

FORAGING ECOLOGY OF BATS IN SAN FRANCISCO, CALIFORNIA

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Biology: Ecology and Systematic Biology

by

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San Francisco, California

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CERTIFICATION OF APPROVAL

I certify that I have read Foraging Ecology of Urban Bats in San Francisco by Jennifer Joy Krauel, and that in my opinion this work meets the criteria for approving a thesis submitted in partial fulfillment of the requests for the degree: Master of Science in Biology: Ecology and Systematic Biology at San Francisco State University.

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2009

Little is known about the foraging requirements of bats in densely populated urban settings. This study seeks to understand the distribution and abundance of bat foraging activity in San Francisco natural areas, how characteristics of natural areas influence the observed patterns of distribution and foraging activity, species-specific responses to those characteristics, and seasonal patterns in distribution and abundance of bat foraging activity. Twenty-two parks were surveyed quarterly during 2008-2009 using Pettersson D240x acoustic monitoring equipment. Four species were confirmed (*Tadarida brasiliensis*, *Myotis yumanensis*, *Lasiurus blossevillii*, and *Myotis lucifugus*.) Results indicate that amount of forest edge and distance to water were the factors best explaining species richness and foraging activity. This study shows that bats are present even in densely populated urban centers, although at reduced species richness, and that habitat factors explaining their community composition and activity patterns are similar to those documented in less urbanized environments.

I certify that the Abstract is a correct representation of the content of this thesis.

Chair, Thesis committee

Date

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Introduction

Conservation in the 21st century is increasingly about managed areas, not wild lands. Although ecology has traditionally focused on the latter, understanding how to maintain diversity in managed areas is a progressively more important research priority. While most taxa show a decrease in species richness and abundance with increasing urbanization, responses can be variable and difficult to translate into management guidelines (Andren 1994; Debinski and Holt 2000). Factors that may influence diversity can become politically charged, for example the controversy over native vs. introduced plants (Connor et al. 2002), and determination of appropriate uses of natural areas (e.g. off-leash dogs, mountain bikes). The management challenges in these urban wild lands thus become more complex with fewer options, and the need for research-based recommendations becomes even more important. However, as urban densities are increasing but human interactions with nature are decreasing, these urban core areas offer the most opportunities for access to nature, education and conservation outreach (Niemela 1999).

A growing body of research illuminates the effects of increasing urbanization on natural communities (Blair 1996, Clergeau et al. 1998, Blair 1999, Clark et al. 2007).

Nevertheless, factors promoting diversity and abundance in urban taxa can be confusing. Many studies have reported a positive relationship between patch size and species richness, supporting an approach based on the concept of urban parks as islands

(Gavareski 1976, Faeth and Kane 1978, Nupp and Swihart 2000, Crooks et al. 2004, Smith 2007), but others show contradictory responses (Debinski and Holt 2000).

Connectivity between parks and the permeability of the inter-park urban matrix also contribute to species richness (Debinski and Holt 2000, Fernandez-Juricic 2000, Fenter 2007, Hodgkison et al. 2007), especially for less mobile species (Bolger et al. 2001).

Other factors influencing species richness in different taxa include structural diversity of vegetation (Carrascal et al. 2002, Evans et al. 2009), number of nectar-producing flowering plants (Clark et al. 2007), proportion of park that is natural or forest (Bolger et al. 2001), patch age (Crowe 1979, Bolger et al. 2008), tree height (MacGregor-Fors 2008), or degree of human disturbance (Ficetola et al. 2007). In some cases, factors that promote species richness in one taxa decrease it in other taxa (Ficetola et al. 2007). In addition, the importance of factors may also vary across seasons, and most studies do not examine effects throughout the year (but see Bolger et al. 2000).

Species richness in urban mammals is often affected by different factors than apply to other vertebrates (Sorace 2001, Moreno-Rueda and Pizarro 2009). At a local scale, patch size is often cited as positively correlated with richness (Vandruff and Rowse 1986, Dickman 1987, Dunstan and Fox 1996, Nupp and Swihart 2000), but sometimes the reverse is true (Bowers and Matter 1997, Pardini 2004). Habitat-related factors that are important to urban mammal species richness include vegetation density (Dickman 1987, Hodgkison et al. 2007, Croci et al. 2008), native grass cover, the number of hollows

(Hodgkison et al. 2007), presence of water (Vandruff and Rowse 1986), patch age and proximity to buildings (Dickman 1987), and the diversity of the herbaceous layer (Andrews and O'Brien 2000, Croci et al. 2008). For most of these species, nesting and foraging resources are provided by the park where they are resident, although little is known about how competition, predation, or social behaviors affect distribution of mammal species and individuals in urban settings. While these patterns are becoming established for many mammals (Baker et al. 2003; Baker and Harris 2007), volant mammals may experience the urban environment in a very different way since they are less affected by habitat fragmentation (Evelyn 2002; Loeb et al. 2009).

While no studies of bats have focused on the urban core, there is a growing body of literature examining factors related to an urbanization gradient. Relative to less urbanized areas, some more urbanized areas have increased diversity (De Cornulier and Clergeau 2001, Gehrt and Chelsvig 2003, Johnson et al. 2008) while others have reduced diversity (Geggie and Fenton 1985, Kurta and Teramino 1992, Gaisler et al. 1998, Avila-Flores and Fenton 2005, Hourigan et al. 2006, Duchamp and Swihart 2008) and others found no relationship between urbanization and diversity (Loeb et al. 2009). In most habitats, bats are limited more by roost availability than food availability (Fenton 1990), but there is some evidence to show that this is not the case in urban areas (Duchamp et al. 2004). Urban areas are characterized by many trees and by structures that may provide a greater variety of roosting options (Evelyn 2002; Loeb et al. 2009). In addition, urban areas tend

to have reduced insect diversity and abundance relative to surrounding rural areas (Frankie and Ehler 1978, Nuckols and Connor 1995) and bat activity is often directly related to insect activity and mass (Avila-Flores and Fenton 2005; Bell 1980; Scanlon and Petit 2008). This suggests that urban bats may be limited more by access to food resources than roost resources.

Given that their diet is comprised of insects, and that roost availability is less likely to limit distribution of urban bats, it is possible that their distribution is driven by ecological factors that influence insect abundance. There is some evidence that habitat features that enhance insect abundance (e.g. edge habitat and water sources) may lead to higher bat activity. For example, forest edge habitat is important for flying insects (Lewis 1969, Fried et al. 2005) and insect diversity and abundance is often higher near water (Fukui et al. 2006). Studies of urban bat foraging activity have reported a strong correlation between activity and amount of forest edge (Walsh et al. 1995, Vaughan et al. 1997, Everette et al. 2001, Gehrt and Chelsvig 2003) and proximity to water (Lewis 1967, Nagraeff and Brigham 1995, Walsh and Harris 1996, Vaughan et al. 1997, Lesinski et al. 2000, Russo and Jones 2003, Hourigan et al. 2006, Zukal and Rehak 2006, Whitford 2009). These habitat factors are, of course, important for additional reasons beyond insect abundance; bats may also prefer edges because they cannot forage within the forest clutter as efficiently (Grindal and Brigham 1999; Sleep and Brigham 2003) and water importance is also due to water for drinking (Adams and Simmons 2002).

Unlike many urban areas where the urban bat community may be influenced by bats from surrounding suburban or agricultural areas (Avila-Flores and Fenton 2005; Gehrt and Chelsvig 2003). San Francisco offers an ideal opportunity to study the effects of core urban habitats. It is relatively small land area, yet is the second-most densely populated area in North America, after New York City. San Francisco is situated at the end of a peninsula, with salt water on three sides, which can be an effective barrier for even volant species, although some species have been known to cross the ocean during migration (Cryan and Brown 2007). Unlike other urban areas studied, there is not a significant amount of agricultural area surrounding the city; the approach over the peninsula passes through suburban areas and through wild land owned by the San Francisco water district (9,307.77 ha) and the Mt. San Bruno natural area (941.30 ha).

This study aims to identify foraging area characteristics important for San Francisco bat communities and to provide baseline data on bat species diversity and community composition. Specifically, I seek to determine (1) the distribution and abundance of bat foraging activity in San Francisco natural areas; (2) which characteristics of natural areas influence the observed patterns of distribution and foraging activity; (3) species-specific responses to those characteristics; and (4) seasonal patterns in distribution and abundance of bat foraging activity.

Methods

Study area

San Francisco's climate is defined as a coastal Mediterranean climate with dry mild summers and wet mild winter (Ritter 2006). This particular climate has a dry season lasting typically from May until October and a wet season from November until April. From late October through March, San Francisco receives an average of 95% of its annual rainfall (Null 1999). Wind and fog are common. These may influence bat activity as bats have been shown to be less active in moderate to strong winds (Rydell 1989, Boonman 1996, Russo and Jones 2003) and fog (Pye 1971, Ciechanowski et al. 2007).

The wild lands in the city itself consist of a set of federally managed areas, collectively called the Golden Gate National Recreation Area (GGNRA) and a set of 31 parks managed by the city of San Francisco that have areas designated as Significant Natural Areas (hereafter called "natural areas"), ranging in size from 0.3 acres to over 300 acres. Natural areas are defined as having remnant fragments of the Franciscan Landscape (Forman 1995) that have been largely unchanged by human activity. These undeveloped natural areas are not pristine and many are dominated by non-native plant species. They also contain a mosaic of coastal scrub, perennial grasses, chaparral, riparian wetlands, and native patches of coastal live oak and laurel trees, which support many sensitive plant and animal species (Connor et al. 2002). San Francisco residents and visitors have access

to these natural areas for passive recreational purposes such as hiking, nature watching, and dog walking.

I studied twenty-two parks. Fifteen parks were chosen to enable comparison with three earlier studies (McFrederick and LeBuhn 2006, Fenter 2007, Clarke et al. 2008). I added seven additional parks randomly selected to provide a suitably large sample size (Figure 1, Appendix 1). Three of the additional park sites were added after the first quarter, including two sites in the Presidio of San Francisco and one over a private reservoir adjacent to a natural area in the study.

Seventeen species of bats, all insectivorous, are known to occur along the central coastal region of California. An earlier survey (Pierson and Rainey 1995) found at least five different species in the Presidio of San Francisco: Big brown bat (*Eptesicus fuscus*), Red bat (*Lasiurus blossevillii*), Hoary bat (*Lasiurus cinereus*), Mexican free-tailed bat (*Tadarida brasiliensis*), and at least one species of *Myotis*. Museum records document the presence of California myotis (*Myotis californicus*) and Yuma myotis (*Myotis yumanensis*) in San Francisco County (Pierson and Rainey 1995). Other species that could possibly occur in San Francisco include Pallid bat (*Antrozous pallidus*), Silver-haired bat (*Lasionycteris noctivagans*), Long-eared myotis (*Myotis evotis*), Little brown bat (*Myotis lucifugus*), Fringed myotis (*Myotis thysanodes*), Long-legged myotis (*Myotis*

volans), Townsend's big-eared bat (*Corynorhinus townsendii townsendii*), and Mastiff bat (*Eumops perotis*).

Bat activity and diversity

I conducted acoustic monitoring surveys of each site for one night every quarter during the period of May 2008 through April 2009. For each quarterly round, recording dates were as close together as possible, usually on subsequent nights. I only sampled on nights with winds less than 20 mph, and tried to keep conditions consistent between nights within quarters. Parks were visited in random order. To determine the sampling area within each site, I used GIS software (ArcMap version 9.2, Esri, Redlands, CA USA) to identify forest and water edges which would be most likely to attract foraging bats within each park (Furlonger et al. 1987, Lesinski et al. 2000, Everette et al. 2001, Gehrt and Chelsvig 2003, Sparks et al. 2005). Multiple random locations were generated along those edges in each park (Beyer 2004) and were sequentially evaluated on site. I selected the first adequately secure location for each park. Detectors were set up at heights ranging from 1-3 meters, depending on the location, and facing perpendicular to the expected bat foraging corridor.

To collect each acoustic sample, I used four Pettersson D240X ultrasonic acoustic detectors (Pettersson Elektronik AB, Upssala, Sweden) connected to iRiver IPF digital recorders (iRiver America, Vancouver, WA). The detector used on a given park night

was chosen at random. I calibrated detectors using an ultrasonic emitter at the start of the study and periodically thereafter. Detectors and recorders were placed in a plastic waterproof casing inside a metal cage to deter vandalism. Lab and field tests showed that the housing did not affect the recordings or quality of recorded bat calls. These data will be published elsewhere. Detectors were configured to automatically trigger upon detection of ultrasonic noise, and to record time-expanded 1.7-second call sequences in each file on the recorder.

After the equipment was retrieved the next day, I analyzed the recorded bat call files using Sonobat software (Szewczak 2008), discarding files not representing recognizable bat calls, for example, insect activity or wind noise. For bat activity, I evaluated the number of recognizable call sequence files per park night, where each call recording was considered to be a pass by one or more foraging bats (Fenton 1970). This number does not represent the number of animals in the area, but rather a relative measure of bat foraging activity at a particular location (Hayes 2000). For species richness, I evaluated the number of separately identified species per park night. The total richness value for each park represents the cumulative number of species recorded in that park over the course of the year. I identified calls to species qualitatively based on lowest apparent frequency, highest apparent frequency, characteristic frequency (the frequency of the call at its lowest slope, or the lowest frequency for consistent FM sweeps), frequency with the greatest power, call duration, and upper and lower call slope (O'Farrell et al. 1999,

Szewczak and Weller 2006). Dr. Joseph Szewczak, Humboldt State University, California, confirmed species identifications.

All three members of the acoustically similar species group of *Tadarida brasiliensis*, *Eptesicus fuscus*, and *Lasiurus cinereus* were expected in this study area. Because neither *E. fuscus* nor *L. cinereus* were confirmed in this study, the equipment was tested in a nearby area to verify that those species would be recognizable if present. Both species have been reported in San Francisco (Pierson and Rainey 1995) as well as in the surrounding areas (Heady and Frick 2000, Cryan and Brown 2007, Mudd 2007). While no recorded calls were a strong match for *E. fuscus*, some calls recorded in this study were highly suggestive of *L. cinereus*. However, because attributes of some of their calls can overlap strongly with those of *T. brasiliensis*, for the purposes of species richness estimates in this study I assigned all to be the most commonly present and most acoustically variable species of that group, *T. brasiliensis*. There was no other group of indistinguishable calls observed in the study.

Afternoon and morning temperature, average and maximum wind speed, cloud cover, and precipitation were recorded for each park night, as was temperature, humidity, wind speed, and precipitation at a citywide, not park-specific, level for each night (Weather Underground 2009).

Insect abundance and diversity

Insect abundance and diversity were addressed using sticky traps constructed of one 8.5 x 11 inch transparency sheet wrapped around a small water bottle and covered with aerosol Tangle Trap (Tanglefoot, Grand Rapids, MI). Traps were suspended from trees in non-illuminated areas. While all insect-sampling methods are biased toward certain types of insects (Kunz 1988), field studies have shown that sticky traps did not catch significantly different orders of insects or numbers of insects relative to suction or intercept traps (Sleep and Brigham 2003). Insect abundance as measured by these traps was negligible, even with four traps per park night. Sampling was discontinued during the final quarter and no analysis was done.

Park characteristics and analysis

I calculated park size, proximity to water, and proximity to large parks (> 100 ha) using ArcMap (Appendix 1). Proximity was measured as the distance from the recording location to the edge of the nearest body of water or large park. I used data supplied by the San Francisco city parks to determine the area of native vegetation and the amount of forest edge within each park (EIPAssociates 2005). While most tree-covered areas in San Francisco are smaller than may be generally considered as “forest”, I defined forest edge in this study to be the perimeter distance around polygons outlining tree-covered areas

inside a park. Where a park was adjacent to golf courses or other open space, I used ArcMap to re-calculate park size to include those open spaces, and revise the estimate for forest edge to include these open spaces. Unlike many areas, golf courses in San Francisco are not permitted to use pesticides, so they are likely to support an insect fauna that could be used as foraging areas for bats. I estimated the amount of forest edge in golf courses by calculating a percentage of forest edge per area based on a representative golf course for which I had forest edge metrics available (Presidio), and applied that to other golf courses adjacent to study areas.

To model which of these park characteristics are best at explaining differences in foraging activity between parks, I built a priori models based on linear and generalized linear regression using SAS (SAS 9.2, 2008). To measure total activity, I pooled the number of calls across all four recording nights from each park. I modeled total foraging activity as well as species-specific activity for the two most common bats, *Tadarida brasiliensis* and *Myotis yumanensis*, representing 98.9% of all classified call sequences. Total activity and total *T. brasiliensis* activity in each park were natural log transformed and modeled (PROC REG). Three park sites were not sampled in the first quarter, so I accounted for uneven sampling rates in those parks by forcing the number of sampling intervals into the models. One park site, Lobos Creek in the Presidio, was removed from all regression models as an outlier due to extremely high activity levels on one night. The activity level of *M. yumanensis* could not be normalized and was, therefore, modeled

as a negative binomial distribution in a generalized linear model (PROC GENMOD). I used park size, amount of forest edge, proximity to water, proximity to large parks, and percent native vegetation as possible explanatory variables for all models. I transformed explanatory variables to approach normality and screened them for multicollinearity using Pearson correlation matrices and the variance inflation factor. I examined the pattern of the residuals for each regression model and found no evidence to suggest that linear or generalized linear regression was not the appropriate model for these data. I used second-order Akaike's Information Criterion (AICc), calculated Akaike weights to select the most parsimonious model given the data, and computed model-averaged estimates for parameters appearing in the most parsimonious models (Burnham and Anderson 2002). Exploratory analyses of effects of temperature and other climatic variables showed no significant effect on activity or species richness within quarters and were not pursued further. I considered between-quarter effects on activity by graphing activity for each park over time as well as using repeated measures ANOVA and Tukey post-hoc tests in SPSS (SPSS Release 11.5.0, 2002). Activity numbers were too low for species other than *T. brasiliensis* to test for statistical significance.

To measure species richness, I counted the accumulated number of species in each park over the entire study period. Since species richness could not be transformed to approach a distribution enabling a linear or logistic regression analysis, I modeled species richness predictors using Discriminant Function Analysis with cross validation in SPSS using the

number of species found in each park as the grouping variable, and the same set of transformed explanatory variables as used in the activity models.

Results

From May 2008 through April 2009, over 85 park nights, I recorded 5,592 bat passes representing at least four separate bat species (Appendix 2). I classified 4,700, or 84% to be those of *Tadarida brasiliensis* or bats using calls not possible to distinguish from that species. I also captured 831 recordings (14.9%) of *Myotis yumanensis*, 16 recordings (0.29%) of *Lasiurus blossevillii*, and 6 recordings (0.11%) of *Myotis lucifugus*. I was unable to classify 31 bat passes to these or any other expected species because the recording was not of sufficient quality.

For the activity level of all species combined, the models containing only amount of forest edge or park size were most parsimonious, followed by models combining edge or size singly with each of the other parameters (Table 1). AICc model weight for edge was 0.196, and for edge and size was 0.166. Because *T. brasiliensis* represented such a significant proportion of the activity, the species-specific model results were similar; size alone was the most parsimonious model (weight = 0.187) followed by edge alone (weight = 0.146). Distance to the nearest large park alone was the fourth most likely model (weight = 0.065). Models for *M. yumanensis* were somewhat different, with edge and distance to water the most parsimonious model (weight = 0.211), followed by both edge and distance to water plus park size (weight = 0.104, Table 1).

In calculations for model averaging for parameters in all models, none of the parameters are significant since all span zero at the 95% confidence interval (Table 2).

Graphs of activity over time for each park, based on total activity and for each species, showed the highest activity in the fall, and the lowest activity in the winter (Appendix 3). Fall activity was significantly higher for *T. brasiliensis* than in winter or spring (Tukey, Mean difference_{winter,fall} =2.38 $P < 0.0001$ and Mean difference_{spring, fall} =1.59, $p=0.017$, $n=22$).

I detected all four species in only two of the 22 parks, Pine Lake and the Twin Peaks reservoir (Appendix 2). Two additional parks had three species each (*T. brasiliensis*, *M. yumanensis*, and *L. blossevillii*), five parks had two species (*T. brasiliensis* and *M. yumanensis*), and 13 parks had only one species (*T. brasiliensis*). Tests of dimensionality for the discriminant analysis of species richness indicate that two dimensions are identified, with two variables, distance to water and edge, together explaining 100% of the variance (Table 3).

Discussion

This is the first foraging ecology study of bats focused on core urban parks. I found that the amount of forest edge, park size, and distance to water are important characteristics in explaining the distribution of bat foraging activity and species richness in San Francisco parks, which is consistent with findings from other bat foraging studies on the urban-rural gradient (Walsh et al. 1995, Vaughan et al. 1997, Everette et al. 2001, Gehrt and Chelsvig 2003). Also, species richness was lower than reported in surrounding areas. However, the unusual absence of *Eptesicus fuscus* and the dominance of *Tadarida brasiliensis* contrast sharply with community composition reported in other temperate North American cities. Seasonal results were also surprising, as high *T. brasiliensis* activity in the fall contrasted with the expected resource-based peak in spring and with a previous study in the area showing peak activity in winter (Pierson and Rainey 1995).

Park characteristics

The relative importance of edge as a factor explaining bat foraging activity agrees with the results of many other urban studies (Walsh et al. 1995, Vaughan et al. 1997, Everette et al. 2001, Gehrt and Chelsvig 2003, but see Hourigan et al. 2006, Rhodes and Carferall 2008). Edge habitat has been found to contain more insects (Lewis 1969, Fried et al. 2005), and since bats tend to be opportunistic foragers (Ober and Hayes 2008), edge would thus be more attractive for foraging insectivorous bats. While few studies of other taxa have specifically measured the amount of edge habitat in urban settings, the amount

of forest edge in my study parks is highly correlated with forest area, which has been shown to influence the richness of other taxa. For example, the amount of forest area was negatively related to urban ant species richness (Clarke et al. 2008), but positively related to bird species richness (Bolger et al. 2001). Since *T. brasiliensis* forages over large areas and flies well above the canopy (Russo and Jones 2003), it is presumably not limited to individual parks and can choose those with greater amounts of forest edge. Note that since *T. brasiliensis* dominated this study, factors explaining general foraging activity are more likely to apply to *T. brasiliensis* than to other taxa in this study.

Proximity to water, in combination with amount of forest edge, best explains differences in species richness among parks in San Francisco, and also appeared in multiple models explaining activity patterns for *Myotis yumanensis*. Several other studies have found proximity to water to be an important factor explaining bat activity along the urban-suburban gradient (Geggie and Fenton 1985, Furlonger et al. 1987, Negraeff and Brigham 1995, Walsh and Harris 1996, Vaughan et al. 1997, Lesinski et al. 2000, Everette et al. 2001, Russo and Jones 2003, Sparks et al. 2005, Zukal and Rehak 2006, Whitford 2009). *Myotis* feed near and over water (Fenton and Barclay 1980, Brigham et al. 1992, Evelyn et al. 2004, Ober and Hayes 2008) and proximity to water probably enhanced the ability of this species to forage in several parks in my study sufficiently to increase species richness therein.

Park size is an important factor for many taxa (Gavareski 1976, Faeth and Kane 1978, Nupp and Swihart 2000, Crooks et al. 2004, Smith 2007). Park size was also an important factor in this study, but primarily for models explaining *T. brasiliensis* activity. Distance to the nearest large park was also a factor in the *T. brasiliensis* models, although of lesser importance. Park size is correlated with amount of forest edge in this study ($r = -0.612$, $p = 0.003$). The large foraging area for *T. brasiliensis* (Russo and Jones 2003) would suggest they might favor bigger parks featuring more forest edge. Avila-Flores and Fenton (2005) report a relationship between activity and park size, which may reflect the difference between park sizes and foraging ranges of bats. While percent native plants in each park is important to conservation efforts and for some mammalian taxa (Hodgkison et al. 2007) it was not an important factor in explaining bat foraging activity or species richness.

That the factors important for explaining bat foraging and diversity differ from or even contradict factors important to other taxa is a strong signal that conservation efforts aimed at maintaining diversity in urban settings need to have a broad focus. For example, I found that even mid-sized parks can be important to bats when managed to maximize water access and forest edge. Pine Lake Park in San Francisco is a medium-sized park (37.19 ha) with a small lake and abundant non-native forest. Despite heavy recreational use, it supported the highest bat species richness in the city; all four species were found there. This contrasts sharply with results from studies of invertebrate taxa in

the same park that showed very low levels of activity and diversity for ants and bees (McFrederick and LeBuhn 2006, Fenter 2007, Clarke et al. 2008). Thus, it is important to consider the needs of a diverse suite of species when setting conservation priorities (Chase et al. 2000).

Species-specific responses

Models explaining activity for *Tadarida brasiliensis* and *Myotis yumanensis* differed.

Activity pattern differences are likely attributable to differences in their ecological

profiles. *T. brasiliensis* have wings with a high aspect ratio, a high wing loading

(Wilkins 1989), and consequently forage over the canopy and over large distances

(Wilkins 1989, Russo and Jones 2003). Documented foraging ranges of this species are

considerably larger than the area of this study, and *T. brasiliensis* has been reported from

a wide variety of habitats throughout its foraging range (Avila-Flores and Fenton 2005).

This suggests that *T. brasiliensis* has the capability to gather resources from multiple

parks in San Francisco. In contrast, the low aspect ratio and low wing loading noted in

Myotis bats (*M. yumanensis* and *M. lucifugus* in this study) make them better adapted for

foraging in cluttered areas (Aldridge 1986). The documented foraging range for *M.*

yumanensis in this region (2-4 km, Evelyn et al. 2004) is less than the study area.

However, the largest distance to water for any park in this study was approximately 2 km,

which suggests that *Myotis* bats are not limited by commuting distances between sites.

This species also forages preferentially over and near water (Fenton and Barclay 1980,

Brigham et al. 1992, Evelyn et al. 2004, Ober and Hayes 2008). *M. yumanensis* is known to prefer areas with very large roost trees (Evelyn et al. 2004). Thus, future studies should examine the presence of large roost trees in parks as a possible explanatory variable for *M. yumanensis* presence.

I was unable to model activity patterns for the other two species found in this study, *Lasiurus blossevillii* and *Myotis lucifugus*, because they represented an insignificant percentage of vocal records and were found in less than 20% of sites (Rickman and Connor 2003). However, three of the four sites where *L. blossevillii* was recorded in this study were adjacent to lakes along the central spine of the city, and one recording was from a park without water but at a higher elevation known for attracting migrating birds (Mt. Davidson). None were detected at lakes closer to the ocean, including one lake closest to a known roosting location for *L. blossevillii* in Golden Gate Park (Orr, 1950). *M. lucifugus* was found in only two parks, both with lakes nearby, but with such low activity levels that it is difficult to draw any conclusions from those records.

Species richness was lower in San Francisco than previously measured in nearby areas (Heady and Frick 2000, Mudd 2007). I was particularly surprised not to find *Eptesicus fuscus*. Many other studies of bats in urban temperate areas report the near-commensal species *E. fuscus* (North American cities) or its congener *E. serotinus* (European cities) as being present and often very common (Gaisler et al. 1998, Lesinski et al. 2000, Everette

et al. 2001, Johnson et al. 2008, Loeb et al. 2009). *E. fuscus* is one of the most widely distributed and commonly detected species in California, reported as common in the nearby Santa Cruz mountains south of the study area (Heady and Frick 2000, Mudd 2007) as well as to the north and east (Pierson et al. 2004, Rainey et al. 2006). *E. fuscus* has been reported previously in the Presidio of San Francisco (Pierson and Rainey 1995) but was not recorded at that location during this study, including during recording sessions conducted outside of the quarterly dates included in this analysis. The *E. fuscus* echolocation call repertoire is somewhat variable and can overlap with *T. brasiliensis*, so it is possible that some less characteristic *E. fuscus* calls were attributed to *T. brasiliensis*, but the absence of any typical *E. fuscus* calls was still surprising. These bats can be somewhat sensitive to degree of urbanization (Duchamp et al. 2004, Avila-Flores and Fenton 2005) and insect abundance (Avila-Flores and Fenton 2005) and perhaps less tolerant of pollution (Kalcounis-Rueppell et al. 2007). It is possible that the extremely high level of urbanization and low insect levels in the core city area restrict these bats to the suburban areas.

Seasonality

In Mediterranean climates with mild rainy winters and warm dry summers, insect activity is expected to occur all year but peak in late spring and early summer (Evans and Hogue 2004). Since bat activity is related to insect activity (Bell 1980, Avila-Flores and Fenton 2005, Scanlon and Petit 2008b) bat activity should be higher in May than in September,

but this is the opposite of what this study found. Overall bat activity was highest in September, dropped off considerably in December and March, and then increased somewhat in May. However, other studies have shown that insect abundance tracked temperature but not precipitation (McIntyre et al. 2001) and that mass and diversity of insects was higher during warm months, as was bat activity (Scanlon and Petit 2008a). In San Francisco, temperatures are highest in September (Ritter 2006).

All four species of bat found in San Francisco during this study were active during the winter of 2008-2009. Many *Tadarida brasiliensis* populations in North America are migratory (Wilkins 1989). Pierson and Rainey (1995) found *T. brasiliensis* activity lowest during the summer months in the Presidio of San Francisco and speculated that *T. brasiliensis* overwinter in areas like San Francisco, along the coast, before migrating to the warmer central California valley to breed in the summer. However, my results show the opposite pattern, with the highest *T. brasiliensis* activity in September and significantly lower in May and December. Elevated activity levels in the late summer/early fall could indicate local breeding, but it is not possible to verify this with acoustic-only surveys. Another possible explanation for the higher activity levels in September would be an increase in insect activity, which was not detected with traps.

Habitat characteristics that contribute to diversity and abundance of mammalian species in urban settings are not necessarily the same as those favoring plants, arthropods, or

birds, the most commonly studied taxa (Soule et al. 1988, Bolger et al. 2000, Bolger et al. 2001). Bats, as volant and nocturnal mammals, offer an even greater challenge for urban conservation. Maintaining forest patches and water elements in urban parks should be part of management priorities. Although the urban environment may not be ideal habitat, bats are clearly able to survive there. As humans become increasingly urban (United Nations. Dept. of International Economic and Social Affairs. et al.), understanding urban bats is important not only to ensure their continued survival but also to encourage people to appreciate and value them.

Model	K	AICc	Δ AICc	W_i
Total Activity				
Edge	3	19.078	0.00	0.196
Size	3	19.406	0.33	0.166
Edge DistPark	4	21.137	2.06	0.070
Size Edge	4	21.519	2.44	0.058
Edge Dist H ₂ O	4	21.667	2.59	0.054
Edge NativePl	4	21.839	2.76	0.049
DistPark	3	21.932	2.85	0.047
Effort	2	22.013	2.93	0.045
Size DistPark	4	22.256	3.18	0.040
Size NativePl	4	22.280	3.20	0.039
Size Dist H ₂ O	4	22.321	3.24	0.039
Dist H ₂ O	3	23.307	4.23	0.024
NativePl	3	23.459	4.38	0.022
<i>Tadarida brasiliensis</i> Activity				
Size	3	22.619	0.00	0.187
Edge	3	23.117	0.50	0.146
Effort	2	24.701	2.08	0.066
DistPark	3	24.750	2.13	0.065
Edge DistPark	4	25.100	2.48	0.054
Size Edge	4	25.285	2.67	0.049
Size NativePl	4	25.342	2.72	0.048
Size DistPark	4	25.445	2.83	0.046
Size Dist H ₂ O	4	25.636	3.02	0.041
Edge NativePl	4	25.650	3.03	0.041
Edge Dist H ₂ O	4	25.868	3.25	0.037
NativePl	3	25.923	3.30	0.036
Dist H ₂ O	3	26.361	3.74	0.029
DistPark NativePl	4	26.748	4.13	0.024
Dist H ₂ O DistPark	4	26.984	4.36	0.021

<i>Myotis yumanensis</i> Activity				
Edge Dist H ₂ O	3	83.269	0.00	0.211
Size Edge Dist H ₂ O	4	84.687	1.42	0.104
Edge	2	84.816	1.55	0.097
Edge NativePl	3	85.408	2.14	0.072
Dist H ₂ O	2	86.048	2.78	0.053
Size Edge NativePl	4	86.320	3.05	0.046
Edge Dist H ₂ O NativePl	4	86.358	3.09	0.045
Edge Dist H ₂ O DistPark	4	86.769	3.50	0.037
Size Edge DistH ₂ O DistPark	5	86.806	3.54	0.036
Size Dist H ₂ O	3	87.019	3.75	0.032
Dist H ₂ O DistPark	3	87.163	3.89	0.030
Size	2	87.237	3.97	0.029
Size Edge	3	87.588	4.32	0.024
Edge DistPark	3	87.630	4.36	0.024

Table 1. AICc values and weights for the top-ranking models (within 10 percent of $W_{i_{\max}}$) explaining the influence of habitat variables on total activity and species-specific activity for 21 parks in San Francisco, California, in 2008-2009. Model rankings were based on Akaike's Information Criterion corrected for small sample size (AICc). K = the number of estimable parameters in approximating model. Total activity and *Tadarida brasiliensis* activity models included an additional variable, Effort, used to account for unequal sampling effort in three parks. $\Delta AICc$ = the difference in value between AICc of the current model versus the best-approximating model (AIC_{\min}) for each set of models. W_i = Akaike weight, the probability that the current model (i) is the best approximating among those considered for each group (Burnham & Anderson 2002). One park, Lobos Creek in the Presidio, was removed from this analysis as an outlier.

Model-averaged parameters	Model Averaged Estimate	Uncond. Std. Error	95% CL Upper	95% CL Lower
Total Activity				
Size (m ²)	0.27	0.19	0.67	-0.13
Edge (m ²)	-468.82	270.67	94.19	-1031.82
Distance H ₂ O (m)	-0.02	0.03	0.04	-0.08
Distance Lg. Pk. (m)	0.00	0.00	0.00	0.00
Pct Native Plants	0.85	1.58	4.13	-2.43
<i>Tadarida brasiliensis</i> Activity				
Size (m ²)	0.29	0.19	0.70	-0.11
Edge (m ²)	-417.96	304.83	216.09	-1052.02
Distance H ₂ O (m)	-0.02	0.03	0.05	-0.08
Distance Lg. Pk. (m)	-0.00019	0.00031	0.00046	-0.00083
Pct Native Plants	1.21	1.71	4.76	-2.33
<i>Myotis yumanensis</i> Activity				
Size (m ²)	-0.37	1.31	2.35	-3.09
Edge (m ²)	-5061.24	4230.94	3739.12	-13861.60
Distance H ₂ O (m)	-0.19	0.19	0.21	-0.59
Distance Lg. Pk. (m)	0.00	0.00	0.01	-0.01
Pct Native Plants	3.41	3.59	10.88	-4.07

Table 2. Model averaged parameter estimates with unconditional standard errors and 95% confidence intervals (Burnham & Anderson 2002) explaining total activity and activity of most common species at 21 parks in San Francisco, California, in 2008-2009. One park, Lobos Creek in the Presidio, was removed from this analysis as an outlier.

Function	Eigenvalue	% of Variance	Canonical Correlation	Standardized Canonical DF Co-efficient: Edge	Standardized Canonical DF Co-efficient: Distance to Water
1	3.686	98.2	0.887	0.758	0.907
2	0.069	1.8	0.254	0.719	-0.518

Table 3. Discriminant Function Analysis results explaining patterns of bat species richness in 22 parks in San Francisco, California, in 2008-2009. Results are statistically significant for functions 1 through 2 (Chi-square 29.000, DF=6, P <0.001).



Figure 1. Map of San Francisco parks surveyed in 2008-2009.

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Appendix 1: Park Characteristics

Park	Forest edge (m)	Park size (ha)	Distance to Large Park (m)	Distance To water (m)	Percent Native plants
Billygoat Hill	434	0.31	2,091	756.69	3.73%
Bernal Hill	570	9.76	2,033	2,064.39	1.20%
Buena Vista	2,556	14.59	320	1,660.38	18.40%
Corona Hts	1,284	5.09	831	1,276.29	3.39%
Edgehill	457	0.51	2,631	962.33	0.00%
Green Belt	3,272	57.28	1,074	338.04	7.81%
Glen Canyon	5,114	47.52	2,360	2.78	52.31%
Golden Gate	58,216	411.91	336	2.62	29.58%
GG Heights	581	2.28	1,787	728.58	8.18%
Grandview	438	1.79	1,066	741.04	81.87%
Hawk Hill	233	1.60	2,154	769.50	3.38%
Kite Hill	204	0.93	1,352	607.67	0.97%
Lake Merced	497,866	364.89	40	39.84	51.81%
Mt. Davidson	3,171	15.95	2,916	535.26	8.94%
McLaren	34728	134.75	135	13.36	7.88%
Mtn Lake	737,386	1999.00	8	15.15	78.18%
Lobos Creek	737,386	1999.00	42	4.04	78.18%
Pine Lake	8,434	37.19	896	440.84	11.81%
Tank Hill	355	1.16	909	311.55	0.37%
Twin Peaks	1,715	24.32	1,891	449.73	54.40%
TP Reservoir	1,715	24.32	1,244	7.44	54.40%
Bayview	3,851	157.93	17	2,220.88	10.21%

Descriptions for parks in San Francisco, California during 2008-2009. See methods for details of park characteristic calculations.

Appendix 2: Species results for individual parks

Park	Total TABR	Total MYYU	Total LABL	Total MYLU	Taxa
Billygoat Hill	55	0	0	0	1
Bernal Hill	9	0	0	0	1
Buena Vista	476	0	0	0	1
Corona Hts	31	0	0	0	1
Edgehill	51	0	0	0	1
Green Belt	1	0	0	0	1
Glen Canyon	45	1	0	0	3
Golden Gate	1389	20	0	0	2
GG Heights	164	0	0	0	1
Grandview	40	0	0	0	1
Hawk Hill	17	0	0	0	1
Kite Hill	33	0	0	0	1
Lake Merced	449	5	0	0	2
Mt. Davidson	274	0	1	0	2
McLaren	410	0	3	0	3
Mtn Lake	296	28	0	0	2
Lobos Creek	496	537	0	0	2
Pine Lake	79	82	11	1	4
Tank Hill	9	0	0	0	1
Twin Peaks	102	0	0	0	1
TP Reservoir	68	158	1	5	4
Bayview	206	0	0	0	1

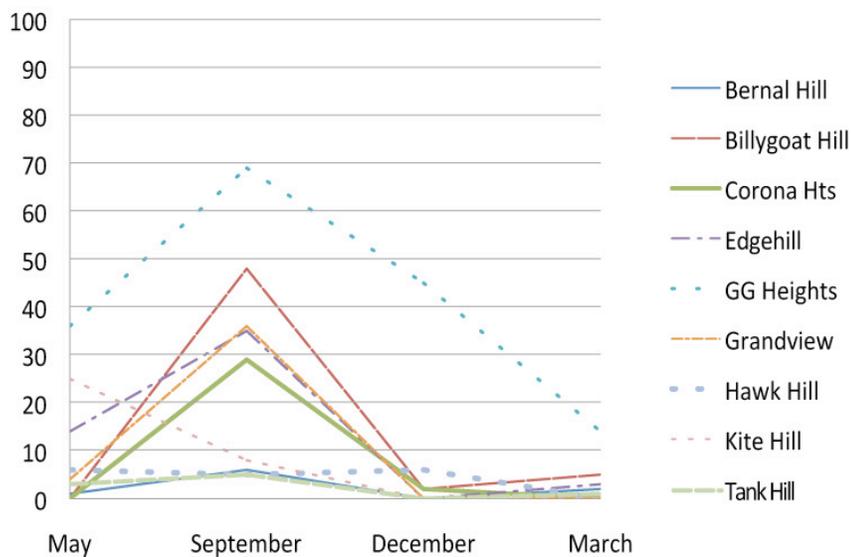
Total activity values for parks in San Francisco, California for each bat species found during 2008-2009. Taxa = maximum number of species found over the study period in each park. TABR = *Tadarida brasiliensis*, MYYU = *Myotis yumanensis*, LABL = *Lasiurus blossevillii*, MYLU = *M. lucifugus*.

Appendix 3: Seasonal Activity

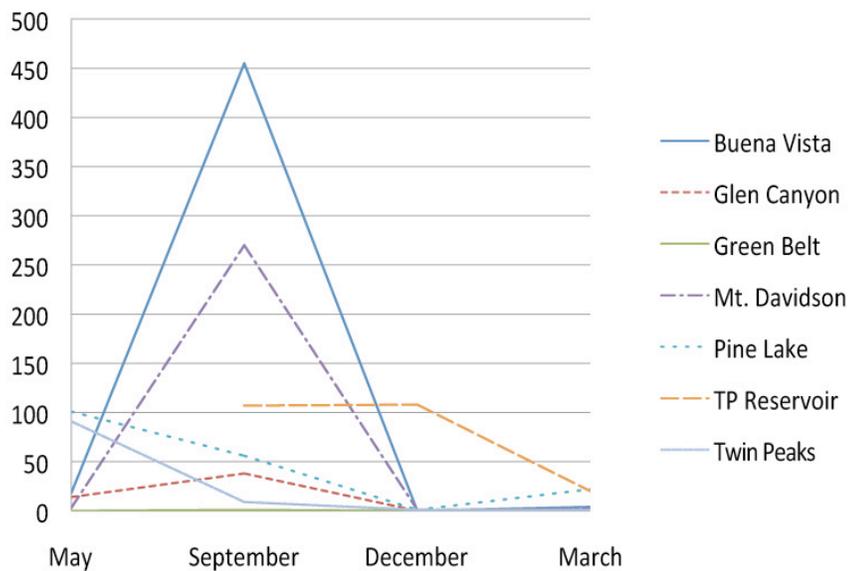
The graphs below illustrate seasonal activity for all species combined. Parks are grouped by size, where large parks > 1,000 ha, medium parks > 100 ha, and small parks < 100 ha.

Activity peaks for most parks in the fall. For *Tadarida brasiliensis*, activity is significantly higher in the fall than in spring or winter.

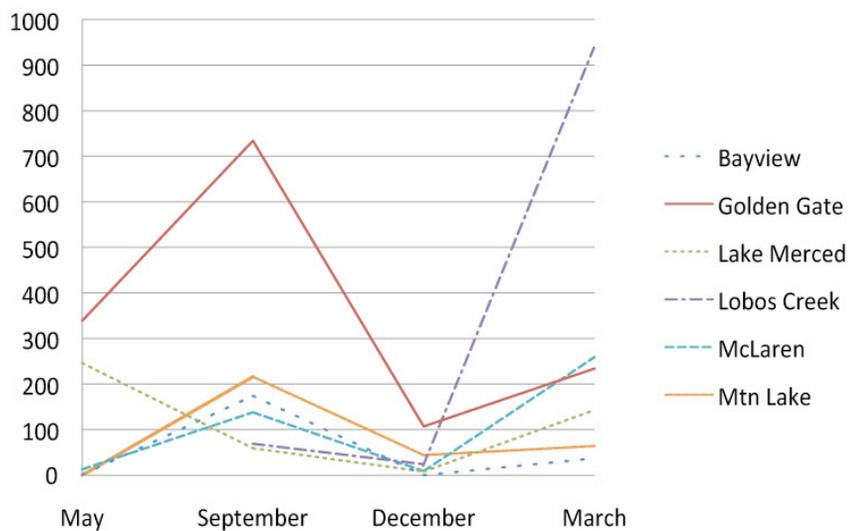
Seasonal Activity: Small Parks, All Species



Seasonal Activity: Medium Parks, All Species



Seasonal Activity: Large Parks, All Species



Appendix 4: Species Accumulation Curve

I used EstimateS for Macintosh (Colwell 2005) to generate an Incidence-based Coverage Estimator (ICE) for species richness based on means of randomized runs. This estimator provides a smoothed species accumulation curve based on randomized runs of collected data and predicts the number of species expected. To measure species richness, I counted the accumulated number of species in each park over the entire study period. The randomized species richness curve predicts a total of 4.5 species.

