

Estimating density of a forest-dwelling bat: a predictive model for Rafinesque's big-eared bat

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Abstract Data on species distribution and abundance are the foundation of population ecology. However, due to difficulties in surveying bats, abundance estimates for tree-roosting microchiropterans are non-existent. Therefore, our objective was to develop methods for estimating colony abundance and density, taking as our model Rafinesque's big-eared bat *Corynorhinus rafinesquii*, a species of conservation concern found in cypress-gum swamps of the southeastern United States. We searched 123 transects at eight study sites in the Coastal Plain of Georgia, USA to locate and characterize diurnal summer roosts of *C. rafinesquii*. We modeled the relationship between the number of bat colonies and landscape-scale habitat variables with zero-inflated negative binomial regression and used Akaike's information criterion to select the most parsimonious models. We generated a predictive density map to identify areas of high colony density and to estimate overall abundance. Colony density was predicted by the duration of wetland flooding, wetland width, and study site. Application of the regression model to a GIS indicated there were 3,734 colonies containing 6,910 adult bats on the eight study sites. Predicted density ranged from 0.07 colonies/ha and 0.07 adult bats/ha in saturated wetlands to 0.47 colonies/ha and 1.18 adult bats/ha in semi-permanently flooded wetlands. This study is the first to estimate density and abundance of forest-dwelling microchiropterans over a large area. Such data can serve as a baseline for future work

on population trends in *C. rafinesquii*. In addition, our approach could be replicated for other bat species with moderately cryptic roosts.

Keywords Abundance · Chiroptera · *Corynorhinus rafinesquii* · Cypress-gum swamp · Spatial modeling · Zero-inflated negative binomial

Introduction

Bats populations have come under increasing pressure due to long-standing challenges such as habitat loss and hunting pressure (Fenton 1997) as well as new threats such as White-Nose Syndrome (Frick et al. 2010) and wind turbines (Kunz et al. 2007). Wind turbines primarily kill tree-roosting bats, and the number of fatalities is potentially large (Kunz et al. 2007). Despite estimates of the number of fatalities, population-level impacts are unknown due to a total lack of population estimates for tree-roosting microchiropterans (Arnett et al. 2011). Despite the need for information, estimating the abundance of forest-dwelling bats has proven particularly difficult (O'Shea et al. 2003; Kunz et al. 2009) and remains the primary obstacle to understanding the population ecology of forest-dwelling bat species (Brigham 2007).

While a handful of studies have developed predictive geographic models of bat presence (e.g., Jaberger and Guisan 2001; Greaves et al. 2006), spatial models estimating bat density and abundance have not been developed due to the technical challenges involved. While many types of observations can be used in presence models, abundance estimates require counts of animals, estimates of detection probability, and area surveyed (Williams et al. 2002). However, there are few methods for estimating detection

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probabilities or area occupied for forest-dwelling bats. Abundance estimates cannot be obtained from acoustic surveys (Hayes 2000), mist net or harp trap surveys (Weller 2007), or telemetry studies (Willis et al. 2006). Furthermore, assumptions of mark-recapture models are unlikely to be met (Kunz et al. 2009, but see Vonnhof and Fenton 2004).

In contrast, repeated roost surveys within an area could, theoretically, generate counts of bats, detection probabilities, and a known area. Roost searches for tree-cavity-roosting microchiroptera have rarely been attempted (but see Sedgely and O'Donnell 1999; Gooding and Langford 2004). However, many bat species use roosts that are accessible for searches and could benefit from such surveys (e.g., *Balionycteris maculata*, *Myotis austroriparius*, *Myzopoda aurita*, *Rhynchonycteris naso*, *Saccopteryx bilineata*). We developed methods for estimating bat abundance from roost surveys using Rafinesque's big-eared bat, *Corynorhinus rafinesquii*, a small, insectivorous vespertilionid restricted to the southeastern United States (Jones 1977). In the Coastal Plain, it is most commonly associated with bottomland forests and swamps where it roosts in hollow trees (Clark 2003). Roost trees typically have basal hollows, making the roosts and occupants relatively conspicuous (Carver and Ashley 2008). Accessible roosts make repeated roost surveys feasible, enabling density estimates, which, combined with habitat data, could be the basis for a geographic model of bat density. Therefore, our objectives were to (1) develop a model predicting abundance of *C. rafinesquii* colonies from habitat data and generate predictive maps in a geographic information system (GIS) and (2) estimate colony abundance and density on selected study sites.

Methods

Study area

The study was conducted at eight sites in the Coastal Plain of Georgia, USA (32°N, 83°W). This is a subtropical region consisting of low, rolling hills and sandy soils derived from marine sediments (Wharton 1978). Annual precipitation exceeds 120 cm and low-lying areas of poorly drained clays support an abundance of ponds, swamps, bogs, pocosins, and other wetlands. All study sites were state-managed and located within a major river floodplain with cypress-gum swamps and bottomland hardwoods as major habitat components. Sites included Moody Forest Natural Area, Ocmulgee Wildlife Management Area (WMA), Tuckahoe WMA, Beaverdam WMA, Chickasawhatchee WMA, Clayhole Swamp WMA, Little Satilla WMA, and River Bend WMA. Sites were selected to achieve wide

geographic distribution across the Georgia Coastal Plain and to ensure inclusion of sites with forested cypress-gum swamp habitat across a range of ages. Major river systems influencing study sites included the Altamaha, Flint, Little Satilla, Ocmulgee, Oconee, and Savannah rivers (Fig. 1). Study areas ranged from 1,416 ha (River Bend WMA) to 8,597 ha (Ocmulgee WMA) with area in cypress-gum swamp habitat ranging from 535 ha (Moody Forest Natural Area) to 2,178 ha (Chickasawhatchee WMA).

Transect searches

We searched for *C. rafinesquii* roost trees at three sites during summer 2007 and at the other five sites during summer 2008. Given that *C. rafinesquii* is found in forested wetlands (Clark 2003), we stratified the study areas by forested wetland categories defined and mapped by the US Fish and Wildlife Service's National Wetland Inventory (NWI; Cowardin et al. 1979). We selected three palustrine, forested wetland categories that differ by surface water duration: saturated, seasonally flooded, and semi-permanently flooded.

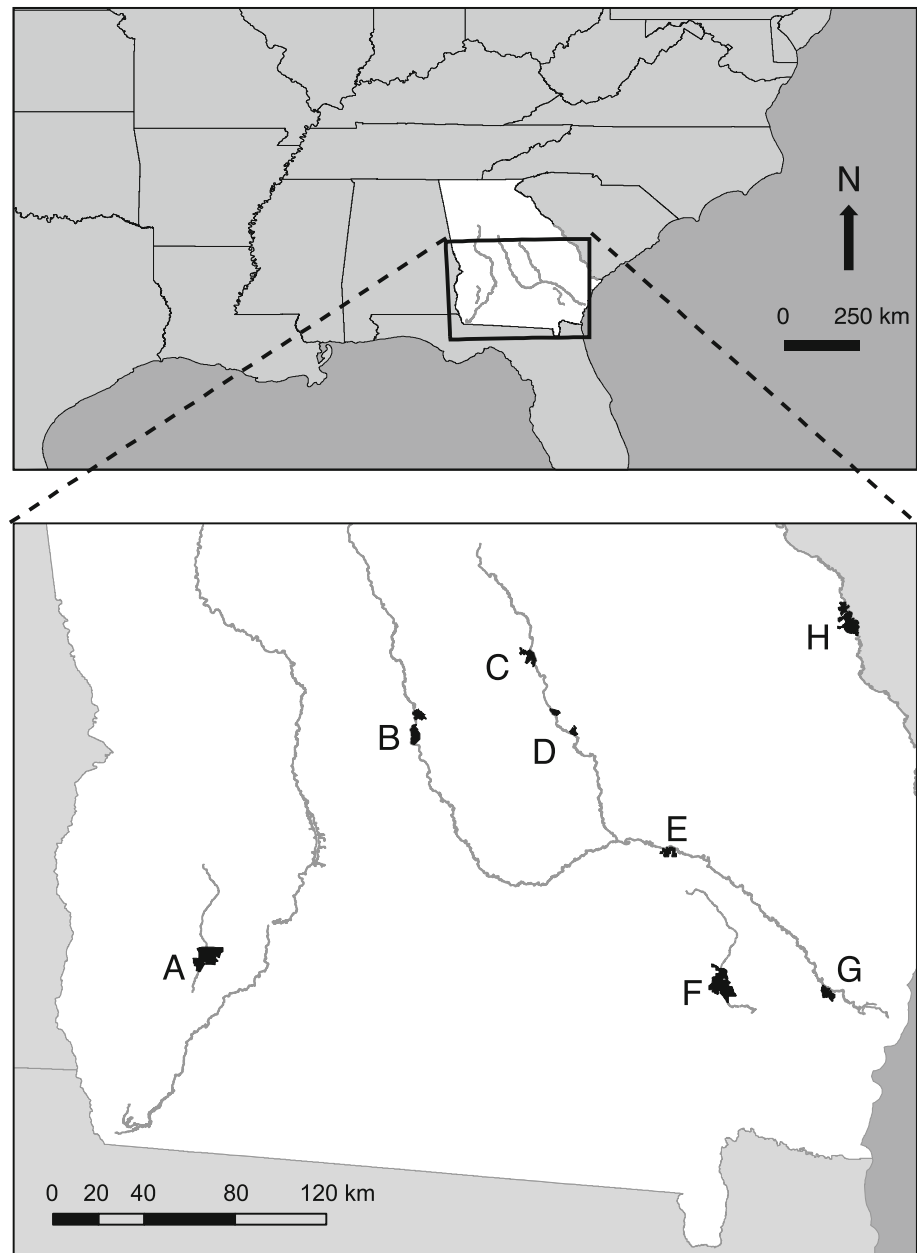
We created 500 m long linear transects along the approximate center of all wetland areas using ArcMap (version 9.2, ESRI Inc., Redlands, CA). We selected transects from each wetland category using stratified random selection (Williams et al. 2002). We over-sampled semi-permanently flooded wetlands relative to their area to approximate an optimal allocation of survey effort (Williams et al. 2002) based on our expectation that roost density in this wetland type would be higher and more variable (Gooding and Langford 2004; Trousdale and Beckett 2005). By combined area, the study sites were 38 % saturated, 36 % seasonally flooded, and 26 % semi-permanently flooded while transects were 21 % saturated, 30 % seasonally flooded, and 49 % semi-permanently flooded.

We walked each transect and searched for trees with basal hollows within 15 m of the transect. When a hollow tree was located, we inspected the cavity using a spotlight and mirror and counted the number of visible bats. We were able to distinguish adult and juvenile bats by pelage color (Jones 1977). Each transect was searched three times, 3–20 days apart, to improve the accuracy of our estimates. In addition, during the second set of transect searches of 2008, each tree was independently searched by two workers so we could estimate detection probabilities (MacKenzie et al. 2002).

Model development and analysis

To inform our habitat-abundance model, we weighed evidence for competing hypotheses regarding the landscape-

Fig. 1 Study sites and associated river systems in the Coastal Plain of Georgia, USA used to examine summer roost-site selection by *Corynorhinus rafinesquii* in 2007–2008. *A* Chickasawhatchee Wildlife Management Area (WMA) in the Flint River basin, *B* Ocmulgee WMA on the Ocmulgee River, *C* Beaverdam WMA on the Oconee River, *D* River Bend WMA on the Oconee River, *E* Moody Forest Natural Area on the Altamaha River, *F* Little Satilla WMA on the Little Satilla River, *G* Clayhole Swamp WMA on the Altamaha River, and *H* Tuckahoe WMA on the Savannah River



level ecological forces that affect colony abundance. Although the term colony is sometimes used to denote a socially related unit, we defined a bat colony as one or more bats in a single roost at the time of observation. While the variable of interest in our analysis was average number of colonies on a transect after three surveys, our regression models required the response variable to be an integer. Therefore, we used total number of colonies after three surveys as the response variable in our regression models and then divided our density estimates by the number of surveys to obtain average density estimates.

For our analysis, we explored common regression models for count data (Atkins and Gallop 2007). Because

our data included excess zeros and overdispersion (Clement 2011) we selected zero-inflated negative binomial (ZINB) regression. ZINB models are mixture models combining logistic regression to model excess zeros, also known as inflation, and negative binomial regression to model the count data (Lambert 1992). The biological interpretation is that logistic regression predicts areas of non-habitat (excess zeros) and negative binomial regression predicts the number of bat colonies in habitat identified by logistic regression. Because the number of colonies/transect varied among study sites, we included study site as a random effect in the ZINB model (Min and Agresti 2005). All statistical analysis was performed in Program R

2.11.0 (R Development Core Team 2011) primarily using a function for mixed-effects ZINB models available from Atkins and Gallop (2007).

Because the ZINB model corresponds to two biological concepts, presence and abundance, we weighed evidence for two corresponding sets of hypotheses relating landscape-level forest characteristics to presence and abundance of *C. rafinesquii* colonies. Specific hypotheses were that colonies would be present in areas of cypress-gum swamp (Clark 2003) or forested wetland (Clement 2011), or that colony presence would be random with respect to these habitats. These two habitats overlap ecologically and spatially, but are not identical. Cypress-gum swamps are defined by the dominant tree species and delineated by the Natural Resource Spatial Analysis Laboratory (NARSAL 1998). In contrast, forested wetlands are defined by the duration of surface water and delineated by the National Wetland Inventory (Cowardin et al. 1979; USFWS 2004). Simultaneously, we compared hypotheses that, where present, colony abundance would be higher where foraging habitat is greater (Carter 2006), commuting costs are lower (Miles et al. 2006), water is available (Watrous et al. 2006), anthropogenic disturbance is lower (Sparks et al. 2005), alternate roosting habitat is greater (Brigham et al. 1997), wetlands retain water longer (Clement 2011), or that colony abundance would be random with respect to these factors. We also developed a global model of colony abundance, which included all uncorrelated (Pearson $R^2 < 0.25$) predictor variables. For analysis, we pooled data across years. We checked for adequate fit of the global model with a Pearson χ^2 test and by visually comparing actual counts of colonies to the fitted values from the best model.

We used Akaike's information criterion corrected for small sample bias (AIC_c) to assess evidence for models, with the lowest AIC_c indicating the best supported model (Burnham and Anderson 2002). We evaluated the relative strength of evidence for each model by calculating AIC weights (w_i ; Burnham and Anderson 2002). We did not perform model averaging because it is not appropriate for mixed models (Grueber et al. 2011). We calculated Nagelkerke's R^2 to quantify the variation explained by each model (Nagelkerke 1991).

We assessed model precision by calculating 90 % confidence intervals for coefficients based on a t -statistic with $n - 1$ degrees of freedom. For the zero-inflated portion of the results, we transformed the log-odds coefficients to the probability of colony presence in each habitat type (Atkins and Gallop 2007). For random effects, we exponentiated the log-odds coefficients to obtain odds ratios that express how much more or less likely colony absence is at each site. For the count portion of the results, we exponentiated the coefficients to obtain a factor expressing the effect of

predictors as a percentage change in colony abundance, given that habitat is present. Confidence limits that encompass 0 indicate that estimates are not precise enough to conclusively determine the direction of the relationship between the predictor and colony abundance.

Spatial modeling

We created a GIS database with nine layers relevant to our hypotheses. We used 1:24,000 scale NWI wetland data (USFWS 2004) and 30 × 30 m resolution, 44-class land-cover data (NARSAL 1998). The landcover type at the center of each transect was determined and a dummy variable coded the transect as cypress-gum swamp or other forest cover type. The NWI wetland category of each transect was also coded with dummy variables.

We examined the hypotheses that bats select roost sites in proximity to alternate roosts or foraging habitat by calculating the percent of potential roosting and foraging habitat within a 1,000 m radius of the transect center. We selected a 1,000 m radius because alternate roosts for this species are typically within 1,000 m (Trousedale et al. 2008; Rice 2009) and most foraging bouts occur within 1,000 m of the roost (Hurst and Lacki 1999; Menzel et al. 2001). Roosting habitat has been described as either cypress-gum swamp (Gooding and Langford 2004) or forested wetland (Clement 2011), so we used each as a measure of roosting habitat. Because *C. rafinesquii* in the Coastal Plain forages in stands of sapling pine in preference to other stand types (Menzel et al. 2001), we estimated foraging habitat by the percent of the area that was pine (loblolly [*Pinus taeda*], slash [*P. elliotii*], shortleaf [*P. echinata*], or longleaf [*P. palustris*]). To quantify the distance to travel corridors, water resources, and anthropogenic disturbance, we calculated the distance from the transect midpoint to the closest road open to vehicle passage, the closest permanent water source, and the closest urban area >30 ha. We also estimated width of the NWI wetland containing each transect to differentiate defined sloughs from floodplains. We define a slough as a natural trough that commonly holds water despite lacking an inlet or outlet to a permanent water body (Georgia Forestry Commission 2009). We used the Spatial Analyst Zonal Geometry tool in ArcMap to approximate wetland width. We limited this measurement to the area within 250 m of each transect on the assumption that local wetland width was more relevant to roost selection than conditions further away.

After characterizing habitat at the study sites, we exported habitat attributes (wetland width, etc.) to Program R where we weighed evidence for ZINB models, as described above. We applied the results of the best supported ZINB model to the habitat attributes of each 30 m cell of spatial data to estimate colony abundance in each

cell using the Spatial Analyst Raster Calculator tool in ArcMap. As previously mentioned, the ZINB regression modeled the total number of colonies on each 1.5 ha transect after three surveys. However, our goal was to estimate the average number of colonies and then project the model onto 30 m (0.09 ha) map units. Therefore, we translated the ZINB results into map units by multiplying (total colonies/1.5 ha) by 0.09 ha/1.5 ha/3 surveys. We summed abundance in all map cells to obtain total abundance estimates. We used bootstrapping with 10,000 replicates to estimate 90 % confidence intervals for the number of colonies. We also mapped the best supported ZINB model by applying the model to each 30 m raster cell, using the Spatial Analyst Raster Calculator in ArcMap.

Estimated colony numbers based on surveys of trees with basal hollows are biased low for two reasons. First, observers may fail to detect bats that are present (MacKenzie et al. 2002). Second, some bats roost in trees without accessible basal hollows (Trousdale and Beckett 2005). To account for imperfect detection, we used a detection rate derived from the surveys performed by two independent observers (mean 0.96; 95 % confidence interval 0.87–0.99; details in Clement 2011). We incorporated uncertainty around the estimate of detection probability during the bootstrapped estimation of abundance by sampling the log-odds of detection from a normal distribution and then applying an inverse-logit transformation to obtain the probability of detection. To account for bats roosting in trees without basal hollows, we divided abundance estimates by the rate of use of basal hollows derived from data on 17 bats radio-tracked for ≥ 3 days (mean 0.61; 95 % confidence interval 0.46–0.76; M. Clement, unpublished data). We sampled the rate of use of basal hollows from a beta distribution as part of the bootstrapped estimation of abundance. Correcting for these two factors yielded a corrected estimate of colonies on the eight sites.

We estimated the number of bats in these colonies by multiplying colonies in each wetland category by the average adults/colony in that wetland category. We did not directly model the number of bats with the ZINB model because the distribution was bimodal (one peak for small bachelor colonies and one peak for large maternity colonies) and therefore not conducive to modeling. We calculated density by dividing number of colonies or bats by ha of forested wetland.

Results

Of the 123 transects we searched, 41 were occupied by 179 bat colonies containing 512 bats. Transects with bats were characterized by narrow, semi-permanently flooded

Table 1 Means and standard deviations of variables measured on transects with and without *Corynorhinus rafinesquii* roost trees

Variable	Unoccupied (<i>n</i> = 82)		Occupied (<i>n</i> = 41)	
	$\mu(X)$	SD	$\mu(X)$	SD
Cypress-gum (Y/N)	0.59	0.50	0.80	0.40
Semi-permanently flooded (Y/N)	0.40	0.49	0.68	0.47
Seasonally flooded (Y/N)	0.29	0.46	0.29	0.46
Saturated (Y/N)	0.30	0.46	0.02	0.16
Distance to roads (m)	453	440	494	415
Distance to water (m)	628	467	509	338
Distance to urban (m)	8,865	3,833	9,778	4,763
Wetland width (m)	212	125	131	97
Area pine (%)	18.7	13.8	14.5	9.7
Area swamp (%)	43.0	22.1	41.1	21.2
Area wetland (%)	41.0	24.4	33.9	22.1

wetlands, and cypress-gum swamps (Table 1). We excluded swamp landcover from the global model because it was correlated with wetland category ($R^2 = 0.36$). The Pearson Chi-square goodness-of-fit test for the global model indicated a good fit between the model and the data ($\chi^2 = 7.72$, $df = 8$, $P = 0.461$).

The best supported model predicted the presence of bat habitat from wetland categories and the number of colonies from wetland width (Table 2). This top model received 95.5 % of the AIC_c weight and therefore was the only model in the confidence set. The results indicated that semi-permanently flooded wetland was twice as likely as seasonally flooded wetland and 20 times as likely as saturated wetland to be appropriate roosting habitat (Table 3). Study sites differed substantially in the probability of forested wetlands being suitable habitat for bats, with wetlands at the site with the highest colony density being 12.1 times more likely to be suitable, and wetlands at the site with the lowest colony density being 3.1 times less likely to be suitable, relative to an average site. Furthermore, within appropriate habitat, wetland width had the greatest effect on colony abundance, reducing colony abundance by 6.0 % for every 10 m increase in width (Fig. 2).

Average predicted density, corrected for imperfect detection and roosts in trees without basal hollows, was highest in semi-permanently flooded wetlands, with over six times as many colonies and almost 17 times as many adult bats as saturated wetlands (Table 4). Density varied among study sites, with 2.6 times higher colony density and 3.6 times higher bat density at the site with the highest densities relative to the site with the lowest densities. Extrapolated to the full area of the eight study sites, the best supported model estimated that the sites held 3,734

Table 2 Best supported zero-inflated negative binomial models used to predict *Corynorhinus rafinesquii* colony abundance

Colony presence variables	Colony abundance variables	<i>K</i>	AIC _c	ΔAIC _c	<i>w_i</i>	<i>R</i> ²
Wetland forest type	Wetland width	7	313.52	0.00	0.955	0.357
Wetland forest type	Pine forest area	7	321.47	7.95	0.018	0.310
Wetland forest type	Wetland forest area	7	322.60	9.08	0.010	0.303
Wetland forest type	Global	14	322.92	9.40	0.009	0.399
Wetland forest type	None	6	325.48	11.96	0.002	0.271
Wetland forest type	Cypress-gum swamp area	7	325.80	12.28	0.002	0.283
Wetland forest type	Distance to roads	7	326.32	12.80	0.002	0.280
Wetland forest type	Distance to water	7	327.48	13.96	0.001	0.273
Wetland forest type	Distance to urban	7	327.56	14.03	0.001	0.272
Wetland forest type	Wetland forest type	8	329.25	15.73	0.000	0.276
Land cover type	Global	13	329.91	16.39	0.000	0.346
None	Global	12	338.67	25.14	0.000	0.277
Land cover type	None	5	349.97	36.45	0.000	0.079
None	None	4	357.33	43.81	0.000	0.000

The table shows variables, number of parameters in the model (*K*), Akaike's Information Criterion adjusted for small sample size (AIC_c), difference in AIC_c (ΔAIC_c), model weights (*w_i*), and Nagelkerke's *R*² values. Study site was included as a random effect in the colony presence portion of all models

Table 3 Coefficient estimates and 90 % upper and lower confidence intervals (CI) for the top model predicting roost abundance of *Corynorhinus rafinesquii*

Model portion/variable	Coefficient	Standard error	Probability appropriate habitat (%)	Change in colony abundance, given presence (%)	Lower CI (%)	Upper CI (%)
Logistic						
Semi-permanently flooded	−0.314	0.477	57.8		38.4	75.0
Seasonally flooded	1.178	0.572	29.7		7.0	70.3
Saturated	3.800	1.169	3.0		0.0	31.5
Negative binomial						
Intercept	2.069	0.205				
Wetland width (10 m units)	−0.062	0.015		−6.0	−8.3	−3.7

colonies (bootstrap 90 % confidence interval of 2,598–5,774), or 0.23 colonies/ha for the three wetland categories combined (Table 4). Using the average adults/colony in each wetland category, we estimated there were 6,910 adult bats (4,912–10,605) on the study sites or 0.43 adult bats/ha.

We projected model results onto maps to show spatial patterns of density (Fig. 3). All sites were primarily composed of large areas of low colony density (<0.20 colonies/ha). Clayhole Swamp WMA, Chickasawhatchee WMA, and River Bend WMA also had substantial amounts of wide, semi-permanently flooded wetlands predicted to support medium colony density (0.20–0.75 colonies/ha). Beaverdam WMA, Moody Forest, Ocmulgee WMA, and Tuckahoe WMA were the only sites with noticeable areas of narrow, semi-permanently flooded wetlands predicted to support high colony density (0.76–2.57 colonies/ha). Few

colonies were found at Little Satilla WMA and predicted densities were generally low.

Discussion

Estimates of bat abundance

Corynorhinus rafinesquii is generally considered uncommon throughout its range (Loeb et al. 2011), although in certain areas it may be captured in greater numbers than other bat species (Medlin and Risch 2008; Clement and Castleberry 2011) suggesting it may be locally common. Based on available records of bats in trees, caves, and anthropogenic roosts, Arroyo-Cabrales and Ticul Alvarez Castaneda (2008) estimated the total population at <10,000 adults. We observed over 500 bats on our transects and

over 300 bats that were found elsewhere on our study sites (Clement 2011). We estimated that there were 6,910 adult bats on 16,016 ha of forested wetlands at our study sites alone. Our estimate suggests that more than 10,000 *C. rafinesquii* exist given that numerous other populations are known from forested wetlands throughout the Atlantic Coastal Plain and Mississippi River Valley (Clark 2003).

Bat abundance has been estimated previously for some conspicuous foliage-roosting megachiroptera (e.g., Wiles and Johnson 2004) and at a small scale for some tent-roosting species (Foster 1992; Vonhof and Fenton 2004). However, ours is the first rigorous estimate for a cavity roosting species over a large area. Our result demonstrates the feasibility of estimating abundance of forest-dwelling bats from roost surveys. Because we used non-random selection of study sites, our scope of inference was limited

to our study sites, but inference could be extended to larger areas with random selection. In addition, because we surveyed different sites in different years, the site effect was potentially conflated with any annual effect. However, given the low mortality and reproductive rates of bats, interannual differences should be small in most years (Barclay and Harder 2003).

Predictors of bat density and abundance

Although *C. rafinesquii* typically roost in water tupelo (Carver and Ashley 2008), cypress-gum swamp habitat was not the best predictor of roosting habitat. Despite including non-preferred tree species and more area, forested wetland data was a better predictor. Wetland category was likely a more powerful predictor because water tupelo prevalence was closely related to wetland categories, with water tupelo composing 4 % of hollow trees in saturated wetlands, 50 % in seasonally flooded wetlands, and 75 % in semi-permanently flooded wetlands. At 3,944 ha, this last category narrowly delineated areas with dense water tupelo, while the 9,085 ha of cypress-gum swamp included large areas with few water tupelo trees. Additionally, silvicultural best management practice guidelines in Georgia proscribe harvesting within sloughs, which generally are semi-permanently flooded wetlands (Georgia Forestry Commission 2009). As a result, sloughs often contained numerous large trees whereas surrounding areas supported few large trees.

Although colony abundance was higher in narrower wetlands, it seems unlikely that bats are attracted to wetlands due to their width, per se. Rather, wetland width likely was a surrogate for water persistence as narrow wetlands tended to be deeper sloughs that held water longer

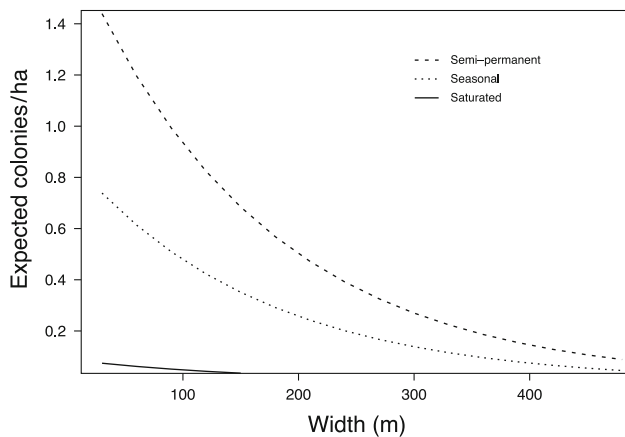


Fig. 2 Predicted density (colonies/ha) for *Corynorhinus rafinesquii* by wetland hydroperiod and width

Table 4 Estimated abundance and density of *Corynorhinus rafinesquii*

Location	Area (ha)	Number of colonies	Colony density	Number of bats	Bat density
Site					
Beaverdam	1,259	181	0.14	373	0.30
Chickasawhatchee	4,117	1,138	0.28	2,547	0.62
Clayhole Swamp	1,558	292	0.19	645	0.41
Little Satilla	2,111	301	0.14	431	0.20
Moody Forest	588	213	0.36	430	0.73
Ocmulgee	1,358	375	0.28	716	0.53
River Bend	1,043	165	0.16	326	0.31
Tuckahoe	3,983	1,070	0.16	1,443	0.36
Total	16,016	3,734	0.23	6,910	0.43
Wetland category					
Saturated	6,309	458	0.07	458	0.07
Seasonal	5,763	1,431	0.25	1,779	0.31
Semi-permanent	3,944	1,845	0.47	4,673	1.18
Total	16,016	3,734	0.23	6,910	0.43

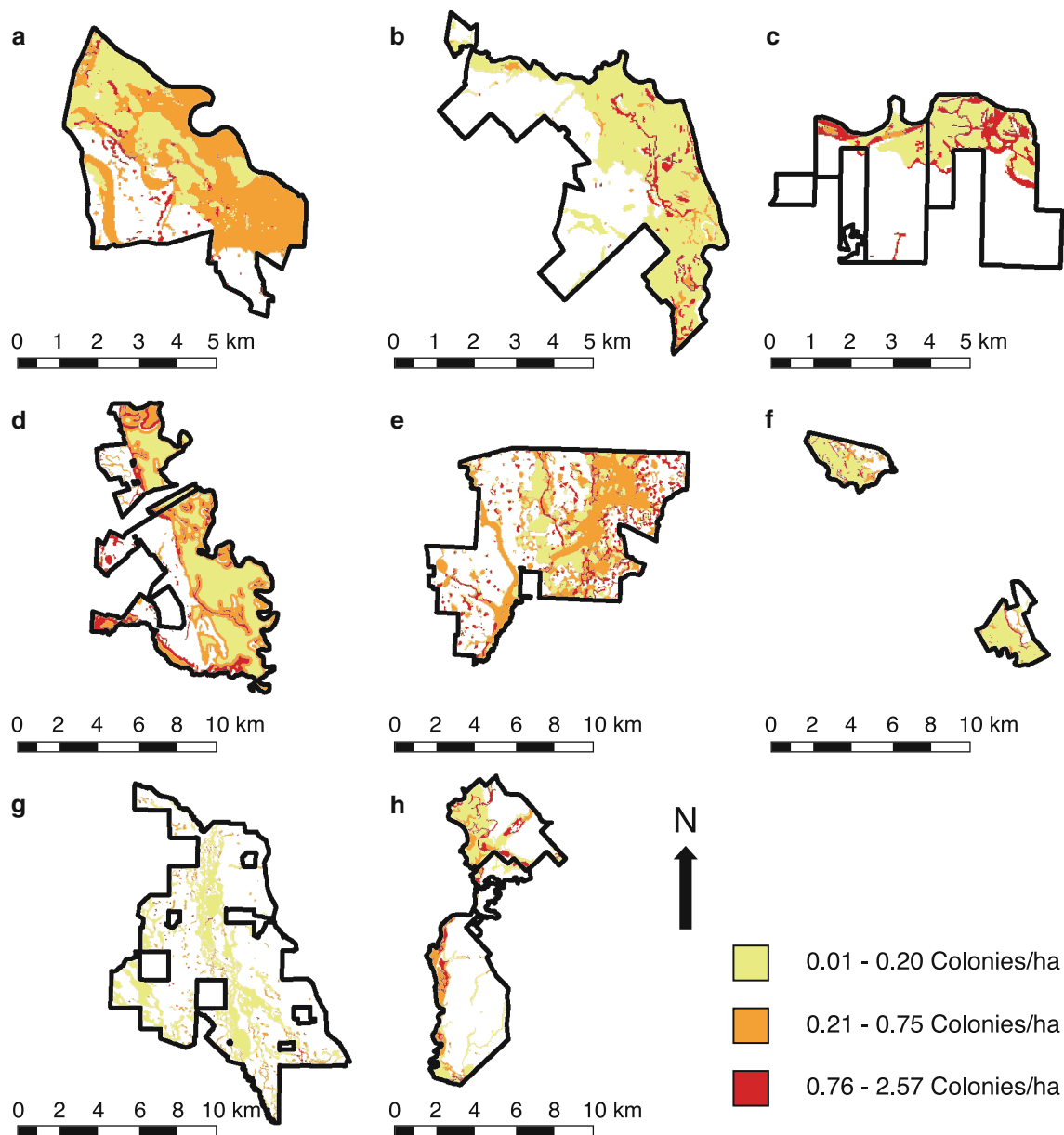


Fig. 3 Colony density maps for *Corynorhinus rafinesquii* at eight sites in the Coastal Plain of Georgia: **a** Clayhole Swamp Wildlife Management Area (WMA), **b** Beaverdam WMA, **c** Moody Forest

Natural Area, **d** Tuckahoe WMA, **e** Chickasawhatchee WMA, **f** River Bend WMA, **g** Little Satilla WMA, **h** Ocmulgee WMA

during summer and wider wetlands tended to be floodplains that held water for shorter periods of time, regardless of their NWI category. Effectively, the width variable served as a supplement to the wetland category variable, with narrow wetlands providing the water regimen necessary for the hydrophilic tree species used as roosts (Hook 1984).

Wetland category and width have not been used in previous geographic models of bat presence. Among models predicting bat presence, the most common significant predictors have been elevation and forest area, followed by temperature, distance to water, and anthropogenic development (Jaberg and Guisan 2001; Ford et al.

2005; Greaves et al. 2006; Milne et al. 2006; Watrous et al. 2006; Duff and Morrell 2007; Rebelo and Jones 2010). Forest area and distance to water were poor predictors in our study, perhaps because both were abundant and also because forested wetland categories provided more precise habitat descriptions. Although *C. rafinesquii* has been reported to avoid developed areas (Jones 1977), there was little development on our study sites. We did not explore elevation or temperature because there was little variation across our study sites, in contrast to studies conducted in mountainous regions that encompassed areas of high variability (e.g., Jaberg and Guisan 2001).

Our results indicated a strong site-specific effect. The difference in colony density across sites likely was due to differences in the prevalence of large, hollow water tupelo. Other studies have found bats are more likely to be present where preferred roost structures are abundant (Crampton and Barclay 1998; Russo et al. 2004). Similarly, *C. rafinesquii* probably select individual trees that meet their roosting needs and therefore achieve greater density where more roosts are available. Microsite variables that affect the presence of *C. rafinesquii* are known (Clement and Castleberry 2012), but measurement costs for a large-scale project would be prohibitive. A GIS data set that accurately represented the availability of large, hollow trees might better predict bat colony density and reduce the site-specific effect, but such detailed forest data were not available.

Variation in the number of suitable trees among sites was likely due to differences in historical land use and the natural range of water tupelo. Tree harvesting practices typically affect the densities of large, hollow trees (Graves et al. 2000). While we did not document harvesting history, sites had diverse ownerships and presumably different management histories. Additionally, Little Satilla WMA lies outside the core range of water tupelo (Johnson and Beaufait 1965). As a result, only 16.5 % of hollow trees surveyed at that site were water tupelo, compared to 60.4 % at the other sites combined. Other bats, such as the New Zealand long-tailed bat *Chalinolobus tuberculatus* are also less likely to be present outside the range of preferred roost tree species (Greaves et al. 2006). Overall, the substantial differences between sites indicate that extrapolations beyond the eight study sites might be imprecise and should be interpreted with caution. However, for a site inside the range of water tupelo and with a homogenous land use history, the model should identify areas of greatest suitability for *C. rafinesquii*.

Conclusions

Given the vulnerability of bat populations to decline, more investigation of the population ecology of bats is warranted (O'Shea et al. 2003). Population estimates play a vital role in a number of standard conservation methods, including assessing population trends, population viability analysis, adaptive resource management, and more (Williams et al. 2002). The lack of abundance estimates for bats has been described as the greatest limitation on our understanding of bat ecology (Brigham 2007). Despite this need, abundance estimates remain elusive (Kunz et al. 2009).

Our results provide the first rigorous abundance and density estimates over a large scale for a tree-cavity-dwelling bat. Our predictive spatial model can be used to assess species status, locate areas of ecological importance,

and support conservation planning and management (Guisan and Thuiller 2005). Our abundance and density estimates can serve as a baseline for future work on population trends or adaptive resource management of *C. rafinesquii*. Furthermore, our field techniques could be adapted to numerous bat species (e.g., Foster 1992) enabling more wide-spread studies on the population ecology of bats.

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References

- Arnett EB, Huso MMP, Schirmacher MR, Hayes JP (2011) Altering turbine speed reduces bat mortality at wind-energy facilities. *Front Ecol Environ* 9:209–214
- Arroyo-Cabres J, Ticol Alvarez Castaneda S (2008) *Corynorhinus rafinesquii*. IUCN Red List of Threatened Species, Gland, Switzerland. <http://www.iucnredlist.org/apps/redlist/details/17600/0>
- Atkins DC, Gallop RJ (2007) Rethinking how family researchers model infrequent outcomes: a tutorial on count regression and zero inflated models. *J Fam Psychol* 21:726–735
- Barclay RMR, Harder LD (2003) Life histories of bats: life in the slow lane. In: Kunz TH, Fenton MB (eds) *Bat ecology*. University of Chicago Press, Chicago, pp 209–253
- Brigham RM (2007) Bats in forests: what we know and what we need to learn. In: Lacki MJ, Hayes JP, Kurta A (eds) *Bats in forests: conservation and management*. Johns Hopkins University Press, Baltimore, pp 1–16
- Brigham RM, Vonnhof MJ, Barclay RMR, Gwilliam JC (1997) Roosting behavior and roost-site preferences of forest-dwelling California bats (*Myotis californicus*). *J Mammal* 78:1231–1239
- Burnham KP, Anderson DR (2002) *Model selection and multimodel inference: a practical information-theoretic approach*, 2nd edn. Springer, New York
- Carter TC (2006) Indiana bats in the Midwest: the importance of hydric habitats. *J Wildl Manage* 70:1185–1190
- Carver BD, Ashley N (2008) Roost tree use by sympatric Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) and southeastern myotis (*Myotis austroriparius*). *Am Midl Nat* 160:364–373
- Clark MK (2003) Survey and monitoring of rare bats in bottomland hardwood forests. In: O'Shea TJ, Bogan MA (eds) *Monitoring trends in bat populations of the United States and territories: problems and prospects*. U.S. Geological Survey, Fort Collins, Colorado, pp 79–90
- Clement MJ (2011) *Roosting ecology of Rafinesque's big-eared bat and southeastern myotis in the Coastal Plain of Georgia*. Doctoral Thesis. University of Georgia, Athens, Georgia, USA
- Clement MJ, Castleberry SB (2011) Comparison of survey methods for Rafinesque's big-eared bats. In: Loeb SC, Lacki MJ, Miller DA (eds) *Conservation and management of eastern big-eared bats: a symposium*. U.S. Forest Service Southern Research Station, Clemson, SC, pp 147–157
- Clement MJ, Castleberry SB (2012) Summer tree roost selection by Rafinesque's big-eared bat. *J Wildl Manage*. doi:10.1002/jwmg.456

- Cowardin LM, Carter V, Golet FC, LaRoe ET (1979) Classification of wetlands and deepwater habitats of the United States. U.S. Department of the Interior, Washington, DC
- Crampton LH, Barclay RMR (1998) Selection of roosting and foraging habitat by bats in different-aged aspen mixedwood stands. *Conserv Biol* 12:1347–1358
- Duff AA, Morrell TE (2007) Predictive occurrence models for bat species in California. *J Wildl Manage* 71:693–700
- Fenton MB (1997) Science and the conservation of bats. *J Mammal* 78:1–14
- Ford WM, Menzel MA, Rodrigue JL, Menzel JM, Johnson JB (2005) Relating bat species presence to simple habitat measures in a central Appalachian forest. *Biol Conserv* 126:528–539
- Foster MS (1992) Tent roosts of Macconnell's bat (*Vampyressa macconnelli*). *Biotropica* 24:447–454
- Frick WF, Pollock JF, Hicks AC, Langwig KE, Reynolds DS, Turner GG, Butchkoski CM, Kunz TH (2010) An emerging disease causes regional population collapse of a common North American bat species. *Science* 329:679–682
- Georgia Forestry Commission (2009) Georgia's best management practices for forestry. Georgia Forestry Commission, Macon
- Gooding G, Langford JR (2004) Characteristics of tree roosts of Rafinesque's big-eared bat and southeastern bat in northeastern Louisiana. *Southwest Nat* 49:61–67
- Graves AT, Fajvan MA, Miller GW (2000) The effects of thinning intensity on snag and cavity tree abundance in an Appalachian hardwood stand. *Can J For Res* 30:1214–1220
- Greaves GJ, Mathieu R, Seddon PJ (2006) Predictive modelling and ground validation of the spatial distribution of the New Zealand long-tailed bat (*Chalinolobus tuberculatus*). *Biol Conserv* 132:211–221
- Gruerber CE, Nakagawa S, Laws RJ, Jamieson IG (2011) Multimodel inference in ecology and evolution: challenges and solutions. *J Evol Biol* 24:699–711
- Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. *Ecol Lett* 8:993–1009
- Hayes JP (2000) Assumptions and practical considerations in the design and interpretation of echolocation-monitoring studies. *Acta Chiropterol* 2:225–236
- Hook DD (1984) Waterlogging tolerance of lowland tree species of the South. *South J Appl For* 8:136–149
- Hurst TE, Lacki MJ (1999) Roost selection, population size and habitat use by a colony of Rafinesque's big-eared bats (*Corynorhinus rafinesquii*). *Am Midl Nat* 142:363–371
- Jaberg C, Guisan A (2001) Modelling the distribution of bats in relation to landscape structure in a temperate mountain environment. *J Appl Ecol* 38:1169–1181
- Johnson RL, Beaufait WR (1965) Water tupelo (*Nyssa aquatica* L.). In: Fowells HA (ed) *Silvics of forest trees of the United States*. U.S. Department of Agriculture, Washington, DC, pp 284–286
- Jones C (1977) *Plecotus rafinesquii*. *Mammalian Species* 69:1–4
- Kunz TH, Arnett EB, Erickson WP, Hoar AR, Johnson GD, Larkin RP, Strickland MD, Thresher RW, Tuttle MD (2007) Ecological impacts of wind energy development on bats: questions, research needs, and hypotheses. *Front Ecol Environ* 5:315–324
- Kunz TH, Betke M, Hristov NI, Vonnhof MJ (2009) Methods for assessing colony size, population size, and relative abundance of bats. In: Kunz TH, Parsons S (eds) *Ecological and behavioral methods for the study of bats*. Johns Hopkins University Press, Baltimore, pp 133–157
- Lambert D (1992) Zero-inflated Poisson regression, with an application to defects in manufacturing. *Technometrics* 34:1–14
- Loeb SC, Lacki MJ, Miller DA (2011) Conservation and management of eastern big-eared bats: an introduction. In: Loeb SC, Lacki MJ, Miller DA (eds) *Conservation and management of eastern big-eared bats: a symposium*. U.S. Forest Service Southern Research Station, Clemson, SC, pp 1–12
- MacKenzie DI, Nichols JD, Lachman GB, Droege S, Royle JA, Langtimm CA (2002) Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83:2248–2255
- Medlin RE Jr, Risch TS (2008) Habitat associations of bottomland bats, with focus on Rafinesque's big-eared bat and southeastern myotis. *Am Midl Nat* 160:400–412
- Menzel MA, Menzel JM, Ford WM, Edwards JW, Carter TC, Churchill JB, Kilgo JC (2001) Home range and habitat use of male Rafinesque's big-eared bats (*Corynorhinus rafinesquii*). *Am Midl Nat* 145:402–408
- Miles AC, Castleberry SB, Miller DA, Conner LM (2006) Multi-scale roost-site selection by evening bats on pine-dominated landscapes in southwest Georgia. *J Wildl Manage* 70:1191–1199
- Milne DJ, Fisher A, Pavey CR (2006) Models of the habitat associations and distributions of insectivorous bats of the Top End of the Northern Territory, Australia. *Biol Conserv* 130:370–385
- Min Y, Agresti A (2005) Random effect models for repeated measures of zero-inflated count data. *Stat Model* 5:1–19
- Nagelkerke NJD (1991) A note on a general definition of the coefficient of determination. *Biometrika* 78:691–692
- NARSAL (1998) Landsat landcover 44 class. Natural Resources Spatial Analysis Laboratory, University of Georgia, Athens, GA. <http://gis1.state.ga.us/download.asp?dataID=18756>
- O'Shea TJ, Bogan MA, Ellison LE (2003) Monitoring trends in bat populations of the United States and territories: status of the science and recommendations for the future. *Wildl Soc Bull* 31:16–29
- R Development Core Team (2011) R: a language and environment for statistical computing. The R Foundation for Statistical Computing, Vienna. <http://www.r-project.org>
- Rebelo H, Jones G (2010) Ground validation of presence-only modelling with rare species: a case study on barbastelles *Barbastella barbastellus* (Chiroptera: Vespertilionidae). *J Appl Ecol* 47:410–420
- Rice CL (2009) Roosting ecology of *Corynorhinus rafinesquii* (Rafinesque's big-eared bat) and *Myotis austroriparius* (southeastern myotis) in tree cavities found in a northeastern Louisiana bottomland hardwood forest streambed. Master of Science Thesis. University of Louisiana at Monroe, Monroe, Louisiana, USA
- Russo D, Cistrone L, Jones G, Mazzoleni S (2004) Roost selection by barbastelle bats (*Barbastella barbastellus*, Chiroptera: Vespertilionidae) in beech woodlands of central Italy: consequences for conservation. *Biol Conserv* 117:73–81
- Sedgeley JA, O'Donnell CFJ (1999) Factors influencing the selection of roost cavities by a temperate rainforest bat (Vespertilionidae: *Chalinolobus tuberculatus*) in New Zealand. *J Zool* 249:437–446
- Sparks DW, Ritzi CM, Duchamp JE, Whitaker JO (2005) Foraging habitat of the Indiana bat (*Myotis sodalis*) at an urban–rural interface. *J Mammal* 86:713–718
- Trousdale AW, Beckett DC (2005) Characteristics of tree roosts of Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) in southeastern Mississippi. *Am Midl Nat* 154:442–449
- Trousdale AW, Beckett DC, Hammond SL (2008) Short-term roost fidelity of Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) varies with habitat. *J Mammal* 89:477–484
- USFWS (2004) National wetland inventory database. U.S. Department of Interior, Washington, DC. <http://gis1.state.ga.us/download.asp?dataID=39621>
- Vonnhof MJ, Fenton MB (2004) Roost availability and population size of *Thyroptera tricolor*, a leaf-roosting bat, in north-eastern Costa Rica. *J Trop Ecol* 20:291–305

- Watrous KS, Donovan TM, Mickey RM, Darling SR, Hicks AC, Von Oettingen SL (2006) Predicting minimum habitat characteristics for the Indiana bat in the Champlain Valley. *J Wildl Manage* 70:1228–1237
- Weller TJ (2007) Assessing population status of bats in forests: challenges and opportunities. In: Lacki MJ, Hayes JP, Kurta A (eds) *Bats in forests: conservation and management*. Johns Hopkins University Press, Baltimore, pp 263–292
- Wharton CH (1978) *The natural environments of Georgia*. Georgia Department of Natural Resources, Atlanta
- Wiles GJ, Johnson NC (2004) Population size and natural history of Mariana fruit bats (Chiroptera: Pteropodidae) on Sarigan, Mariana Islands. *Pac Sci* 58:585–596
- Williams BK, Nichols JD, Conroy MJ (2002) *Analysis and management of animal populations*. Academic Press, San Diego
- Willis CKR, Voss CM, Brigham RM (2006) Roost selection by forest-living female big brown bats (*Eptesicus fuscus*). *J Mammal* 87:345–350