

Estimating Probabilities of Detection for Bat Echolocation Calls: An Application of the Double-Observer Method

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Abstract

Differential detectability is an issue of great practical importance in bat species (Order Chiroptera) surveys. Bat echolocation recorders increasingly are being used in survey efforts, but recorder-based surveys have not measured differences in detection probability quantitatively. A recently developed avian survey technique uses 2 observers at a site to estimate the probability of detection by comparing birds recorded independently by the 2 observers. We applied this method to bat surveys using remotely operated Anabat echolocation recorders. We placed 2 detectors at each sample point, which were randomly selected from forested habitat within 2 watersheds in Indiana and 2 in Missouri. The first detector was oriented toward the most open area of forest and the second was set 5 m away and oriented toward the most open area that allowed sampling of an area distinct from the first detector. We estimated detection probabilities using the Huggins closed-capture model in program MARK. We compared models of detection probability using the corrected quasi-likelihood Akaike's Information Criterion adjusted for overdispersion (QAIC_c). The best models accounted for detector placement and region but not species. Overall probability of detection for bats using 2 detectors was 0.62 in Indiana and 0.42 in Missouri. Results confirmed that a second detector increased the probability of detecting different species of bats at a site. Future regional comparisons should account for differences in detection probability to avoid biases associated with surveys relying solely on recorded calls. (WILDLIFE SOCIETY BULLETIN 34(2):408–412; 2006)

Key words

ANABAT, bats, Chiroptera, detection probability, echolocation calls.

Bats (Order Chiroptera) are cryptic animals and difficult to survey effectively. When compared to manual capture techniques, remotely placed acoustic detectors that record bat echolocation calls allow researchers to more efficiently survey multiple areas (Murray et al. 1999, Miller 2001). Acoustic surveys rely on counts of bat passes (Krusic et al. 1996, Crampton and Barclay 1998, Menzel et al. 2002, Patriquin and Barclay 2003), bat calls (Broders 2003), or time blocks during which bat calls are detected (Miller 2001) for calculation of activity indices (Fenton 1970, Miller 2001). These indices typically are used to compare bat activity levels among habitats, study areas, and species. Acoustic surveys also may be used to assess a species' occurrence at a site, which can then be used as a response variable in models of species–environment relationships (Ekman and de Jong 1996, Russ and Montgomery 2002). Regardless of whether the goal is a measure of activity or occurrence, subsequent statistical comparisons rely on the assumption that the probability of detection is constant throughout the study and equal among all categories being compared. One concern that repeatedly arises from these types of surveys is how to account for variation in the probability of detecting bat calls (Hayes 1997, 2000; Gannon et al. 2003; O'Shea et al. 2003).

Within a forest, many factors can affect the detectability of bat calls (Hayes 2000, Weller and Zabel 2002). Differences in vegetative clutter may deflect echolocation calls to different degrees (Patriquin and Barclay 2003). Additionally, the vertical

structure of a forest may influence the height at which bats forage (Kalcounis et al. 1999, Weller and Zabel 2002). Call intensity and reaction to forest structure differ among species (Brigham and Sleep 2003) and geographical location (O'Farrell et al. 2000, Murray et al. 2001), and other sources of intraspecific variation (Betts 1998, Kazial et al. 2001) could further affect detectability within a species. When possible, attempts are made to standardize sampling protocols to limit the influence of these sources of variation (Krusic et al. 1996, Humes et al. 1999, Menzel et al. 2002, Patriquin and Barclay 2003). However, the effectiveness of standardization in equalizing detection probability is untested for acoustic bat surveys, and many sources of variation likely exist that are either unknown or unmeasured. Thus, differences in activity values could be due to differences in the probability of detection rather than actual differences in activity (Humes et al. 1999, Hayes 2000, Gannon et al. 2003, O'Shea et al. 2003).

Recently, methods have been adapted to account for variation in the probability of detection when conducting acoustic sampling of bird populations (Nichols et al. 2000, Farnsworth et al. 2002, Moore et al. 2004). Nichols et al. (2000) describe a method that relies on 2 independent observers simultaneously sampling the same site, counting individual animals, and identifying them to species. The counts of each observer are compared over multiple sites after all surveys are completed. These comparisons are then formatted into encounter histories of detected (1) or not detected (0) for each observer and analyzed using standard closed population models.

We applied this technique to estimate the probability of

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recording echolocation calls of different species of bats during a night of sampling by using 2 detectors at a sample point. Our goals were to compare the probability of detection using either 1 or 2 detectors at a sample site and to test for differences in detectability between 2 study areas and among 5 species of bats common to both areas.

Methods

We collected recordings over an entire night at a total of 469 locations in 2 separate portions of the Central Hardwood Region: in forested areas of the Middle Wabash–Little Vermillion and Wildcat Creek watersheds in west-central Indiana, USA, and in the St. Francis and Black River watersheds in southeastern Missouri, USA. Dates of sampling spanned 2 years: between 27 June and 23 August 2002 and 19 May and 18 August 2003. We randomly selected locations of sample sites within forest areas and apportioned them among 3 classes of forest patch size: 1–25 ha, 25–100 ha, and >100 ha. The dominant forest vegetation in study areas of both states is composed primarily of a variety of oak (*Quercus* spp.) and hickory (*Carya* spp.) species. Additionally, forests in the Indiana study region contained more soft-mast trees, primarily American elm (*Ulmus americana*), sugar maple (*Acer saccharum*), silver maple (*A. saccharinum*), and white ash (*Fraxinus americana*), whereas Missouri forests contained coniferous trees, primarily short-leaf pine (*Pinus echinata*).

We housed Anabat detectors and Zero Crossing Analysis Interface Modules (ZCAIMs; Titley Electronics, Ballina, NSW, Australia) in plastic containers with a 45° polyvinyl chloride (PVC) elbow on one end. We aligned detector microphones with the PVC elbow leaving a 1-cm gap between the elbow and detector microphone. We elevated each container 1 m off the ground using either a PVC stand or a rope suspension system (Fig. 1a,b).

We identified sequences of bat calls to species using a discriminant function model (Britzke et al. 1999). We used measured parameters from a known-call library to construct linear discriminant functions using MINITAB, version 13.2 (2002; MINITAB Inc., State College, Pennsylvania). We entered corresponding parameters from calls collected during the study into these functions to identify each individual call. We then identified a call sequence by taking the mode of the species assignments for calls within that sequence. Sequences were deemed unidentified if the mode of identified calls either was <4 or <60% of all calls in the sequence.

To adapt the double-observer method for surveys using remotely operated bat detectors, we treated each detector as an observer at a point count. We set bat detectors to sample spatially independent portions of the same site (Fig. 1c) for 1 night. At each site, we oriented the primary detector toward the most open area of the forest. We positioned the secondary detector 5 m behind the primary detector and then oriented it toward the most open area of the forest within a 180° radius centered on the direction opposite to the primary detector (Fig. 1c). The orientation of the secondary detector prevented spatial overlap of the recording area between the 2 detectors (Fig. 1c). We expected this restriction in orientation to cause a lower probability of detection for the secondary detector because this detector would often be oriented toward a less open area than the primary detector.

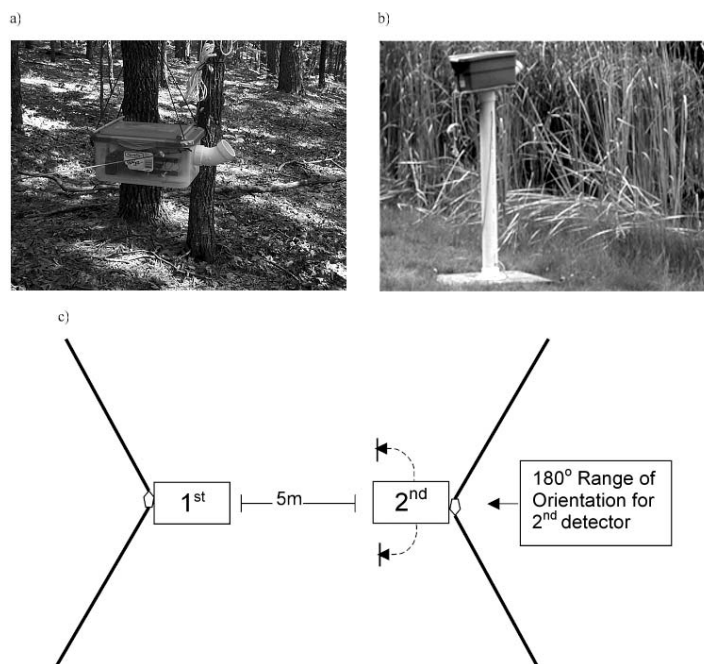


Figure 1. Photograph of the setup for acoustic detectors in Mo. (a) and in Ind., USA (b), and a schematic of the orientation of two detectors at a sample site (c). The orientation of the second detector is restricted to 180° to ensure independent areas are sampled at a site.

Encounter histories contained 2 sampling occasions, one for each detector at a site. Because individual bats could not be distinguished by their echolocation calls, the encounter history did not incorporate the number of calls recorded. Instead, we treated each new species encountered during a night as an independent encounter, so we treated multiple identifications of the same species by the same detector at a site as a single occurrence. We included region and species identification of each encounter history as potential covariates. However, we made no effort to account for potential variation between years because 1) our detectors were calibrated annually to maintain consistent sensitivity levels and 2) we believed between-year variation would be inconsequential relative to other factors such as site-specific vegetation characteristics and nightly environmental conditions.

We calculated detection probability estimates from encounter histories using the Huggins (1989) closed-capture model implemented in program MARK (White and Burnham 1999). We used the quasi-likelihood Akaike's Information Criterion corrected for overdispersion ($QAIC_c$) to select the model that best fit the data (Hurvich and Tsai 1989, Anderson et al. 1994). We considered models with $\Delta QAIC_c$ values <4 to be competing and we consolidated parameter estimates based on these models through model averaging based on $QAIC_c$ weights (Burnham and Anderson 2002). We estimated the probability of detection for each detector: p_1 for the primary detector and p_2 for the secondary detector. We compared detection probabilities using a 2-tailed Student's *t*-test (Zar 1999). We calculated a combined detection probability (\hat{p}) for both detectors as $\hat{p} = 1 - (1 - \hat{p}_1)(1 - \hat{p}_2)$. We calculated asymptotic variance for the combined detection probability using the estimator given by Cook and Jacobson (1979):

$$\text{var}(\hat{p}|x_{..}) = \frac{(1 - \hat{p})^2 \hat{p}}{x_{..}}$$

$$\left[\frac{1}{\hat{p}_1 \beta_1} + \frac{1}{\hat{p}_2 \beta_2} + \frac{1}{\hat{p}_2(1 - \hat{p}_1) \beta_1} + \frac{1}{\hat{p}_1(1 - \hat{p}_2) \beta_2} \right],$$

where $\beta_i = x_{i.}/x_{..}$, $x_{i.}$ is the number of encounter histories for detector i and $x_{..} = x_{.1} + x_{.2}$.

Results

Acoustic surveys across the 2 study regions resulted in 249 encounter histories for 5 species of bats: *Eptesicus fuscus*, *Lasiurus borealis*, *Myotis lucifugus*, *Myotis septentrionalis*, and *Myotis sodalis* (Table 1). The best models of detection probability assumed variation by region and order of detector placement (Table 2). Four models had nearly equivalent ΔQAIC_c values (Table 2). Based on estimates averaged among competing models, the probabilities of detection appeared to be greater for both primary (0.40 ± 0.070 SE) and secondary detectors (0.36 ± 0.070 SE, $n = 165$) in Indiana when compared to those in Missouri (0.30 ± 0.11 SE, $n = 84$; 0.23 ± 0.087 SE, $n = 84$). However, pair-wise statistical comparisons between regions for both primary and secondary detectors show that these estimates are not significantly distinguishable ($t_{148} = 0.81$, $P = 0.419$; $t_{212} = 1.13$, $P = 0.259$). Additionally, we found no differences between primary and secondary detectors within either region (Ind., $t_{327} = 0.41$, $P = 0.684$; Mo., $t_{140} = 0.46$, $P = 0.642$). By using 2 detectors configured as described in our study, the probability of detecting a species at a site (0.62 ± 0.087 SE, $n = 165$) in Indiana was greater than that of the primary detector alone ($t_{161} = 1.93$, $P = 0.056$). For detectors in Missouri, the combined detection probability (0.46 ± 0.17 SE, $n = 89$) was not a significant improvement over the primary detector alone ($t_{80} = 0.81$, $P = 0.418$).

Species differences were not included in the best models of detection probability (Table 2). For illustration we estimated the species-specific detection probabilities for Indiana, while incorporating differences in detector placement (Fig. 2). Looking at each species individually, the probability of detection was highest for *L. borealis* and *M. sodalis* and lowest for *E. fuscus* and *M. lucifugus* (Fig. 2).

Discussion and Management Implications

The method described above provided us with a coarse estimate of overall detection probability for our respective study areas. With this information we were able to confirm that our probability of detecting bats through echolocation recordings was <1 in both of our study areas. We also were able to assess the relative benefit of adding a second detector to our sampling locations. Our models

Table 1. Number of bat encounter histories for 2 study regions (Mo. and Ind., USA) by species during 2002–2003.

Species	Indiana	Missouri	Combined
<i>Eptesicus fuscus</i>	32	6	38
<i>Lasiurus borealis</i>	28	26	54
<i>Myotis lucifugus</i>	24	4	28
<i>Myotis septentrionalis</i>	41	29	70
<i>Myotis sodalis</i>	40	19	59
Total	165	84	249

Table 2. Relative performance of competing models measuring the probability of detecting bat echolocation calls for 2 study regions (Mo. and Ind., USA) and 2 detectors during 2002–2003.

Model ^a	ΔQAIC_c ^b	QAIC_c weight	Parameters
Region + detector	0.0000	0.2506	3
Region + detector + (region \times detector)	0.0073	0.2496	4
Detector	0.0599	0.2432	2
Region	0.0882	0.2398	2
Region + detector + species	7.4423	0.0061	7
Region + detector + species + (region \times detector)	7.4831	0.0059	8
Species	7.8759	0.0049	5

^a Factors for each model that were allowed to influence the estimated probability of detection.

^b Models are ranked according to their adjusted ΔAIC_c value (ΔQAIC_c).

suggest that an additional detector increased our ability to detect bats present in Indiana by approximately 1.6 times. Due to the low probability of detection for the primary detector in Missouri, we concluded that a second detector also was biologically relevant there, even though its contribution was not statistically significant. Importantly, we also identified regional differences in the probability of detecting bats, even though sampling methods were consistent between regions. We believe that these differences are most likely due to differences in forest stand composition. Although both study areas are dominated by hard-mast species, forests in the Indiana study area contained more soft-mast trees such as maple (*Acer* spp.), whereas Missouri forests contained more pine (*Pinus* spp.). Thus, future comparisons of bat communities between the 2 regions will need to account for differential detectability.

Most studies using acoustic sampling for bats openly acknowledge that unknown detection probabilities are a potential source of bias in their results and conclusions (Krusic et al. 1996, Crampton

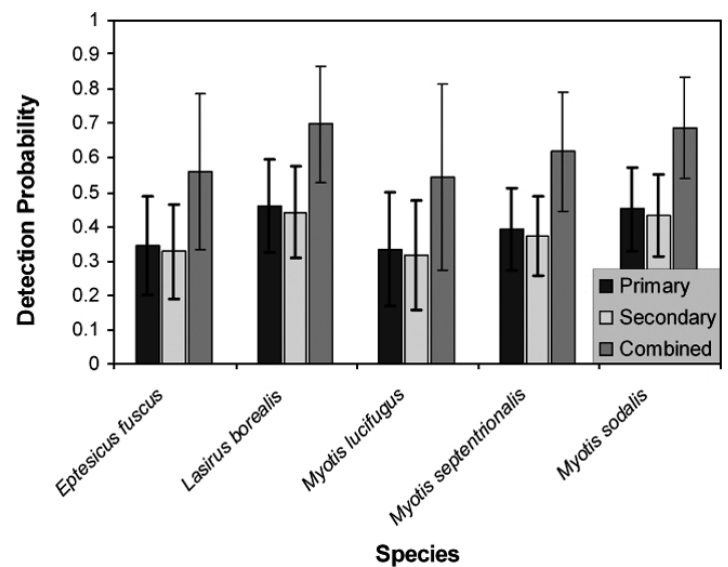


Figure 2. Species-specific probabilities of detection and associated standard errors for Indiana study region. Model assumed a detector by region interaction. Five bat species were included: *Eptesicus fuscus*, *Lasiurus borealis*, *Myotis lucifugus*, *Myotis septentrionalis*, and *Myotis sodalis*.

and Barclay 1998, Humes et al. 1999, Menzel et al. 2002, Patriquin and Barclay 2003). Incorporating detection probabilities into analysis of bat call counts allows researchers to make more informed decisions about resource allocation, increase robustness of species occurrence surveys, and strengthen comparisons of bat activity indices from different habitats or regions.

Previous researchers have noted the need for estimation of detection probabilities in bat echolocation surveys (Hayes 2000, Gannon et al. 2003, O'Shea et al. 2003). Detection probabilities can be estimated using multiple detectors, as demonstrated in this paper, or by repeatedly surveying a site over a specified time period (Nichols et al. 2000, Tyre et al. 2003). Increases in both the number of encounter histories and the number of sampling occasions within an encounter history improves one's ability to account for relevant changes in detection probability (Tyre et al. 2003). However, with all ecological studies, funds are limited relative to study objectives, and few studies will be able to record at the same location with multiple detectors for multiple nights.

In the current study, our objective was to complete a species occurrence survey. We sampled each site for a single night, while we used 2 detectors at each site. We sacrificed our ability to distinguish between night-to-night temporal variation and site-specific variation in order to include more sample locations in our study. This approach is not appropriate for all studies, especially those measuring bat activity levels, because activity can vary greatly at the same location on different nights (Hayes 2000). However, sampling the same sites on multiple nights, even with 1 detector, should allow estimation of detection probability.

Depending on the question of interest, there are several statistical models that allow incorporation of detection probability. For example, species-occurrence surveys may be analyzed with a zero-inflated binomial (ZIB) model (Tyre et al. 2003) instead of more traditional logistic regression modeling. The ZIB model estimates the rate of false-negative errors resulting from a failure to detect a species at an occupied site. For comparisons of activity indices, an application of the zero-inflated Poisson model may be appropriate (Welsh et al. 1996). Both of these models allow the

inclusion of site-specific covariates to help limit potential bias due to variation between sites.

Using raw count data may appear to be a more straightforward method of estimating bat activity. However, for both mark-recapture studies and bird point counts, use of raw count data requires more assumptions than probabilistic methods that account for detection probability (Nichols and Pollock 1983, MacKenzie and Kendall 2002). We expect the same to be true for estimates of bat activity based on echolocation call counts. As with all calculations of detection probability, actual abundance of the study organism can influence its probability of detection. This is an even greater concern for bat echolocation studies because the inability of echolocation recordings to distinguish among individual animals prevents estimates of per capita detection probabilities. Instead, detection probabilities for a particular species or species group will be estimated from individual bat passes or from time blocks during a temporal sequence. Thus, estimates of bat activity are not actual measures of bat abundance (Hayes 2000, Gannon et al. 2003).

We recommend that future studies account for probability of detection when using echolocation detectors for species occurrence surveys or when making comparisons of bat activity levels. Echolocation surveys that ignore potential differences in the probability of detection risk drawing erroneous conclusions. This is especially true when making comparisons between areas that may differ in vegetative density or species that differ substantially in call intensity.

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