28 nights)

Species	Adult males	Adult females	Juvs	Unk	Total	% of Total (95% *CI*)
Myotis volans	57 (52)	132 (126)	45 (44)	2 (2)	236 (225)	37% (34–41%)
Eptesicus fuscus	68 (43)	45 (12)	24 (14)	0	137 (69)	22% (19–25%)
Myotis lucifugus	27 (11)	27 (3)	23 (6)	0	77 (20)	12% (10–15%)
Lasionycteris noctivagans	26 (24)	23 (17)	17 (11)	0	66 (52)	10% (8–13%)
Lasiurus cinereus	31 (27)	2 (1)	19 (15)	3 (3)	55 (46)	9% (7–11%)
Myotis evotis	22 (22)	5 (3)	11(10)	0	38 (35)	6% (4–8%)
Myotis ciliolabrum	7 (4)	5 (4)	1 (0)	1 (1)	14 (9)	2% (1–4%)
Myotis thysanodes	4 (3)	4 (1)	2 (1)	0	10 (5)	2% (1-3%)
Corynorhinus townsendii	1(1)	0	0	0	1 (1)	0.2% (0.03–0.9%)
Total					634 (462)	

taken from August to early October, likely during migration. However, two females captured on 8 July 2003 and 7 July 2005 were lactating, indicating local reproduction. Adult male silver-haired bats and hoary bats were captured each month from June through September. All but one of the adult hoary bats captured > 2000 m was male; all of the juvenile hoary bats at higher elevations were taken after the first week of August. Although males were predominant in long-eared myotis and fringed myotis (*Myotis thysanodes*) at elevations > 2000 m, presence of juveniles was noted for both species at these higher sites, and one lactating female long-eared myotis was captured on 5 July 2005. We also found a maternity colony of little brown bats in a building at 2,704 m elevation (captures not included in calculations). The mountain zone had higher species diversity (Simpson's Index=0.78) and greater equitability of distribution of individuals among species (0.50) than the city.

Roosts of big brown bats in buildings

General characteristics and distribution of big brown bat roosts

We radio-tagged 148 adult female big brown bats to locate maternity roosts. Roosts of five bats were not located. The remaining 143 bats led us to 115 buildings. No tracked bats led us to colonies in natural structures. We also discovered buildings used by big brown bats through local knowledge and project publicity. We documented colonies (≥ 10 bats) in 96 buildings by both methods (the initial 115 buildings included some used by <10 bats). Colonies of big brown bats occupied buildings with a variety of uses. The 96 buildings with colonies of ten or more bats included: 51 single-family residences; 11 apartment, townhouse, or condominium multi-family complexes; ten churches or associated structures; three bat boxes on buildings; five university buildings (football stadium, three administrative buildings, one vacant classroom building under renovation); four restaurants; two office buildings; and single buildings used as a public school, private pre-school, fraternity house, fire station, park picnic pavilion, research laboratory, small historic outbuilding, garage, barn, and a burned shell of a small derelict building. Ninety-two of the 96 roosts were used by people regularly, many on a daily basis. The age distribution of buildings peaked with structures erected during 1970–1979 (Fig. 2a), with a median construction date of 1966. Roosts in buildings occurred throughout the city, but an area of greater concentration was apparent in northern Fort Collins (Fig. 3a). In cases where we could determine the roosting site within a building, only 23% were in attics (*CI* 16–31%, n=110, including sites occupied by <10 bats); most roosts were in cracks in walls, compartments above soffits, spaces between walls and exterior chimneys, and similar places.

Colony size and composition

The *GM* evening emergence count of big brown bats in colonies occupying buildings during June was 47 adults (*CI* 39–56; based on the highest count at 53 roosts, out of 133 counts made in June of all years). The distribution of counts showed typical colony sizes of 20–50 adult bats, with few colonies exceeding 100 bats and a maximum count of 219 at a church recreational hall (Fig. 2b). Most young emerged in flight in late June and early July each year, based on age composition of bats captured at buildings and foraging areas (Fig. 4). The percentages of captured bats that were juveniles were notable in mid-July and peaked during the last 10 days of that month (Fig. 4).

Big brown bats used buildings as maternity roosts to give birth and nurse young, with sex and age composition of colonies favoring adult females and juveniles. We captured 5,466 bats (including recaptures) at 39 buildings in Fort Collins on 181 occasions in June and July, 2001–2005. The composition by age and sex was 3,984 adult females (73%), 1,362 volant juveniles (25%; 678 juvenile males and 684 juvenile females), and 120 adult males (2%). Most (92.5%) of the adult females caught when reproductive condition was most obvious (10 June to 20 July each year) were pregnant or lactating (2,333 of 2,521 captures). We did not detect colonies of adult males. Most males likely roosted in the mountains or solitarily in the city, as supported by the male-skewed adult sex ratios at higher elevations (Table 2) and anecdotal accounts. For example, in summer 2005 we were notified on three different dates about a lone bat roosting under eaves (6 m above ground) over a patio. We captured and tagged the bat each time, and each was a different adult male.

Roosts of big brown bats in buildings did not include colonies of other species. We captured 15 little brown bats on 13 nights during evening emergence at big brown bat roosts (out of 7,303 captures of big brown bats at 41 roosts on 196 nights over the 5 years); some may have entered nets from outside rather than from inside the roost. We did not find colonies of little brown bats within the city, but two colonies were found in buildings outside city limits. A maternity colony of western small-footed myotis also was observed at a residence outside city limits.

Seasonal use of buildings by big brown bats

Bats roosted in buildings from early spring to early autumn. The earliest we observed bats at maternity roosts was 26 March in 2003. We maintained PIT tag readers at two roosts continuously for 1 year in 2004–2005. The larger colony included 132 PIT-tagged bats known alive at the start of monitoring, whereas the smaller colony had 21 PIT-tagged bats. Attendance patterns of these marked bats at the larger colony showed few active in early autumn, none in winter, few in early spring, and maximum numbers in summer (Fig. 5a). A similar pattern was also evident at the roost used by the smaller number of bats, although one adult female was recorded during winter (Fig. 5b).

We radio-tagged 56 big brown bats (48 adults and eight volant juveniles) at roosts in late August through October in 2002–2004 to determine post-maternity season movements. Signals from these bats were no longer detected in the city on dates ranging from 20 August to 6 October, with a mean date of 14 September across the 3 years (*CI* 11–17 September). Twenty-four of the bats (22 adults and two juveniles, both sexes) were subsequently located

Fig. 2 Characteristics of colonies of big brown bats (*Eptesicus fuscus*) occupying buildings in Fort Collins, Colorado. **a** Ages of buildings (by decade of construction) occupied by maternity colonies (≥ 10 bats) during 2001–2005. **b** Distribution of maternity colony sizes in buildings, based on highest count at evening emergence in June when juveniles were not yet volant, from a sample of 133 counts at 53 roosts 2001–2005. **c** Distribution of distances to the roost from initial capture sites for radio tagged adult female bats ($n=57$) on the day following capture over water

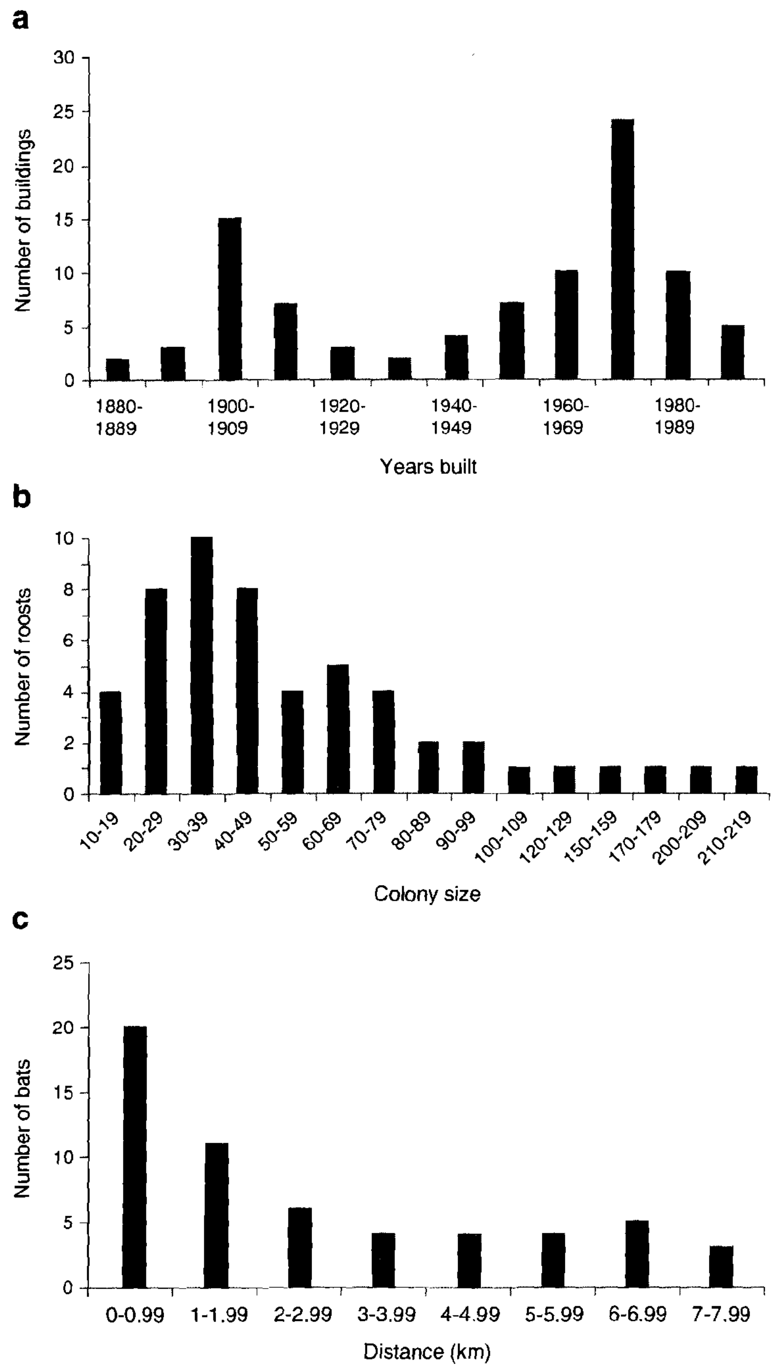
at autumn roosts and presumed hibernation sites in rock crevices at higher elevations (1,852–2,876 m) in the mountains, ranging up to 87 km from Fort Collins (see Neubaum et al. 2006).

Bats used certain buildings at times other than the peak periods of birthing and lactation. Two case histories illustrate differing patterns of use. The first involved a marked reduction in use coincident with the time of birthing and lactation. We monitored tagged bats at a small structure (the oldest building in the city) beginning in May each summer, 2002 through 2005 (we PIT tagged 174 bats at this roost and readers recorded bats 6,856 times). Each summer the bats stopped using the building abruptly in the third week of June: activity stopped on 19 June 2002, 16 June 2003, 20 June 2004, and 21 June 2005, with only 0–2 bats recorded after these dates each year (except an 8-day period in July 2005). The second case history involved intermittent and minor use of a building after lactation and fledging of young. Bats roosted in a 10-cm high space between a roof and an internal high-peaked ceiling in a 27 year-old single-family house. The roost was discovered through radio-tracking of an adult female on 2 July 2001, when 8 bats were counted at the evening emergence. Residents reported low numbers of bats using the roost, primarily beginning in July in each subsequent year. We captured and PIT-tagged four bats at emergence on 1 August 2003: all were post-lactating females. A tag reader was placed at this site on 20 July 2004. The four bats tagged in 2003 used the building intermittently in summer 2004, and were recorded on 22 of 50 days between 20 July and 8 September. In 2005 the tag reader was in place continually between 23 May and 9 September. Tagged bats were not detected until 8 July. Bats were present on 27 of the next 31 days, then absent the rest of the summer.

Attrition of roosts and fates of bats at exclusion

We followed the fates of colonies in 65 buildings known as roosts in 2001 and 2002. Owners attempted to exclude bats from 23 of the buildings (35%) by the end of the study. In four cases exclusion was unsuccessful, and in 4 cases results were unknown to us. In 15 cases bats were successfully excluded by intentional structural modification (sealing cracks or otherwise blocking entry); in two cases bats were unintentionally excluded by renovation for other purposes. Thus 26% (17 of 65) of the roosts were removed from availability within 0–4 years of their discovery by us (14 were removed within 0–1 year). We obtained information about use of alternate roosts by PIT-tagged bats after exclusion at seven buildings. In four cases (309 bats were PIT-tagged at the four buildings), we detected 52 excluded bats later crossing PIT-tag readers at nearby roosts (mean distance 0.79 km, *CI* 0.50–1.1 km from the original roost, range 0.13–1.3 km for distances between 11 alternate roosts and the site of exclusion); we did not discover alternate locations of most individuals.

Exclusion at one building provided a detailed case study on subsequent fates of bats. LTR was a farmhouse built in 1890 and since surrounded by residential and light industrial development. Owners reported bats roosting there for at least 40 years. We counted 156 bats at emergence in June 2001. Owners sealed the main entrance used by bats in autumn 2001 after bats had left for the season, but installed an exterior bat box at the sealed entrance to serve as an alternative roost. Bats returned in 2002 and used the roost via other access points not thoroughly sealed in 2001, with only occasional use of the bat box. A


a
Number of buildings
30
25
20
15
10
5
0
1880-1889
1900-1909
1920-1929
1940-1949
1960-1969
1980-1989
Years built
b
Number of roosts
10
8
6
4
2
0
10-19
20-29
30-39
40-49
50-59
60-69
70-79
80-89
90-99
100-109
120-129
150-159
170-179
200-209
210-219
Colony size
c
Number of bats
25
20
15
10
5
0
0-0.99
1-1.99
2-2.99
3-3.99
4-4.99
5-5.99
6-6.99
7-7.99
Distance (km)

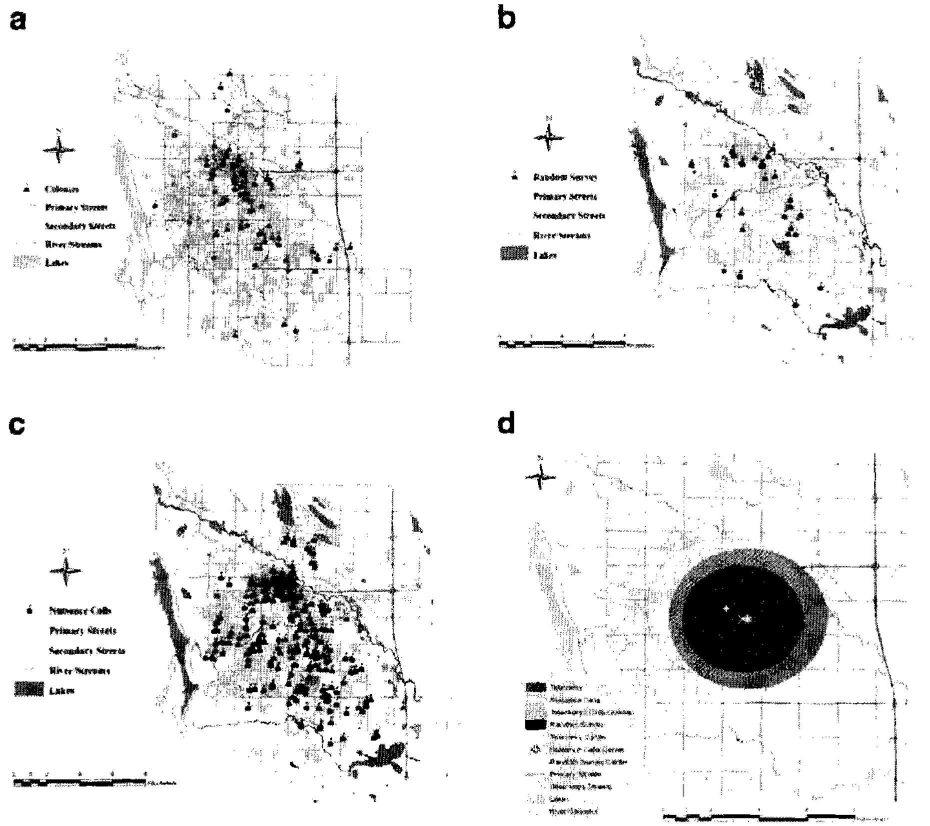


Fig. 3 Distributions of buildings with bat colonies in Fort Collins, Colorado, as determined by (**a**, *upper left*) radiotracking adult females to roosts after capture during foraging; (**b**, *upper right*) searches of randomly selected buildings (includes indications of use by bats without sightings); (**c**, *lower left*) locations of nuisance call records received by public health surveillance agents; and (**d**, *lower right*) centroids and ± 1 SD for locations of roosts based on radiotelemetry (asterisk), random surveys of buildings (X), and addresses of reports of nuisance bat incidents (+)

total of 267 PIT-tagged bats used the building in 2001 and 2002. A complete sealing was done in autumn 2002. In 2003 the bats did not use the house, but the bat box was used by 146 PIT-tagged bats from 25 April to 6 June. Use was abruptly discontinued on 6 June, suggesting that the bats had shifted to alternate roosts to give birth and rear young. Bats returned to the bat box in lower numbers in June 2004, when three pregnant females were captured there and radio-tagged to determine locations of alternate colony sites. These bats led us to two buildings. One (MEV) was an expensive (> twice the median home value for the city) home built in 1999 in a subdivision bordering the grounds of building LTR and 0.14 km away. There bats roosted in areas accessed under the ceramic tile roof, including 82 individuals first PIT-tagged at LTR. The other location was a wood-frame residence (building CHI) on a small farm 0.74 km away, where 134 PIT-tagged bats from the original roost were detected. This site had been known to harbor bats for at least 23 years, and it is likely that bats regularly moved between buildings LTR and CHI prior to the exclusion. We detected 136 of the original 268 PIT-tagged bats from Building LTR in the two alternate roosts, and found that 80 of these were detected at both alternate roosts in 2004 or 2005,

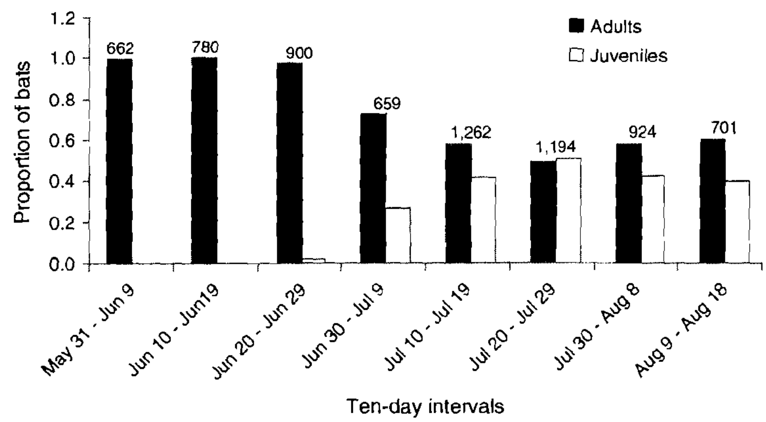


Fig. 4 Seasonal pattern in proportions of big brown bats (*Eptesicus fuscus*) captured emerging from roosts in buildings or while foraging that were adults or volant juveniles (sample sizes appear above vertical bars), Fort Collins, Colorado, USA, cumulative 2001–2005

including 80 of the 82 recorded at Building MEV. In 2002 there were 99 adult female bats at LTR that were captured and showed evidence of reproduction. We recaptured 27 of these at the two alternate roosts during 2004 and all were reproductive, providing no evidence of long-lasting effects of exclusion on reproduction (reproduction was not assessed in 2003). In 2005 another 36 adult female bats originally tagged at LTR were captured at the alternate roosts and assessed for litter size. Mean litter size was 1.14 (*CI* 1.02–1.26), similar to that of pregnant females assessed at the same time period but unknown to be subject to exclusion in prior years ($\bar{X} = 1.10$, *CI* 1.03–1.18, n=72). PIT reader records showed a minimum-number-alive of 51 of these 99 bats at alternate buildings in 2004 (51.5%). This would be roughly equivalent to an annual survival of adult females of at least 0.72.

Deaths of bats at roosts

We entered roosts in 18 attics and barns, some on multiple occasions. We found very few carcasses within these roosts, typically noting from zero to about ten (larger numbers in attics with the largest colonies). Carcasses were often mummified, and could have accumulated for years. It is unlikely that carcasses would be removed from within the attic roosts by larger scavengers because of limited access, and we saw no signs of scavengers. The small numbers of carcasses included neonates and juveniles that were not completely grown. Because most roosts were not in barns or attics, they could only be observed for carcasses on the ground around their openings. We maintained tag readers at 44 buildings for variable lengths of time over the five summers, and visited these during the day 3,757 times. We also captured bats at 40 buildings on 280 occasions over five summers. Captures involved from 3 to 15 observers and began under full light conditions. We never saw multiple carcasses within or outside big brown bat roosts. We interpret this lack of observations as evidence that no serious epizootics or poisonings occurred.

Predators were infrequently observed at evening emergences of bats. We noted domestic cats stalking beneath exit points at three roosts, and documented cats successfully catching bats at evening emergences below two roosts. Cats were also frequently reported in association with bats in public health nuisance call records (see below). Screech owls (*Megascops asio*) were observed outside two roosts, and one screech owl attacked a big

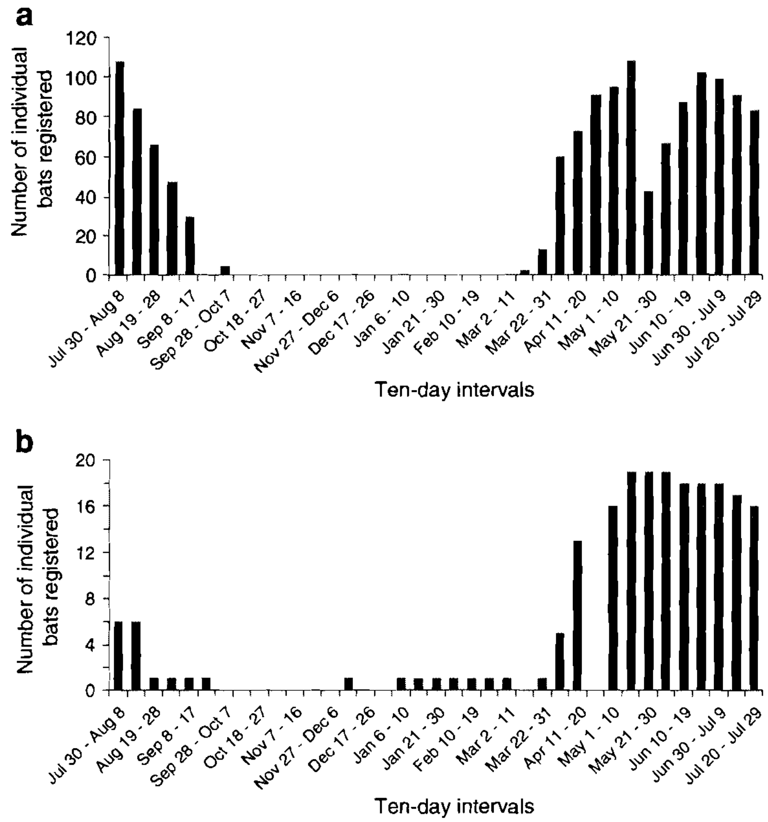


Fig. 5 Attendance patterns (number of individuals per 10 day interval) of individually identifiable PIT-tagged big brown bats (*Eptesicus fuscus*) registered by tag readers at two colony sites monitored over a full annual cycle in Fort Collins, Colorado, 2004–2005 (6–10 January 2005 excluded). (**a**) Building PET with 132 tagged bats known alive at the onset of monitoring, and (**b**) building GBH with 21 tagged bats

brown bat in our net. Great horned owls (*Bubo virginianus*) were observed at two buildings adjacent to big brown bat maternity roosts. We did not observe intentional killing of bats at roosts by people.

Surveys of randomly selected buildings for use by bats

We surveyed exteriors of 406 randomly selected buildings for evidence of bat use on 27 days during summer 2004. These included 327 single-family homes, 33 businesses, 18 apartment buildings, 18 duplexes or town homes, six outbuildings, two schools, and two churches. We found evidence of occupancy by bat colonies at 12 buildings, with three housing a bat colony at the date of discovery. Thus about 3% of the buildings in Fort Collins may be used by big brown bat colonies at some point within a summer (if the detectability of use rather than occupancy is close to one; Electronic Supplementary Material), but only 0.7% may be occupied on any given day (3 of 406). Alternatively, guano or other signs may have accumulated from use over longer periods by single bats or very small groups. If this were true, then use of buildings by maternity colonies at some time during the summer would likely be lower than 3%.

Indeed, we obtained evidence of minor use by bats at an additional 20 of the randomly selected buildings. In these cases the likely use was as a night roost (guano below porch overhangs) or occasional use by solitary bats during the day. Assuming no false positives, an additional 4.9% of the buildings (20 of 406) in Fort Collins showed evidence of minor use by bats. The buildings with evidence of use of any kind were located in parts of the city consistent with areas where radio-tracking and local knowledge also yielded evidence of colonies in buildings (Fig. 3b).

Movements of big brown bats

Movements of bats among buildings

Most of the bats radio-tagged in summer (95 of 143 bats tracked to roosts) occupied a single building over the life spans of the transmitters. However, 48 adult females roosted in more than one building, averaging 2.8 (± 1.1 *SD*) buildings per individual. Distances between buildings for each movement averaged 0.43 km (± 0.49 *SD*, range 0.02–2.6, $n=141$ moves by 48 bats tracked for a mean of 24.1±6.7 days). Only four moves involved buildings separated by over 1.0 km (range 1.1–2.6 km).

We seldom detected movements by PIT-tagged bats among colonies. An analysis of the numbers of detections at each roost monitored each summer (Table 3) showed that about 1–5% of the pool of PIT-tagged bats were detected at roosts other than the single roost they typically occupied or an adjacent building. The *GM* distances of these within-summer movements between roosts were similar to that discovered by radio-telemetry: very few exceeded 1 km (Table 3). Movements to roosts >1 km were highly transient: 28 of the 37 cases involved use of a distant roost on one night, with the remainder involving visits of just 2–8 occasions. Most of the visits were of short duration and during the night. Only five of the 37 cases involved bats that spent at least a full day in the distant roost (three of the five were 1 day, one used the roost on 2 days, and one on six). These rare visits to distant roosts were not a recurring habit peculiar to individuals: only one of 36 bats was documented to visit roosts more than 1 km away in any year other than the one year the move was detected. Thirty of the 37 visits were adult females, and the seven visits by juveniles included both sexes.

Foraging and captures away from diurnal roosts

Big brown bats radio-tagged over water were tracked to roosts that were a *GM* distance of 1.6 km (*CI* 1.2–2.2 km) from the capture site ($n=57$ adult females tracked to the colony the day after tagging), ranging up to 7.9 km away (Fig. 2c). Bats passed multiple colonies closer to foraging sites than their home colonies in the course of foraging. In addition to radio-tagged bats, we captured PIT-tagged bats at foraging and watering areas. Capture sites were a *GM* distance of 1.9 km (*CI* 1.6–2.3; range 0.6 to 6.4 km) from roosts ($n=62$).

We radio-tagged 19 bats at roosts in buildings and tracked them on subsequent nights to locate their foraging areas. Sixteen of these bats were subsequently detected foraging for an average of 4.8 nights each. We took concurrent bearings on 29 occasions and single-bearing readings on 195 occasions. Most of the bats we followed moved from roosts in urbanized areas to foraging areas in city-designated Natural Areas: 91% of the 195 single-bearing location estimates that we acquired overlapped Natural Areas associated with Spring Creek and the Poudre River. Radio signals from tagged bats were seldom obtained over residential or commercial areas, and on the few occasions that bats were detected foraging away from Natural Areas the locations tended to be over parks and lakes. All but one bat was detected east

Table 3 Descriptive summary statistics on detections of big brown bats at roosts in buildings in Fort Collins, Colorado, other than their principal colony site or adjacent buildings, 2002–2005. Roosts where bats were successfully excluded by owners were not entered into computations. *GM* = geometric mean; *CI*=95% confidence interval. Percentages are based on the total number of marked bats detected

Year	N marked bats detected	N detections	N colonies monitored	Distance between monitored colonies	N bats detected at non-adjacent buildings	Distance moved between non-adjacent roosts	N bats detected at roosts >1 km apart
2002	1,105	207,636	13	*GM* 2.92 km *CI* (2.31–3.68) Range 0.13–10.6 km, n=78 possible pairs	40 (3.6%)	*GM* 0.51 km *CI* (0.33–0.78) Range 0.13–7.97 Eleven pairs of buildings	13
2003	1,318	293,464	19	*GM* 3.77 km *CI* (3.32–4.28) Range 0.13–12.0 km, n=171 possible pairs	60 (4.6%)	*GM* 0.45 km *CI* (0.35–0.58) Range 0.13–4.54 Nine pairs of buildings	6
2004	1,333	452,053	17	*GM* 4.16 km *CI* (3.58–4.83) Range 0.14–12.4 km, n=136 possible pairs	19 (1.4%)	*GM* 0.73 km *CI* (0.44–1.21) Range 0.19–6.50 Eight pairs of buildings	5
2005	1,254	386,346	13	*GM* 3.89 km *CI* (3.24–4.67) Range 0.19–10.7 km, n=78 possible pairs	41 (3.3%)	*GM* 0.93 km *CI* (0.73–1.19) Range 0.19–9.5 Nine pairs of buildings	13

and south of the main parts of the city, in the direction of the Poudre River. None of the Natural Areas to the west of the city (Fig. 1a) was used, but these lack extensive riparian vegetation. Some bats made long foraging trips up to 18 km straight line distance from the colony, but near the river. Maximum distances moved between roosts and distant foraging areas averaged 5.9 km. We rarely observed bats foraging in the same areas from night to night. Bats did not restrict foraging to areas near their roosts. We did not observe tagged bats foraging at street lamps. On several nights we followed bats as they moved along Natural Areas on the Poudre River and the movements of these bats spanned the length of the city.

Night roosts

Some structures in the city were used as night roosts (where bats rest between foraging bouts without returning to the colony). One bridge of a major artery over the Poudre River in the older area of the city was used as a night roost by a few big brown bats, but other bridges over the river within the city lacked evidence of night use. Some residents reported nightly accumulations of guano under covered porches, and similar situations were encountered during the searches of buildings at random (see above). At one night roost a high (6 m) porch ceiling served as a trap for warm air. Clusters of at least 12 bats occupied a corner of the porch ceiling over the front door nightly in August beginning 1 to 2 h after sunset, resulting in daily accumulations of fresh guano.

Patterns in public health surveillance of bats for rabies

Species composition, seasonality, and prevalence of rabies in bats

Rabies diagnostic procedures were performed on 136 bats from Larimer County. No bats were submitted from November through March; most (84%, n=112) were submitted in June through August, with a peak in July (35%, n=47). Species composition was consistent with our records from mist-netting bats over water in Fort Collins: 75% were big brown bats, 14% were little brown bats, 6% were silver-haired bats, and other species were less than 3% each (Table 4). Only 11 (8.1%, *CI* 5–14%) of the 136 cases were rabid; nine of these were big brown bats. Six of the nine rabid big brown bats were adult females and 16.2% (*CI* 8–31%) of the total sample of adult female big brown bats from Larimer County

Table 4 Numbers, species, sex, and age composition of bat specimens submitted to the Colorado Department of Public Health and Environment for rabies diagnoses from Larimer County, Colorado, 2000–2004. Most samples came from the cities of Fort Collins and Loveland, Colorado, but precise details of locations were not available. Number of rabies positive samples are given in brackets [ ]

Species	Adult males	Adult females	Juv	Total (% of all bats submitted, 95% *CI*)
Eptesicus fuscus	26 [0]	37 [6]	39 [3]	102 (75%, *CI* 67–82%)
Myotis lucifugus	4 [0]	8 [0]	7 [0]	19 (14%, *CI* 9–21%)
Lasionycteris noctivagans	2 [0]	6 [0]	0	8 (6%, *CI* 3–11%)
Myotis ciliolabrum	0	3 [0]	1 [0]	4 (3%, *CI* 1–7%)
Myotis volans	0	4 [0]	0	4 (3%, *CI* 1–7%)
Lasiurus cinereus	1 [1]	0	1 [1]	2 (1%, *CI* 0–6%)
Myotis evotis	0	1 [0]	0	1 (< 1%, *CI* 0.4–5%)
Total				136

were rabid. No adult male was rabid, but three of the juvenile big brown bats (7.7%, *CI* 3–20% of juveniles) were positive, for an overall proportion of 8.8% (*CI* 5–16%, 9 of 102). Rabid big brown bats were found in April, May, June, July, and August. The two hoary bats submitted were rabid. All other species were negative, including little brown bats. Non-rabid silver-haired bats were reported in May ($n=2$) or during late August through October ($n=5$; one undated), consistent with netting records of passage of this species through the area during seasonal migration. Simpson's indices of diversity (0.42) and evenness (0.25) in public health samples were comparable to those estimated from captures over water in the city.

The seasonal distribution of cases and the dominance of big brown bats among specimens submitted for rabies diagnoses from the other populous counties along the Colorado Front Range Corridor were very similar to the sample from Larimer County. Just three bats (0.5%) were submitted from November through March, and most were submitted from June through August (74%, $n=452$) with a peak in July (35%, $n=214$). Most (73%) specimens from the urban corridor were big brown bats, with a *CI* (69–77%) overlapping those for proportions of bats captured over water and in the Larimer County public health submissions (cf. Tables 1, 4, 5). Other species were represented at somewhat different proportions than in the samples of bats captured over water in Fort Collins, and more species were examined over this broader area (cf. Tables 1 and 5). However, as in the Fort Collins live sample, the next three most abundant species included silver-haired bats, little brown bats, and hoary bats. *CI*s for proportions by species in public health samples in these counties compared with Larimer County were overlapping except for a lower proportion of little brown bats from the other urbanizing counties in the Front Range Corridor (cf. Tables 4 and 5).

The proportion of all big brown bats diagnosed as positive for rabies in the larger sample of bats along the urbanizing Front Range Corridor was 16% (*CI* 13–20%). The sex and age distribution of rabies-positive cases in big brown bats was 19.7% (*CI* 14–27%) in 152 adult females, 14.1% (*CI* 9–23%) in 92 adult males, 15.1% (*CI* 10–23%) in 106 juvenile females and 13.5% (*CI* 8–22%) in 96 juvenile males. Few rabid bats were found among the other species, with the exception of hoary bats and long-legged myotis (Table 5). Six (50%) of the rabid hoary bats were submitted in June, and all were adult females. Most (41 of 50) silver-haired bats were submitted during September and October, and only one was rabid. No little brown bat was rabid. The numbers and proportions of rabies-positive big brown bats submitted from the nine most populous counties did not vary widely during 2001–2005, ranging from 10 to 17 bats with rabies and 11% to 26% of the total submitted each year.

Species composition in diagnostic specimens from Denver County differed from the Fort Collins area and the Front Range Corridor, with fewer species and even greater dominance of big brown bats. Ninety-five specimens were submitted from Denver County during 2001–2005: 82 specimens (86%, *CI* 78–92%) were big brown bats, eight were silver-haired bats, four were hoary bats, and one was a little brown bat. The big brown bat samples were primarily juveniles (51%, *CI* 39–61%; $n=41$) and adult females (32%, *CI* 23–42%; $n=26$). Seven (8.5%, *CI* 4–17%) of the big brown bats were rabid (three juveniles and four adults). Three of four hoary bats were rabid, whereas none of the other two species was rabid. The seasonal pattern of submissions in Denver County was none in November through March, most (82%, $n=76$) in June through August, and a peak (43%, $n=40$) in July.

Seasonality and locations of nuisance complaints in Fort Collins

Public health agents investigated 330 incidents involving bats within the city limits in 2001–2005. Numbers of cases peaked in midsummer, with a near absence during late autumn, winter, and early spring (Fig. 6a). The majority of specimens from these incidents

Table 5 Numbers and proportions of bats by species, sex and age submitted for rabies diagnoses from the nine most populous counties (other than Larimer County) along the urbanizing Colorado Front Range Corridor, 2001–2005. A total of 617 specimens was examined

Species	Number tested	Proportion of all species (95% *CI*)	Number and % rabid	Adult females N (% of adults)	Adult males N (% of adults)	Juveniles N (% of total)
Eptesicus fuscus	451	73% (*CI* 69–76%)	72 (16%)	152 (62%)	92 (38%)	202 (45%)
Lasionycteris noctivagans	50	8% (*CI* 6–11%)	1 (2%)	16 (57%)	12 (43%)	22 (44%)
Myotis lucifugus	43	7% (*CI* 5–9%)	0	18 (62%)	11 (38%)	14 (33%)
Lasiurus cinereus	25	4% (*CI* 3–6%)	12 (48%)	12 (60%)	8 (40%)	5 (20%)
Myotis volans	24	4% (*CI* 3–6%)	5 (21%)	12	6	6
Myotis ciliolabrum	12	2% (*CI* 1–3%)	0	6 (50%)	6 (50%)	0
Myotis evotis	4	0.6% (*CI* 0.2–1.7%)	0	1	2	1
Lasiurus borealis	3	0.5% (*CI* 0.2–1.4%)	0	2	0	1
Myotis thysanodes	2	0.3% (*CI* 0.1–1.2%)	0	0	1	1
Corynorhinus townsendii	2	0.3% (*CI* 0.1–1.2%)	0	2 (100%)	0	0
Nyctinomops macrotis	1	0.1% (*CI* 0.03–1.0%)	0	1	0	0

referred for diagnostic rabies tests were big brown bats, the midsummer peak in cases coincides with the appearance of volant juvenile big brown bats (Fig. 4), and the cold season absence coincides with the lack of winter activity at big brown bat roosts in buildings (Fig. 5). Locations of incidents (Fig. 3c) occurred throughout the city, but were concentrated near the centroid of the distribution of known big brown bat maternity roosts (Fig. 3d). Nearly all incidents were associated with buildings. In 149 cases bats were found outdoors near buildings, but 113 were found inside residences, 51 were reported in businesses, and one was in a motor vehicle (location was unspecified in 16 cases). Most (256) of the incidents involved live bats, but in 74 cases the bat was dead when the complaint was investigated. None of the 330 nuisance calls responded to by public health agents included observations of bat die-offs.

Numbers of big brown bat specimens examined for rabies in the nine urbanizing counties of the Front Range Corridor showed a similar seasonal pattern (Fig. 6b). The peak period of submissions encompassed the dates from 30 June to 8 August of all years combined, similar to the peak period of nuisance bat incidents investigated in Fort Collins (Fig. 6a). Most (64%, *CI* 58–70%) of the big brown bats submitted from the urbanizing counties from 30 June to 8 August were juveniles (144 of 225 bats). In comparison, the cumulative proportion of bats we captured as they emerged from buildings during the period 30 June to 8 August was 43% juvenile (*CI* 41–45%; 1,533 juveniles out of 3,564 bats captured at 34 buildings, 2001–2005). During the peak submission period in the urbanizing counties, 10% of the juvenile specimens (*CI* 6–16%; 14 of 144) were diagnosed as rabid, whereas 14.5% of the adult females (*CI* 8–26%; 8 of 55) and 8% of the adult males (*CI* 2–24%; 2 of 26) were rabid. Thus, juvenile bats were sampled for rabies in

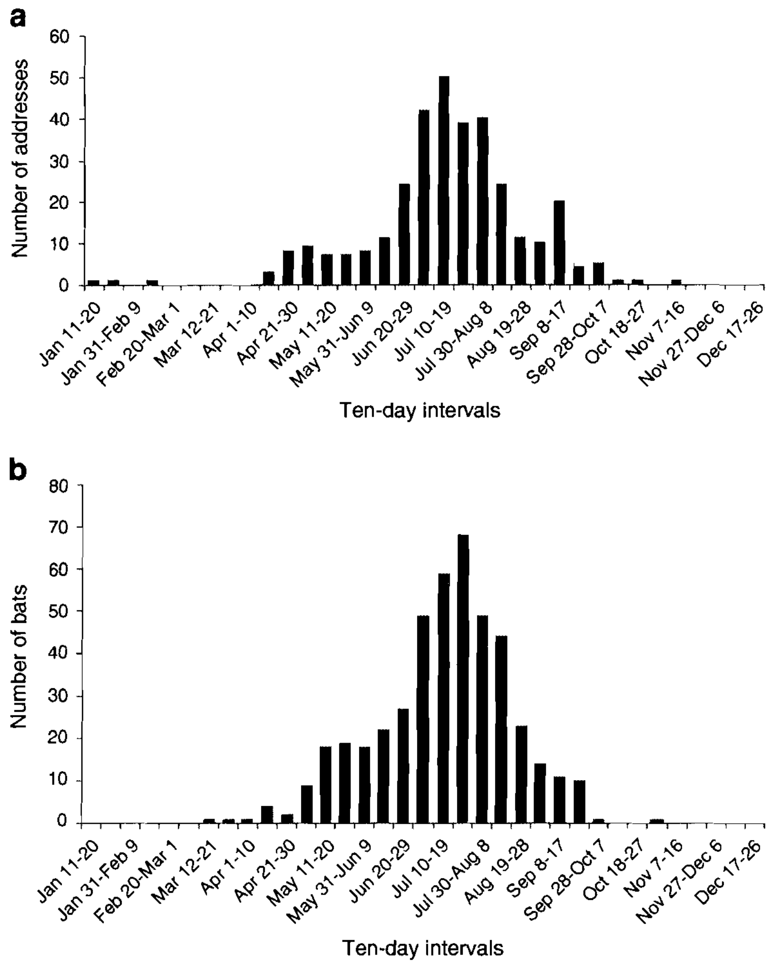


Fig. 6 Seasonal distributions (by 10-day intervals, 2001–2005) of (**a**) numbers of addresses reporting incidents involving bats to public health agents in Fort Collins, Colorado; (**b**) numbers of specimens of bats submitted for rabies diagnoses to the Colorado Department of Public Health and Environment from the nine most populous counties in the urbanizing Colorado Front Range Corridor

greater proportion than their abundance relative to adults, but juveniles did not have a greater prevalence of rabies.

Circumstances of potential human exposure to rabies

Forty-five of 330 incidents investigated in Fort Collins during 2001–2005 involved physical contact between a bat and a human (20) or domestic animals (25). The 20 human-contact cases involved 25 people. Sixteen were adults, six were children ranging from 4 to 15 years of age, and three were age unspecified. In only one case was the contact between bats and humans a *bona fide* bite by a bat, inflicted while the person tried to remove the bat by hand from the wall of a restaurant kitchen. In at least three cases the bat was dead before people handled the carcass. In three other cases the bat flew into or landed on the person and in two cases bats were found in bed with people. One case involved a parent and two children "petting" a disabled bat kept in a cardboard box, and another involved three people passing a live bat around in a tavern. In the remaining ten cases contact was made while people were trying to move or contain the bat. Multiple pets were involved in some cases, with a total potential exposure of ten dogs and 24 cats. Nine of the ten dogs had valid rabies vaccination certificates, with no information available on the tenth. Fourteen of the 24 cats (58%) had valid certificates, six had no or expired certificates (25%), and four had no information.

In addition to the 45 cases with definite contact between a bat and a human or domestic animal, 191 cases were categorized as no contact, 91 were categorized as "possible contact", and three cases were listed as complainant insisting on submitting the bat for rabies testing regardless of lack of exposure. Possible contact cases often involved the simple presence of a bat or bat carcass in an area frequented by pets, or presence of a bat in an area occupied by small children or sleeping adults. Forty-six cases involved possible contact with humans, 45 were with domestic animals, and nine overlapped both categories. Possible contact with pets involved 72 animals, half identified as dogs (n=36) and half as cats (n=36). More dogs (29) than cats (23) in the possible contact cases had proof of current rabies vaccinations. In many cases agent notations implicated cats as having caught the bat or as drawing attention to a debilitated or dead bat on the premises, likely brought in by the cat. Other circumstances in cases of contact or possible contact with humans in the area were varied and are best illustrated by excerpts from agent reports of specific cases (Table 6).

The number of nuisance calls about bats within the city limits was similar each year of the study, with the exception of 2004. The totals for each year were: 54 (2001), 65 (2002), 46 (2003), 105 (2004), and 60 (2005). We attribute the peak in 2004 to local publicity about the health risks of rabies posed by bats. A search of the local newspaper archives (Fort Collins Coloradoan 2007) showed that an article appeared on 23 July 2004 that featured a public warning from local health authorities on the potential dangers posed by exposure to bats in Fort Collins. This appeared during the time of peak emergence of volant young big brown bats when bats are likely most obvious to the public, as described above. In 2004, 66 cases were reported to health authorities after the appearance of this article, whereas fewer cases were reported after this date in the other years, ranging from 6 to 31. The number reported prior to 23 July in 2004 (39) was comparable to numbers prior to that date in all other years of study (range 34–40).

Discussion

This study has revealed some underlying aspects of urban bat ecology that appear to directly influence patterns seen in public health surveillance for rabies (Fig. 7). Below we explore these findings together with pertinent literature for their implications for: (1) patterns of change in bat faunas with increasing urbanization in Colorado and throughout the USA; (2) how use of buildings and (3) movements of the dominant species in urbanizing areas may be derived from natural patterns seen in non-urban areas; and (4) how these ecological factors are manifested in public health surveillance programs for rabies.

Composition of bat faunas and urbanization in Colorado and the USA

As urbanization in the Front Range Corridor progresses, the bat fauna may become increasingly dominated by big brown bats, conforming to more general predictions about homogenization of faunas along rural–urban gradients (McKinney 2006). This homogeni-

Table 6 Incidents of human contact and possible contact with bats excerpted from animal control agent reports in the Larimer County Humane Society records. These accounts include records at locations throughout Larimer County from 1999 to 2005

Date	Animal control agent comments/background
07/3/1999	Three-year-old boy "brought the dead bat to his father after finding it in the yard. He was holding it in his hands."
06/22/2000	"Bat was on ground alive. Kids were messing with it. It bit [15 year old] victim, then died."
07/05/2000	"Subject woke up with bat on his face, grabbed bat and threw into living room."
07/11/2000	40 year old male informant "found bat in river, tried to rescue bat from drowning, bat bit three times, only once drew blood."
07/12/2000	"Kids found bat on ground, picked up bat, then killed bat and took off."
07/14/2000	"Napping in chair, bat landed on her neck."
07/17/2000	"Cat brought in house and killed it; husband saw the bat bite the cat."
07/28/2000	"Bat was being held by many people, all were vagrants. No one was cooperating with names…informants told me that several people have touched the bat and let the bat crawl around on them."
08/12/2000	"Flying around in pediatric ward" of regional hospital.
09/13/2000	"Bat bit [informant] when he tried to get it out of his shoe. Bit on finger."
09/25/2000	"Cat caught bat and brought it into the house." Informant picked it up "not knowing what it was and dropped it again. Husband killed bat on the floor with a mop."
06/19/2003	"Two bats found in toy box in an outside area of child care [center]"
Multiple	Fire station with multiple (21) cases of bats found in sleeping area and living quarters in summers 2002–2004.
07/8/2003	"Picked up injured bat bare handed…someone at party stepped on bat." [Informant kept bat for 3 days before calling authorities].
07/09/2004	Informant "woke up with bat in bed flapping around head and face"
08/02/2004	"Bat found flying around child's bedroom early A.M."

zation may be moderated somewhat by distance to the mountains as source populations of bats. The bat fauna of Fort Collins consisted of seven out of the ten species that we documented in the city and adjacent mountains. Big brown bats were very abundant in the city, particularly adult females and juveniles. Dominance of a single species drawn from adjacent areas is a common feature of many faunal groups within urban and suburban wildlife communities (Adams et al. 2006; McKinney 2006; Shochat et al. 2006). For a wide variety of other animal and plant taxa, urbanized places tend to have less than half the species richness than more natural habitats of a given region (McKinney 2002). With 70% of the species known from the area, the urbanization of Fort Collins has not yet reached this level for bats. These findings contrast with the case of an urban wildlife refuge near Denver, Colorado about three times farther to the adjacent mountains. At the Denver location just three species of bats occurred: 86% of them were big brown bats (97% of big brown bats were adult females and juveniles), with the remainder migratory tree bats (Everette et al. 2001). The species composition of specimens from Denver County submitted to the CDPHE laboratory for rabies diagnoses was identical to the captures in the field study near Denver: 86% of the CDPHE specimens were big brown bats.

Big brown bats can be described as synanthropes or urban exploiters (sensu McKinney 2002, 2006), analogous to birds that naturally nest on cliffs or in cavities but that can adapt to buildings for nest sites and become dominant in cities. We speculate that the adaptability

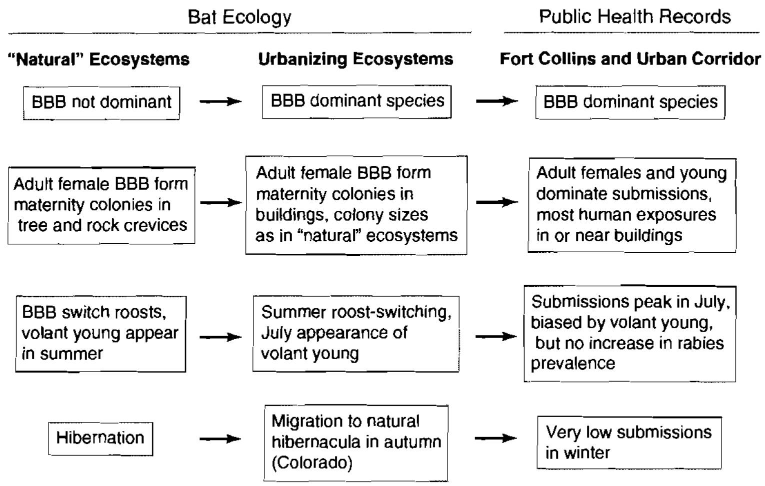


Fig. 7 Summary of the influence of bat ecology on results of the public health surveillance program for rabies in bats in Fort Collins and the urbanizing Front Range Corridor of Colorado. See Discussion for supporting literature citations. Abbreviation: BBB = big brown bat, *Eptesicus fuscus*

of big brown bats in exploiting new roosting opportunities in buildings along with their tolerance of human activities are key to their abundance in USA cities. Maternity colonies of big brown bats have used buildings in Colorado at least as early as 1907 (Warren 1910). The species was very common and colonies were regarded as nuisances in buildings in Fort Collins over 40 years ago (Lechleitner 1969). Similar to findings in Colorado, sampling bats by mist net in the suburban environment at Detroit, Michigan also showed lower diversity than in comparable rural areas, with 83% of captures consisting of big brown bats, and the remaining species migratory tree bats (Kurta and Teramino 1992). Dominance of big brown bats in urban areas in comparison with rural areas has also been noted in sampling through captures in mist nets around Washington DC (Johnson et al. 2008), and in urban parklands in Atlanta GA, Macon GA, Charleston SC and Greensboro NC (83% of captures in the four cities combined; Loeb et al. 2009). Dominance of big brown bats in urban or suburban areas in the USA has also been inferred from studies of bat echolocation activity, including Chicago and surrounding areas (Gehrt and Chelsvig 2004), four cities in the southeastern USA (Loeb et al. 2009), and the Washington DC area (Johnson et al. 2008). In the Washington DC study it was uncertain if the dominance of big brown bats was due to greater natural or anthropogenic roosting opportunities (Johnson et al. 2008). In our area, extensive radio-tracking showed that natural roosts were unimportant for big brown bats.

In addition to abundant roosts, other factors related to development of the landscape likely promoted growth in the Fort Collins big brown bat population (demographics of recruitment and survival in big brown bats in Fort Collins show population growth; O'Shea et al. 2010; 2011). The urbanizing habitat includes greater availability of permanent water for bats from creation of ponds, lakes, reservoirs and canals. The semi-arid landscape has changed due to planting of a diversity of large ornamental and shade trees, shrubs, and lawns throughout the city (Fort Collins has been designated as a "Tree City, USA"; Arbor Day Foundation 2009), and the subsidizing of this vegetation with irrigation and fertilizers. The urbanizing landscape in northern Colorado has much larger above-ground carbon pools, higher annual net primary productivity, and higher soil nitrogen than native habitat (Golubiewski 2006; Kaye et al. 2005). Anthropogenic subsidies may enhance the insect prey base for big brown bats, as has been found for insects and other invertebrates in other urban ecosystems (e.g. Faeth et al. 2005; Falk 1976; McIntyre 2000). The conservation of riparian and floodplain habitats by the Fort Collins Natural Areas program maintains heavily vegetated and structurally diverse areas with abundant riparian trees and shrubs along the Poudre River (Duerksen and Snyder 2005), habitat not present prior to settlement (Knopf 1986; Knopf and Scott 1990).

Roosts of big brown bats in buildings

Maternity colonies of big brown bats in Fort Collins roosted exclusively in buildings, most of which were used by people as residences or for social purposes. We were limited in finding more colonies in buildings only by numbers of radio-transmitters. Some buildings were used by bats only during specific times in the reproductive cycle, and other buildings were used only as night roosts. Although the percentage of buildings used by bats appears low, use of buildings and movements among them clearly put bats and citizens in close proximity and possible conflict. Roosts in Fort Collins were not in particularly old buildings and most were not in attics, contrary to findings in Alberta and Pennsylvania (Schowalter and Gunson 1979; Williams and Brittingham 1997). It is likely that using radiotelemetry in the urban area revealed a wider array of building types and roosting places within buildings than past studies that relied on local knowledge. Three methods of detecting buildings with bat roosts (radio-tracking, random searches, and locations of nuisance calls) all show similar results, with evidence of more roosts in areas closest to the original settlement. Detailed analysis of factors of possible importance in selection of buildings as roosts by big brown bats in Fort Collins were presented elsewhere, and showed that building age was unimportant (Neubaum et al. 2007). Instead, bats roosted in buildings that had larger openings to roosting areas, were slightly warmer, and had openings that were higher than in randomly selected buildings; buildings with roosts were also located closer to areas with roosts in other buildings, with lower building densities, and lower vehicle traffic volumes (these areas tended to be in sections of the city closer to the original settlement sites; Neubaum et al. 2007). The important properties of height, entrance area, and warmer microclimates have been demonstrated for this species at natural roosts in trees and rock crevices (Cryan et al. 2001; Kalcounis and Brigham 1998; Lausen and Barclay 2002, 2003; Vonhof and Barclay 1996). This similarity illustrates that behavioral attributes involved in roost site selection by big brown bats in natural situations (as documented by other studies) seem to persist after colonization of buildings in Fort Collins (Neubaum et al. 2007).

Use of buildings by big brown bats was markedly seasonal, with activity beginning in spring, and peaking in June and July coinciding with birth, nursing, and fledging of young. Colony sizes in June in Fort Collins were similar to reports for other colonies in buildings at widely separated locations in the USA and Canada (Kunz and Reynolds 2003). Reports of colony sizes of big brown bats that occupy natural roosts in trees and rock crevices (e.g., Brigham 1991; Kalcounis and Brigham 1998; Lausen and Barclay 2002; Willis et al. 2006) are also within the range we observed in buildings in Fort Collins, although most colony sizes in natural roosts do not reach the maximum sizes we report. In some cases this may be due to large colonies in natural areas fragmenting into subgroups roosting among individual trees (Willis and Brigham 2004). Evidence of bats in buildings in our area in winter was scant. Despite the exploitation of buildings by maternity colonies, big brown bats apparently have retained the natural local migration pattern of returning to higher elevations for hibernation in rock crevices in autumn (Neubaum et al. 2006): temperature regimes in these rock crevices are ideal for hibernation compared to temperatures in roosts in buildings

(Neubaum et al. 2006). This is unlike the Midwestern USA, where big brown bats more commonly hibernate in buildings (Whitaker and Gummer 1992).

Movements of big brown bats

Under natural conditions in forests, big brown bats frequently move among roosts in trees following a fission-fusion social organization: individual members of a colony will move among cavities in groups of trees in a limited area every 1–5 days, but will not move among trees in different nearby areas occupied by different colonies (Willis and Brigham 2004). This roost-switching behavior has been retained by big brown bats that roost in buildings in Fort Collins. Earlier work (Ellison et al. 2007a) demonstrated that bats in this population often move between adjacent roosts, with rates varying with daily high temperatures. Our study showed that radio-tracked or PIT-tagged bats seldom joined colonies at roosts in buildings greater than 1 km apart (distances between groups of trees used by distinct colonies in forested habitats also are >1 km apart; Willis and Brigham 2004). Roost-switching in the urban environment has advantages and disadvantages for bats in conservation and public health contexts. One advantage to bats is that alternate roosts provide a means for persistence of colonies despite high attrition (35% over 4 years) in roosts. Familiarity with alternate nearby roosting locations favors endurance of colonies after exclusion, but may shift the nuisance to other buildings. We clearly saw this in our detailed case study. Although effects of exclusion may have a short-term impact on reproduction in big brown bats (Brigham and Fenton 1986), we saw no strong evidence for lasting impacts on reproduction or survival. However, a shift to new or seldom-used roosts can call public attention to bats at the new location and perhaps result in additional nuisance complaints or exclusion attempts. Switching roosts during hot weather also may account for some of the mid-summer peak in specimens submitted for rabies diagnoses (see below).

Bats that we radio tracked while foraging primarily used Natural Areas along the Poudre River. This implies that city conservation policies help support the population of big brown bats roosting in buildings in Fort Collins. We seldom tracked foraging bats to urbanized areas and did not see them foraging at streetlamps in the city (reported elsewhere by Furlonger et al. 1987). Low activity over urban habitats was also reported in radiotracking of big brown bats near Indianapolis, Indiana (Duchamp et al. 2004), and echolocation activity of foraging big brown bats in and around Chicago and Washington DC also suggested low use of more urban habitat for feeding (Gehrt and Chelsvig 2004; Johnson et al. 2008). Overall, our findings at Fort Collins conform to a prediction by Geggie and Fenton (1985) that if roosting opportunities limit populations of bats, big brown bats should thrive along the interface between rural and urban settings because they can exploit high roost densities where food availability is not severely diminished by development. The juxtaposition of preserved Natural Areas along the river corridor that runs through the city provides such a configuration in Fort Collins.

Distances travelled from roosts to foraging areas in Fort Collins (mean 5.9 km, range 3.5–12.5 km) overlapped those reported for big brown bats roosting in Denver (mean 14 km, range 9–19 km; Everette et al. 2001). However, these distances are greater than those reported for big brown bats radio-tracked in a less urban area in British Columbia (Brigham 1991) and in Ontario (Brigham and Fenton 1986), and in summaries of natural history observations suggesting 1–2 km between roosts and foraging areas (Kurta and Baker 1990). In our study tagging bats at roosts and subsequently tracking them to foraging sites revealed much longer distances travelled than distances between bats captured at foraging sites and radio-tracked back to roosts or bats registered at roosts through PIT-tag records. Such differences suggest that tracking bats from capture sites back to roosts may impart a low bias to estimates of distances between roosts and foraging areas. Foraging big brown bats in Fort Collins did not show nightly fidelity to the same foraging sites, similar to foraging big brown bats near Indianapolis, Indiana (Duchamp et al. 2004).

Bat ecology and patterns in public health surveillance for rabies

Modern conditions favorable for populations of big brown bats in urbanizing areas of the Colorado Front Range Corridor have placed this species in conflict with humans, both as nuisances and as potential source of exposure to rabies. Prevalence of rabies in bats in the Fort Collins area was similar to that in the other populous Front Range Corridor counties and was consistent with past summaries of prevalence of rabies in bats submitted to the CDPHE laboratory, which ranged from 11% to 19% each year, averaging 17% over a 20-year period (n=2,135 bats; Armstrong et al. 1994; Pape et al. 1999). This proportion, however, is higher than the national trend of 5.8% (out of 20,911 big brown bat specimens examined 1993–2000; Mondul et al. 2003). These "passive surveillance" prevalence data are inherently biased high because other than juveniles, healthy bats are unlikely to be discovered, captured, and submitted to diagnostic laboratories. Instead they represent a sample of bats that are sick, already incapacitated, or not fully developed.

Records of bat submissions for rabies diagnoses, locations of nuisance calls, and our frequent visits to roosts showed no evidence for die-offs of big brown bats from diseases in Fort Collins during 2001–2005. This is notable because the area experienced the arrival of the most intense phase of the North American epizootic of West Nile virus in 2003 (Bode et al. 2006; Gujral et al. 2007; Nemeth et al. 2007) and concern has been expressed about effects of this virus on bat populations (Bunde et al. 2006; Pilipski et al. 2004). The arrival of the epizootic was followed by application of permethrin (a general insecticide) by public health authorities late in summer 2003 and again in 2004 for mosquito control (West Nile virus is mosquito-borne), including some areas where these bats may forage (Bolling et al. 2007). We did not observe any obvious morbidity or mortality of bats at roosts or changes in patterns of submission or nuisance calls in these 2 years. This is consistent with later findings that big brown bats do not show clinical signs of infection after experimental inoculation with West Nile virus and cannot serve as reservoirs for the disease (Davis et al. 2005), and with no evidence as yet for effects of permethrin on bats (Clark and Shore 2001). Our observations of low mortality at roosts is consistent with a general lack of reports of mass die-offs of bats at maternity colonies in the USA other than from climatic factors (freezes and floods), vandalism, or chemical poisoning, up until the recent losses of colonies in hibernation associated with a novel fungal infection (white-nose syndrome; Blehert et al. 2009; Frick et al. 2010). We found no supporting literature for major die-offs of bats from rabies, also consistent with our findings.

Each species of bat found in Colorado harbors distinct genetic variants of rabies virus, indicating little spillover among bat species (Shankar et al. 2005). This is consistent with our observations of buildings used only by single-species colonies. Interestingly, although most human exposure to rabies from bats in the US is through big brown bats, most human deaths due to rabies in the United States are associated with genetic clades of virus variants with subdivisions found in silver-haired bats, hoary bats, and tri-colored bats (*Perimyotis subflavus*; Franka et al. 2006). Silver-haired bats were the second and third most submitted species for rabies diagnoses in the Front Range Corridor and Larimer County, respectively, but had a low prevalence of positive specimens. Silver-haired bats were also the third most abundant species taken in nets over water in Fort Collins, but primarily were taken during migration seasons. Most of the silver-haired bats sampled by the CDPHE rabies laboratory were also taken during autumn migration. This suggests that perhaps during migration silver-haired bats become more obvious to humans by seeking unfamiliar temporary daytime shelters where they may be more conspicuous regardless of health status, as we observed in the case of these bats found over a picnic table and in a door jamb. Such circumstances and the seasonal presence of this species in public health submissions show that human exposures to silver-haired bats can occur in urbanizing settings.

Activity of bats at roosts in buildings in Fort Collins drops substantially in September, radio-tagged bats left the city by mid-September, and most bats were absent throughout the winter. This is reflected in the seasonality of nuisance calls and submissions for rabies diagnoses to public health authorities in Fort Collins, Larimer County, and the Front Range Corridor. This similarity clearly indicates that the potential for most human or domestic animal exposure to rabies from bats in the urbanizing corridor follows the annual ecological cycle of big brown bats. This species roosts in buildings used regularly by people as living quarters or for social functions. Thus the use of buildings as maternity roosts by big brown bats is a major driver for much of the public health surveillance needed against rabies in bats in Colorado. This proclivity to roost in buildings and associated behavior in Fort Collins may explain the dominance of this species in national public health records as well: 20,911 out of 31,380 bats examined in the USA from 1993 to 2000 were identified as this species, and 1,216 out of 1,946 rabid bats were big brown bats (Mondul et al. 2003).

The number of nuisance calls and the number of bats submitted for rabies diagnoses at our study area peaked in July. This may in part be due to shifting of roost locations during periods of high summer temperatures (Ellison et al. 2007a). Nursing females make these moves, and will move large nursing young with them (Ellison et al. 2007a; Mayrberger 2003). July is also when most juvenile bats first emerge from roosts for nightly foraging. Juveniles predominate in the samples of big brown bats submitted for rabies diagnoses in the Front Range Corridor in July. The proportion of the juvenile specimens that was rabid, however, was no greater than in adults. This suggests that newly volant juvenile bats are more likely to be encountered by the public because of disorientation or unfamiliarity with a site (perhaps accompanying a move by mothers), less well-developed flight capability, or morbidity from factors other than rabies. The only major change in temporal patterns of nuisance calls was an increase directly related to local newspaper publicity about dangers of contracting rabies from bats.

A survey of public perceptions and attitudes about bats and rabies among Fort Collins residents showed that 80% of respondents were aware that bats occurred in the city, 98% knew that rabies was transmitted by bites, and 81–89% knew that rabies was fatal if not treated and that bat bites require testing of bats, consultation with a physician, and need for immunization if the bat is rabid (Sexton and Stewart 2007). Awareness and vigilant public health programs probably account in part for the low numbers of human rabies deaths in Colorado and the USA (Mondul et al. 2003; Pape et al. 1999). Despite publicity and a generally knowledgeable citizenry, however, potential human or domestic animal exposures to rabies from bats occurred every year during our study. Many of these incidents were avoidable, as suggested by various case histories we report. Although predation on bats was seldom observed in our study, predation by domestic cats was seen more often than by other animals; domestic cats also were involved in cases where bats were brought into residences, and fewer cats than dogs had evidence for current rabies immunizations. Continued vigilance and education efforts against rabies in urban settings by USA public health agencies is supported by these lapses in preventing exposure or transmission, particularly considering the frequent occupancy by bats of buildings used regularly by people. Urbanization has favored the dominance of a single species of bat in many cities of the USA, and its behavior and annual ecological cycle have brought with it a dangerous disease requiring a vigilant public health surveillance system. The efficacy of this system is attested to by the very low rate of human deaths due to rabies from big brown bats in the US (Mondul et al. 2003). Given that urbanization appears to favor a single widespread and abundant species of bat, efforts to exclude bats from buildings and to continue to inform the public about rabies in bats would appear to have few directly negative impacts on the conservation of bat diversity within Fort Collins and other cities in the USA.

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Electronic Supplementary Material for UECO241

A. AICc Model Selection

For species capture results we modeled probabilities (proportions captured by species, sex or age) as functions of covariates using logistic regression (Proc GENMOD; SAS Institute 2003) . Under the general models probabilities were allowed to vary among categories, whereas under constrained models probabilities were assumed to be constant. Models were ranked using AIC corrected for sample size (AIC_c; Burnham and Anderson, 2002). We also calculated AIC_c differences (Δ_i; difference in AIC_c score between i^{th} and top-ranked model) and Akaike weights (w_i; weight of evidence that the i^{th} model was the best approximating model among the candidate models). The model with the lowest AIC_c score was assumed to be best fitting (Burnham and Anderson, 2002).

Supplementary Table 1 Rankings by Akaike's information criterion adjusted for small sample size (AIC_c--Burnham and Anderson 2002) of top logistic regression models comparing the proportions of female big brown bats captured in Fort Collins, Colorado or adjacent mountains at two elevation zones (< 2000 m and > 2000 m) from 2001 – 2005 (A-D) and frequency of big brown bats among species in the city versus mountain locations (E). Under the general model the probability of a female in the sample is allowed to vary among the three locations, whereas under the constrained model the probability of a female in the sample was assumed to be constant among locations. K is the number of estimable parameters in the model, Δ_i is the difference in AIC_c value between the i^{th} and top-ranked model and w_i is the Akaike weight (probability that the i^{th} model is actually the best approximating model among the candidate models). Abbreviations: EPFU = big brown bats (*Eptesicus fuscus*); LACI = hoary bats (*Lasiurus cinereus*); LANO = silver-haired bats (*Lasionycteris noctivagans*); MYLU = little brown bats (*Myotis lucifugus*); Mtns = mountains.

Comparison	*K*	AIC_c	Δ_i	w_i
A. Adult EPFU Female vs Male at City, Two Mtn Zones				
General model	3	498.88	0.00	1.00
Constrained model	1	552.26	53.38	0.00
B. Adult MYLU Female vs Male at City,Two Mtn Zones				

General model	3	150.12	0.00	1.00
Constrained model	1	181.40	31.28	0.00
C Adult LANO Female vs Male at City, Two Mtn Zones				
General model	3	83.08	0.00	0.98
Constrained model	1	90.92	7.84	0.02
D. Adult LACI Female vs Male at City, Two Mtn Zones				
General model	3	40.37	0.00	0.92
Constrained model	1	45.34	4.97	0.08
E. EPFU vs Other Sp. Captured at City, Two Mtn Zones				
General model	3	1064.70	0.00	1.00
Constrained model	1	1301.69	236.99	0.00

B. Protocol for assessing detectability of use of buildings by bats in random searches

We developed the following method to assess detectability of bat colonies in buildings during ~~or~~ searches of randomly selected buildings. We followed a completely randomized design in selecting buildings from a list maintained by Larimer County that included 65,049 addresses within the city limits. Personnel with field experience in bat natural history visited each randomly selected address, and with permission of the occupants searched the external walls for signs of potential bat use such as openings, stains around openings, sounds of bats vocalizing, and bat fecal pellets (droppings) on the ground near the walls. Occupants were also interviewed about their knowledge of bat occupancy or absence. We limited the search to a period (June 14 to July 20) when maternity colonies were active. The procedure assumes the response variable (occupied, not occupied) is determined without error. Because this will only occur when detection probabilities equal 1.0, we developed a maximum likelihood procedure for estimating detection probability following a site occupancy model approach (MacKenzie et al., 2002). We utilized two observers who searched each building independently on the same date to judge if a maternity colony was present. The observers also noted signs of more limited use by bats (*e.g.*, small numbers of fecal pellets suggesting use by solitary bats). Occupancy by colonies was verified by observing the building on the same or following evening to confirm that bats emerged from the site.

Despite this design and protocol, we were unable to estimate a detectability function for occupancy by colonies because of low numbers of occupied sites and low rates of verification. The number of buildings in which one or more independent observers judged occupancy by a maternity colony was 12 out of the 406 surveyed, with both independent observers agreeing on 10 of the 12 positive cases. However, verification based on exit counts was low: only 1 of 10 was occupied at the time of sampling. Two others of the 12 positive cases found among randomly selected buildings had been previously known to harbor bats from radio-tracking earlier in the study. We also found that false negatives can occur in the surveys for maternity colonies. We counted bats during emergence at only one of 20 buildings observers characterized as having only minor use by bats, and it had a maternity colony of about 30 bats.

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