Mist Net Effort Required to Inventory a Forest Bat Species Assemblage

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ABSTRACT Little quantitative information exists about the survey effort necessary to inventory temperate bat species assemblages. We used a bootstrap resampling algorithm to estimate the number of mist net surveys required to capture individuals from 9 species at both study area and site levels using data collected in a forested watershed in northwestern California, USA, during 1996–2000. The mean number of simulated surveys required to capture individual species varied with species' rarity and ranged from 1.5 to 44.9. We retrospectively evaluated strategies to reduce required survey effort by subsampling data from 1996 to 1998 and tested the strategies in the field during 1999 and 2000. Using data from 1996 to 1998, the mean number of simulated surveys required to capture 8 out of 9 species was 26.3, but a 95% probability of capture required >61 surveys. Inventory efficiency, defined as the cumulative proportion of species detected per survey effort, improved for both the study area and individual sites by conducting surveys later in summer. We realized further improvements in study area inventory efficiency by focusing on productive sites. We found that 3 surveys conducted between 1 July and 10 September at each of 4 productive sites in this 10-km^2 study area resulted in the capture of 8 species annually. Quantitative estimation of the survey effort required to assess bat species occurrence improves the ability to plan and execute reliable, efficient inventories. Results from our study should be useful for planning inventories in nearby geographical areas and similar habitat types; further, the analytical methods we used to assess effort are broadly applicable to other survey methods and taxa. (JOURNAL OF WILDLIFE MANAGEMENT 71(1):251–257; 2007)

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Bats are important components of biodiversity that are often underrepresented in conservation and management plans because of a lack of information on population status and habitat requirements (Pierson 1998, Richards and Hall 1998). Nevertheless, increased interest in bats (Fenton 1997) coupled with their status as species of concern in many areas (Bogan et al. 1996) has increased the number of inventories aimed at documenting species occurrence (Weller and Zielinski 2006). To date, this work has often been conducted with little guidance (but see Resources Inventory Committee 1998, Vonhof 2002) or evaluation of the survey effort required to conduct an accurate inventory. In planning an inventory, an important question is the number of surveys required to detect species with a given level of confidence (Zielinski and Stauffer 1996, Kéry 2002, Sherwin et al. 2003).

Studies of other taxa have evaluated the spatial and temporal replication and survey duration necessary to estimate abundance and establish trends over time (Link et al. 1994, Lewis and Gould 2000, Thompson et al. 2002, Watson 2004) or to estimate number of species detected with increasing effort (Bury and Corn 1987, Block et al. 1994). Evaluations of survey effort necessary to describe bat species assemblages are limited to Australia and the Neotropics (Mills et al. 1996, Moreno and Halffter 2000, Aguirre 2002, Bernard and Fenton 2002). A similar assessment of survey effort has not been made for temperate bat assemblages of North America or Europe despite a large number of surveys conducted in these areas. Estimates of survey effort required to document tropical bat species assemblages provide little guidance for inventories in temperate areas because of differences in species, habitats, and objectives. Tropical areas generally support a larger number of lesser-known bat species, and a frequent objective is to compare the numbers of species present among areas of conservation concern. Hence, the relevant metric for many tropical inventories is the number of species detected for a given level of effort and is frequently addressed using species accumulation curves (Moreno and Halffter 2000, Estrada and Coates-Estrada 2001, Aguirre 2002, Bernard and Fenton 2002).

In temperate areas where the bat fauna generally comprises fewer, better-known species, questions regarding survey effort are typically goal oriented and may focus on efficiency of survey effort. Relevant questions include 1) given a goal of detecting species X, how many surveys are required? or 2) given a goal of detecting Y% of the species in an area, how many surveys should be conducted? Such questions have not been addressed for a temperate bat assemblage and, though conventional species accumulation curves can provide post hoc assessments of survey completeness, they do not do so in a predictive manner.

Activity patterns of temperate bats vary greatly both spatially and temporally (Hayes 1997, 2000). Consequently, multiple surveys are needed to detect individual species and an even greater number to detect all species that use an area. Given limited resources, it is imperative that inventories are both accurate (species are detected and correctly identified) and efficient (measured by species detected/survey). Where-

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as accuracy can be improved simply by increasing the number of surveys (White 2004), the greater challenge is to do so efficiently. We examined sampling accuracy and efficiency using results from mist net surveys conducted in a forested watershed in northern California, USA. Our goals were to quantify the survey effort necessary to inventory the summer bat species assemblage and evaluate practical measures to improve efficiency of inventories in this area.

STUDY AREA

Our study area was within the Pilot Creek watershed in the Six Rivers National Forest in northwestern California (40°37′N, 123°36′W). The watershed was approximately 55 km from the Pacific Ocean at an elevation range of 950–1,320 m. This area was characterized by steep, rugged terrain, commonly gaining 200 m in elevation for each kilometer of distance. This 100-km^2 watershed had hundreds of small tributaries, but only Pilot Creek and the lower reaches of its larger tributaries maintained surface flows throughout summer. Sixty percent of the watershed was late-successional forest, including the headwaters area where our study took place. Vegetation was dominated by Douglas-fir (*Pseudotsuga menziesii*), but white fir (*Abies concolor*) and oaks (*Quercus chrysolepis*, *Q. kelloggii*, and *Q. garryana*) were also common. There were no known caves, mines, bridges, or buildings in our study area.

The nearest weather station was approximately 20 km away at the Mad River Ranger Station (elevation 846 m). Mean annual precipitation during the study was approximately 195 cm, of which 2.0 cm accumulated from June through August. Mean minimum temperatures for June, July, and August were 7.2° C, 9.4° C, and 8.9° C, respectively; mean maximum temperatures were 25.9° C, 30.2° C, and 30.4° C, respectively.

METHODS

We attempted to capture bats in mist nets at water sources and along suspected flight corridors during their summer activity period. We defined a survey as a single night of mist netting at a site. We selected suitable mist net sites that spanned a variety of habitats used by bats, with the goal of maximizing number of species captured in the study area. We conducted surveys to meet the needs of our and 2 other studies (Seidman and Zabel 2001, Weller and Zabel 2001). During 1996–1998 (period 1), we surveyed 9–17 sites per year during June–September (Table 1). In total, we surveyed 28 different sites including 12 sites along Pilot Creek, 2 along perennial tributaries to Pilot Creek, 10 on intermittent streams, 2 on roads, one at a pond, and one at a meadow edge. All survey sites fell within a 9.8-km^2 polygon in the upper half of the watershed. During period 1, we conducted surveys at sites where we suspected capture efforts to be successful and subsequently revisited sites where we captured multiple species or individuals. Such an approach is commonly used to document species presence in an area and we refer to it as conventional methods. By the end of 1997, we had identified 4 sites that were particularly effective. Subsequently, we conducted a disproportionate number of surveys at these sites, which we refer to as focal sites. Three of the focal sites were along Pilot Creek, spaced 570 m and 3.7 km apart; the fourth focal site was at an intermittent stream.

We chose the number, length, and configuration of nets to suit the physical characteristics of each site. Mist nets were 2.6 m high and ranged in length from 6 to 12 m. We used an average of 3.6 nets per survey (SD = 0.8, range = 2–6). Surveys began at sunset and continued for a minimum 3 hours or until an hour passed after the last bat was captured, whichever was longer. We conducted surveys regardless of temperature but not during periods of precipitation. Mean temperature at survey end was 13.0° C (SD = 3.5° C, range = 6.0–24.5° C).

We used survey results from period 1 to explore some of the spatial and temporal effects on survey effort required to capture individual and multiple species of bats. Using all surveys from period 1, we estimated number of annual surveys required to 1) first capture each species and 2) cumulatively detect multiple species. We then evaluated strategies for reducing annual survey effort by comparing these results to several subsets of these data: 1) surveys conducted after 30 June (postJun), 2) surveys conducted after 31 July (postJul), and 3) surveys at focal sites during these date ranges. We selected 30 June to approximate the end date of low nighttime temperatures that can depress bat activity (Maier 1992, Hayes 1997, Erickson and West 2002); 31 July approximated the date when we first captured juveniles. The presence of volant juveniles can increase the number of individuals of a species active in an area (Maier 1992, Schulz 1999) and consequently improve chances of capturing those species. We applied strategies that appeared effective based on results from period 1 in the field during 1999 and 2000 (period 2) to evaluate their applicability.

Additionally, we used results of focal site surveys to evaluate the effort required to assess species richness at individual sites. We sampled from the complete set of surveys conducted at each focal site from 1996 to 2000 to estimate the number of surveys necessary to accumulate species at the site level. We also compared the number of species captured at individual sites using the full data set to postJune and postJuly surveys.

We generated bootstrap estimates (sensu Efron and Tibshirani 1993) of the number of surveys required to meet each objective by randomly drawing from data pools created by subsetting the original data set based on when surveys were conducted and whether all sites or only focal sites were included. The bootstrap routine drew surveys, with replacement, from each pool of surveys and recorded the number of simulated surveys until a particular species was first captured or a specified number of species was captured. When number of species captured was the objective, we made random draws until all species in the pool of surveys were present in the simulated sample. Because a single draw included the complete species assemblage captured at a single site and date combination, interspecific correlations in

Table 1. Number and timing of mist net surveys conducted to capture bats in Pilot Creek watershed, northern California, USA, 1996–2000.

Survey effort	1996	1997	1998	1999	2000
Date of first survey	30 Jun	16 Jun	8 Jun	2 Jul	12 Jul
Date of last survey	18 Sep	8 Sep	6 Sep	30 Aug	7 Sep
No. of surveys on or before 30 Jun	1	6	11	0	0
No. of surveys on or before 31 Jul	13	20	24	5	4
No. of surveys after 31 Jul	10	21	23	7	8
No. of different sites surveyed	9	17	17	4	4
No. of surveys at focal sites	10	19	19	12	12
Total no. of surveys	23	41	47	12	12

occurrence were maintained in the bootstrap samples. We generated summary statistics from the distribution of 10,000 samples from each data pool. We conducted sampling and summary statistics using SAS Release 8.1 (SAS Institute, Cary, NC).

RESULTS

We captured 11 species of bats in 135 surveys over 5 years (Tables 1, 2). We captured 2 species (*Myotis lucifugus* and *Lasiurus blossevilli*) only in 1998; we omitted these species from the 9 core species (sensu Magurran and Henderson 2003) analyzed here. When we included all surveys from 1996 to 2000 in the pool, the mean number of simulated surveys required to first detect a species ranged from 1.5 surveys for *M. californicus* to 44.9 surveys for *L. cinereus.* The 95th percentile, which corresponds to the estimated number of simulated surveys required to ensure a 95% probability of capture, varied from 3 to 136 surveys for those 2 species (Fig. 1). The mean number of simulated surveys required to cumulatively capture all 9 core species was 53 surveys; achieving a 95% probability of capturing the core species would have required 138 surveys (Fig. 2). By comparison, despite up to 47 surveys per year, we captured $\leq$8 core species in the field annually (Tables 1, 2).

Using the data pool from period 1, when we used conventional methods, a mean of 26.3 simulated surveys were required to cumulatively capture 8 of the core species and 61 surveys were required to achieve a 95% probability of capturing those species. The number of surveys required to first capture each individual species was reduced by including only postJune surveys and further reduced by including only postJuly surveys in nearly every case (Table 3). Similarly, including only postJune or postJuly surveys decreased by 18% the mean number of simulated surveys needed to capture 8 species. The simulated effort necessary to cumulatively capture 7 of the core species decreased 16% using postJune data and 29% using postJuly data (Table 3).

Pooling only focal site surveys over all dates reduced the mean number of simulated surveys required to first detect all but 1 individual species (*M. yumanensis*) during period 1 (Table 3). The increase in simulated effort required to cumulatively capture 8 core species by surveying focal sites in period 1 was due to the large number of surveys until the first capture of *M. yumanensis*. By contrast, the simulated effort to capture 6 and 7 species using focal sites in period 1 decreased by 17% and 19%, respectively, when compared to surveys at all sites (Table 3).

Using the data pool from post June surveys at focal sites during period 1 reduced the simulated number of surveys required to capture each species when compared to focal site surveys from all dates and for all species except *M. yumanensis* when compared to post June surveys at all sites (Table 3). However, the simulated number of surveys required to capture 3 individual species (*C. townsendii*, *L. noctivagans*, and *M. yumanensis*) and to cumulatively capture 7 and 8 core species was greater using postJuly than postJune surveys at focal sites (Table 3).

We applied these findings in the field during period 2, when we surveyed each focal site 3 times per year postJune (Table 1). Despite conducting only 12 annual surveys, we captured 8 core species in the field during both years (Table 2). Among the 7 core species that we captured in both

Table 2. Field results, by species, from 135 mist net surveys for bats in Pilot Creek watershed, northern California, USA, 1996–2000.

Species	Species code	No. surveys captured	% surveys captured	Yr captured	No. of surveys until first capture
Myotis californicus	MYCA	92	68.1	All	8
Lasionycteris noctivagans	LANO	59	43.7	All	5
M. evotis	MYEV	39	28.9	All	1
M. volans	MYVO	36	26.7	All	1
M. thysanodes	MYTH	29	21.5	All	10
Eptesicus fuscus	EPFU	19	14.1	All	16
M. yumanensis	MYYU	13	9.6	1997–2000	48
Corynorhinus townsendii	COTO	6	4.4	1996–1998	5
Lasiurus cinereus	LACI	3	2.2	1999–2000	121
M. lucifugus[a]	MYLU	2	1.5	1998	109
Lasiurus blossevilli[a]	LABL	1	0.7	1998	109

[a] We did not consider this species in analysis of core species as described in text.

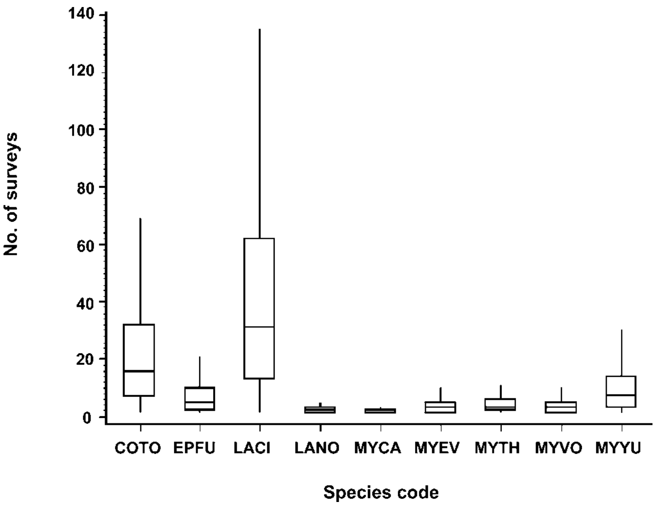

Figure 1. Simulated number of mist net surveys to capture individual bat species in Pilot Creek watershed, northern California, USA, 1996–2000. Species codes as in Table 2.

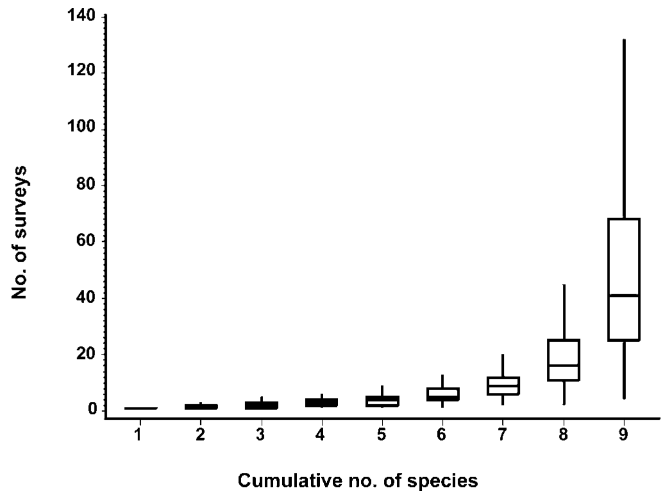

Figure 2. Simulated number of mist net surveys required to accumulate 1–9 species of bats in Pilot Creek watershed, northern California, USA, 1996–2000.

period 1 and period 2, the simulated effort necessary to capture all but one species (*L. noctivagans*) was less in period 2 (Table 3). The mean number of simulated surveys in period 2 required to cumulatively capture 8 core species was 46% as much as the effort required for all sites and dates in period 1. The 95th percentile for the simulated number of surveys required to cumulatively capture 8 species was reached in 26 surveys in period 2 compared to 61 surveys in period 1 (43% of the effort). The strategy used during period 2 was also more efficient at detecting commonly captured species; the mean number of simulated surveys to accumulate 6 species was 71% of that required in period 1 (Table 3) and the simulated effort required to achieve 95% probability of capturing 6 species was 9 surveys in period 2 compared to 14 surveys in period 1 (64% of the effort). Sampling from the pool of post July surveys from period 2 reduced the simulated number of surveys required to accumulate 6–8 species but had mixed effects on individual species when compared to the full set of surveys from period 2 (Table 3).

We conducted 17 field surveys at each of 3 focal sites and 21 surveys at the other focal site between 1996 and 2000. We captured 8 core species at each of the 3 sites along Pilot Creek and 5 core species at the upland site. The simulated mean number of surveys required to capture 8 core species at the 3 sites along Pilot Creek was 18.5 and ranged from 14.1 to 27.2 surveys among the 3 sites. Capture of 7 species required a mean of 9.2 (range = 7.3–12.3) simulated surveys. Capture of 8 core species at the 3 focal sites along Pilot Creek required a mean of 15.9 (range = 12.7–22.7) postJune simulated surveys and 14.2 (range = 13.1–15.9) postJuly surveys. Capture of 5 species at the upland site required a mean of 25.7 simulated surveys.

DISCUSSION

Survey effort necessary to capture bats varied by species, sites surveyed, and time periods over which we conducted surveys. Although we captured the most common species with relatively modest survey effort, pursuit of uncommon species precipitated a sharp rise in required effort. Studies in the Neotropics, where number of species and diversity of habitats were greater, have required 18–70 mist net surveys to capture 90% of the estimated species richness (Moreno and Halffter 2000, Aguirre 2002, Bernard and Fenton 2002). Hence, we were surprised that, using conventional methods, >26 surveys were required to capture 8 of the 9 core species in our relatively small, vegetatively homogenous, study area. This level of spatiotemporal replication was necessary to compensate for our incomplete understanding of the relationship between bat activity and a number of biotic and abiotic factors including weather conditions, insect availability, and reproductive condition of bats (Maier 1992, Hayes 1997, Erickson and West 2002). Additionally, all bats in our study are in the family Vespertilionidae, which are reportedly difficult to capture using mist nets (Kalko 1998, Moreno and Halffter 2000); this may help explain why the levels of effort we observed were comparable to those in Neotropical study areas.

Because the level of effort required to capture uncommon species of bats may exceed the means of some biologists (Weller and Zielinski 2006), it is important to elucidate strategies for improving survey efficiency. In our study area, conducting surveys later in the summer and focusing efforts on the most productive sites reduced the number of surveys required to meet inventory objectives. Although post June surveys consistently reduced effort required to achieve inventory objectives, post July surveys produced mixed results, perhaps as a result of too few total survey nights remaining to capture some species. We generated a relatively complete inventory of the species in our study area using a density of approximately 4 focal sites/10 km^2. Compared to surveying sites of unknown quality, limiting surveys to focal sites improved the rate of species accumulation, saved time, and simplified logistics by eliminating additional site

Table 3. Simulated mean number of mist net surveys required to capture bats in Pilot Creek watershed, northern California, USA, 1996–2000.

Survey goal	Period 1 (1996–1998)						Period 2 (1999–2000)	
	All sites			Focal sites			Focal sites	
	All dates[a]	PostJun	PostJul	All dates	PostJun	PostJul	PostJun	PostJul
Cumulative no. of species								
8	26.3	21.6	21.6	27.2	20.3	26.5	12.0	11.2
7	11.6	9.8	8.2	9.5	7.2	7.7	6.8	6.4
6	6.5	5.7	4.4	5.4	4.2	3.8	4.6	4.4
First capture of species								
Corynorhinus townsendii	18.8	15.4	18.1	7.9	6.0	8.1		
Eptesicus fuscus	7.4	6.2	4.1	6.8	5.2	3.4	5.9	3.8
Lasiurus cinereus							8.2	7.5
Lasionycteris noctivagans	2.2	2.4	2.0	1.8	1.8	1.9	2.7	3.0
Myotis californicus	1.5	1.4	1.2	1.4	1.2	1.2	1.3	1.2
M. evotis	3.5	3.4	2.7	2.5	2.3	2.0	3.4	5.0
M. thysanodes	4.9	4.0	3.6	4.9	3.6	3.5	4.0	3.0
M. volans	4.1	3.9	2.8	2.8	2.4	1.9	2.7	3.0
M. yumanensis	14.2	11.7	9.1	23.9	17.7	24.2	4.8	4.9

[a] Referred to as conventional methods in text.

reconnaissance. Of course, identification of focal sites required a preliminary phase of sampling to identify the most successful sites. When pilot studies are not practical, surveying additional sites, rather than repeated surveys at existing sites, is a more effective inventory strategy for uncommon species (Colwell and Coddington 1994, MacKenzie and Royle 2005).

Despite averaging 4–10 individuals and 2–3 species per survey, each of the 4 focal sites had $\geq$1 survey in which we only captured one bat. Even during the most productive periods (i.e., after 31 Jul) >14 mist net surveys were required to capture all species that occurred at an individual site within this study area. This is similar to the number of mist net surveys required to capture up to 18 species within small habitat patches in tropical Mexico (Moreno and Halffter 2000). By contrast, it has been reported that species richness at a site can be adequately described with 2–3 surveys using bat detectors in Europe (Ahlén and Baagøe 1999) or harp traps in Australia (Mills et al. 1996). Note also that the level of effort necessary to capture species occurring at an individual site approached that required to capture species in the entire study area. Similar results were found in inventories of bats in Mexico (Moreno and Halffter 2000) and *Martes* in California (Zielinski and Stauffer 1996), where the effort necessary for a reliable inventory of an individual stratum approached or exceeded the effort necessary to inventory a larger area comprising multiple strata. This may be because study area inventories incorporate both spatial and temporal replication through the use of multiple survey sites, whereas a site inventory can only include temporal replication.

As with other analytical methods (e.g., species accumulation curves), assessment of inventory completeness and strategies for improving efficiency in our study required an initial survey effort to generate a pool of sample data with which to work. Conventionally, inventory effectiveness has been inferred from species accumulation curves by inspection for inflection points that indicate a decrease in returns on one's survey investment (Bury and Corn 1987, Estrada and Coates-Estrada 2001). In systems with greater species richness, models were fit to species accumulation curves to estimate the number of species expected in an area and inventory completeness was assessed based on detection of a given proportion (e.g., 90%) of the expected species (Soberón and Llorente 1993, Flather 1996, Moreno and Halffter 2000). In our study, rather than determine the number of species detected for a given level of effort, we asked how much effort was required to confidently detect a given species or number of species. Hence, the relationship between species detected and survey effort in our study (Fig. 2) is the inverse of conventional species accumulation curves.

Additionally, our approach provides a probability-based approach to inventory planning and evaluation. Thresholds for proportion of the species assemblage to target can be set a priori in order to identify the number of surveys that might be necessary to meet objectives. For instance, the number of surveys necessary to achieve a 95% probability of capturing a specified number of species could be prescribed as minimum required survey effort. Estimates of required survey effort can simplify planning and allow informed tradeoffs between inventory accuracy and resources available to conduct work. For instance, simulations indicated that capture of 8 of the 9 core species in our study required less than half of the effort necessary to capture all 9 species. If detection of 7 of the core species was considered sufficient, this could be accomplished with a 50–70% further reduction in effort (Table 3).

Our analytical approach also quantifies survey effort necessary to capture individual species when, as in most temperate areas, it is more important to establish which species, rather than how many species, are present (Watson 2004). Establishing the probability of capture or detection with a given level of effort provides a defensible means of quantifying whether sufficient effort has been applied to detect a species, given that it is present (Zielinski and

Stauffer 1996, Kéry 2002, Sherwin et al. 2003). Future projects in nearby areas and similar habitats could use our estimates of sample effort for planning purposes when designing inventories for individual species. However, caution must be exercised when applying our estimates elsewhere because they result from work in a single study area. Similar analytic methods should be applied to data from multiple study areas before meaningful conclusions about capture probabilities, and their variability, for individual species can be made.

Our estimates of required survey effort were based solely on results of mist net surveys. Several studies have concluded that a combination of mist net and acoustic-monitoring surveys provide more complete bat inventories than employing one or the other technique alone (Kuenzi and Morrison 1998, Murray et al. 1999, O'Farrell and Gannon 1999, Duffy et al. 2000). Use of acoustic methods in our study likely would have decreased the number of surveys required to document the presence of some species at both the site and study area level. However, because some species are difficult to detect or identify from their echolocation calls (Murray et al. 1999, O'Farrell and Gannon 1999), capture surveys will continue to be a vital component of bat inventories; and quantifying the effort necessary to do so reliably is important. Further, the analytical approach demonstrated here for assessing required mist net survey effort could be profitably applied to quantify survey effort for other (e.g., acoustic) inventory techniques.

MANAGEMENT IMPLICATIONS

We demonstrated that multiple mist net surveys are necessary to capture most species of bats in a forested area. The strategies we identified for improving inventory efficiency, such as conducting surveys later in the summer and focusing survey effort on productive sites, are likely to be effective in similar habitats and nearby geographic areas, but should be validated first. The goal-oriented analysis of survey effort we introduced is broadly applicable to evaluate completeness and improve efficiency of inventories conducted in other areas, using other survey methods, and for other taxa.

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