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ASSESSING BAT DETECTABILITY AND OCCUPANCY WITH MULTIPLE AUTOMATED ECHOLOCATION DETECTORS

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Occupancy analysis and its ability to account for differential detection probabilities is important for studies in which detecting echolocation calls is used as a measure of bat occurrence and activity. We examined the feasibility of remotely acquiring bat encounter histories to estimate detection probability and occupancy. We used echolocation detectors coupled to digital recorders operating at a series of proximate sites on consecutive nights in 2 trial surveys for the Hawaiian hoary bat (*Lasiurus cinereus semotus*). Our results confirmed that the technique is readily amenable for use in occupancy analysis. We also conducted a simulation exercise to assess the effects of sampling effort on parameter estimation. The results indicated that the precision and bias of parameter estimation were often more influenced by the number of sites sampled than number of visits. Acceptable accuracy often was not attained until at least 15 sites or 15 visits were used to estimate detection probability and occupancy. The method has significant potential for use in monitoring trends in bat activity and in comparative studies of habitat use.

Key words: acoustic detection, Anabat, bat, detection probability, echolocation, occupancy, sampling design

Recent developments in techniques for modeling animal occupancy and detection probability (summarized in Vojta 2005) coupled with existing methods of echolocation detection present an opportunity for the study of bat distribution and habitat use. Conventional capture methods (e.g., mistnetting) and direct surveillance, although widely used to sample bats, are time- and labor-intensive approaches for determining occurrence and activity. In comparison, automated detection and recording of echolocation calls provides an efficient means of sampling bat activity, particularly when done simultaneously at multiple sites and over long time periods (Miller 2001; Murray et al. 1999). However, variability in the likelihood of detecting bats presents a significant problem in analyses of occurrence and activity (Hayes 2000; O'Shea et al. 2003). Detection is not certain even when a species is present at a site, and a naïve estimate of occurrence will underestimate the true occurrence when detectability is less than perfect (MacKenzie et al. 2002). Typically, the likelihood of detecting bats diminishes with distance from the detector and is affected by variables such as vegetation structure (e.g., clutter, canopy height, and canopy closure—Kalcounis et al. 1999; Patriquin et al. 2003; Weller and Zabel 2002). It is important to account for the biases associated with imperfect detection when inferences about occurrence are made from presence–absence surveys.

MacKenzie et al. (2002) showed that the probability of detecting a species can be estimated by repeated surveys of 1 or more sites. Detection probability may then be used to derive an unbiased estimate of occupancy for an aggregate of sampled sites (i.e., landscape unit—MacKenzie 2005) or likelihood of absence at 1 or more sites (Tyre et al. 2003; Wintle et al. 2005). Along similar lines, the double-observer method described by Nichols et al. (2000) also may be used to estimate detection probability. Duchamp et al. (2006) applied this method to bat occurrence data acquired using pairs of echolocation detectors (henceforth detectors) to compare detection probabilities between 2 survey regions. However, their investigation was not aimed at producing detectability-adjusted measures of occupancy, a metric of perhaps more direct interest for studies of bat distribution, habitat use, and trends over time. To our knowledge, a study of associations of bats with forest habitat attributes by Yates and Muzika (2006) is the 1st example of detection-adjusted estimates of bat occupancy using repeated sampling.

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We present an application of the modeling approach proposed by MacKenzie et al. (2002) to a survey for the Hawaiian hoary bat (*Lasiurus cinereus semotus*) in which calls were sampled on consecutive nights (visits) with a linear array of detectors (sites) coupled to automated digital recorders. Our objectives were to examine the feasibility of analyzing remotely acquired detection data to estimate bat detection probability and occupancy. However, although occupancy may be defined simply as the presence of a species, this is a nondiscriminating criterion and may not be appropriate because bats can commute through areas not used for foraging or roosting. Of greater interest are measures of occurrence that indicate higher-order use and selection of habitat (sensu Johnson 1980). Toward this end, we used bat occurrence data acquired at 2 study areas to test a method of identifying the prevalence of high-use areas within a landscape unit based on a predefined threshold level of activity. In addition, we conducted simulation exercises to assess the effects of sampling effort on the estimation of detection probability and occupancy. We interpret our data in the context of allocating the number of visits and sites to sample for a range of conditions that may be encountered in the field.

The Hawaiian hoary bat is the only extant land mammal native to the Hawaiian Islands and was listed as endangered by the United States Fish and Wildlife Service (1970) because of apparent population declines. The absence of other bat species in Hawai‘i makes technical decisions about the identification of species based on calls unnecessary and simplifies the use of recorded calls to estimate occurrence.

MATERIALS AND METHODS

Study area.—Our 2 study areas were located on the northeastern slope of Mauna Kea on Hawai‘i within one of the largest remaining expanses of native rain forest in the state. The vegetation was comprised of mature ‘ōhi’a-lehua (*Metrosideros polymorpha*) with varying amounts of koa (*Acacia koa*) and understory components such as tree fern (hāpu‘u [*Cibotium glaucum*]), matted fern (uluhe [primarily *Dicranopteris linearis*]), and introduced strawberry guava (*Psidium cattleianum*). Sampling locations at the Laupahoehoe Natural Area Reserve (19°57′14″N, 155°16′45″W) were between 760 and 950 m elevation within intact forest of intermediate (~40–60%) canopy closure. The Umikoa study area (19°57′39″N, 155°20′1″W) was situated between 1,080 and 1,240 m elevation within a mix of forest patches and pastures adjacent to intact forest. Sampling was conducted on 11 nights (18–29 September 2006) in Umikoa and 12 nights (10–21 October 2006) in Laupahoehoe, and was limited in time to reduce the effects of seasonal movements (Menard 2001) on estimates of occupancy and detection probability.

Bat detection and threshold activity levels.—Echolocation calls were sampled using Anabat II detectors (Titley Electronics, Ballina, New South Wales, Australia) and recorded onto a compact flash card with a Zero-Crossings Analysis Interface Module (ZCAIM; Titley Electronics, Ballina, New South Wales, Australia), a device that stores call files with associated date and time data for later downloading onto a personal computer (O’Farrell et al. 1999). Detector units were programmed to automatically switch on and off at selected times (predusk and postdawn). Each detector and ZCAIM unit was powered with a 12-V battery permitting operation for up to 2 weeks.

The detector microphone was placed within a ∩-shaped polyvinyl chloride tubing (“bat-hat”) to protect it from the rain (e.g., Arnett et al. 2006). An acrylic-glass plate was used to reflect calls upward into the downward-facing microphone. Each microphone assembly was attached to the top of a 7-m pole and situated above the understory vegetation and within gaps in the forest canopy that were ≥10 m wide. Twelve detectors were used per array, and detectors were spaced at intervals of about 120 m to avoid double counting bats. This spacing was necessary to keep the linear array of detectors to a manageable size in each study area. Call files were processed with Analook software (version 4.9j; Titley Electronics) to filter ambient noise and visually inspected to ensure that residual noise was not interpreted as echolocation calls. Filtered call files were subsequently analyzed with a custom script in SAS (version 8.0—SAS Institute Inc. 2000) that counted the number of bat call pulses per 1-min period.

Activity levels of insectivorous bats are generally associated with insect abundance and may be used to identify areas of high use by bats (Kusch et al. 2004; O’Donnell 2000; Racey and Swift 1985). Bat activity, in turn, may be assessed by the number of files recorded by bat detectors that include echolocation calls (passes—Hayes 1997). However, this metric is susceptible to the arbitrary partitioning of potentially continuous activity. That is, a series of call pulses could be split into any number of call files by chance omissions of intervening pulses or predetermined settings on call file duration. Although we subsequently found that the correlation between the number of call files and pulses was moderately high (e.g., correlations were 0.65 and 0.70 for the detections recorded at the Laupahoehoe and Umikoa study areas), the use of pulse number directly measures the intensity of calling activity and may be less prone to measurement error caused by missed pulses (e.g., small area sampled by a microphone relative to bat movement, bat-detector orientation and distance, ambient noise, etc.) Our approach is similar to that of using file size as a measure of activity (Broders 2003) but has the advantage of being applied to filtered call files and may be less influenced by the interval between pulses (i.e., 2 files of similar size and duration may contain a different number of pulses).

We discriminated among areas of high and low use by examining the incidence of high-activity events as indicated by pulse number. We defined high-activity events as situations when the total number of pulses within each 1-min period exceeded a threshold determined by the median value for each study area. High-activity events were coded as 1 in a matrix that tallied their incidence for each site and each night (i.e., encounter history). Zeros were assigned to matrix cells for periods in which there was no recorded activity or pulse numbers were below the activity threshold. Detection probability and occupancy for each study area were calculated using the program MARK (White and Burnham 1999) based on the model of MacKenzie et al. (2002). These parameters can also be estimated using the program PRESENCE (version 2.0; http://www.mbr-pwrc.usgs.gov/software/presence.html).

Sampling efficiency.—Optimal allocation of survey effort depends on several interrelated components. The primary considerations are statistical in nature and include such factors as acceptable levels of precision and bias, type I and type II error rates, effect size, and power. A study design subsequently must identify the number of survey sites and visits that can be sampled within the logistical constraints dictated by time and cost. Tyre et al. (2003), Field et al. (2005), MacKenzie and Royle (2005), and MacKenzie et al. (2006) addressed these issues, as well as the selection of an optimal number of sites and visits for various sampling designs. We used a simulation exercise to explore the relationship between sampling effort and the precision and bias of detection probability (p) and occupancy (Ψ) estimates. The exercise addressed the hypothetical question: "what if the survey had been done with a smaller set of sites or fewer visits?" Values corresponding to low and high levels of p and Ψ were used to generate artificial data sets representing 4 general combinations of these parameters (i.e., low–low, low–high, high–low, and high–high). Parameters p and Ψ were subsequently reestimated for a range of sample sizes drawn from the data sets. The initial data sets represented various states of "true" p and Ψ (typically unknown) that might be encountered in the field and subsampling reproduced the small samples from which parameters are estimated. The detection probabilities and occupancy values corresponding to low and high levels that were assigned to each simulated data set were 0.2 and 0.8, respectively (although a range of other values is possible). Encounter histories with specified p and Ψ values and data-set sizes were generated from the random deviates of a uniform distribution. Data generation assumed an equal probability of occurrence at all sites and constant p across sites and visits (i.e., the $\Psi(\cdot)p(\cdot)$ model used by MacKenzie et al. [2002]). Subsamples resulting in all zero detection histories or those with no repeat detections at a site were discarded. Data-set generation and simulations were performed with a custom script in the program R (Venables and Smith 2006).

The simulation exercise separately evaluated the effects of the number of visits and the number of sites on estimates of p and Ψ. Simulations that varied both visit and site number were not pursued because of the enormous number of sampling effort and p and Ψ combinations. A fixed total of 15 sites were used in assessing the effects of sampling effort as a function of the number of visits. This number of sites was chosen because use of a greater number of detectors presents relatively greater equipment cost and logistical challenges. Simulations began with a sample size of 30 visits for each of the 4 data sets, and subsampling progressed incrementally with ever-smaller numbers of visits to a minimum of 2 (calculation of p required at least 2 or more visits). Data sets with the specified p and Ψ values were regenerated for each of 1,000 iterations per subsample increment, and p and Ψ were recalculated at each step.

We used a fixed total of 15 visits for the evaluation of sampling effort as a function of site number. This upper limit was selected because preliminary simulations showed that the variance was relatively small above this number. Moreover, battery power for the detectors declined rapidly after about 2 weeks, leading to a decrease in detector sensitivity. Each of the 4 data sets was incrementally subsampled to a minimum of 2 sites (calculation of Ψ requires at least 2 or more sites). Standardizing variance by the corresponding estimate of occupancy to produce a coefficient of variation (*CV*) permitted comparisons of situations in which the initial values of p and Ψ differed between visit and site simulations. Local regression (loess) smoothing splines were used to qualitatively identify the direction of bias in occupancy estimates and changes in variance as a function of sampling effort.

RESULTS

Detection probability and occupancy: field data.—The distribution of pulses was highly skewed with a large proportion of filtered call files comprised of few pulses. For example, at Laupahoehoe, 15% of observations had a single pulse (1st quartile = 2; median = 6; 3rd quartile = 13; maximum = 124). At Umikoa, 16% of the filtered call files had a single pulse (1st quartile = 2; median = 5; 3rd quartile = 13; maximum = 208).

Encounter histories showed that high levels of bat activity were widespread and these events were detected at most (Laupahoehoe) or all (Umikoa) sites. Detection probabilities were estimated to be 0.66 ± 0.046 *SE* and 0.86 ± 0.035 *SE*, and the proportion of sites at which high activity was detected was estimated at 0.82 ± 0.120 *SE* and 1.00 ± 0.000 *SE* at Laupahoehoe and Umikoa, respectively.

Sampling effort and occupancy estimation: simulations.—As expected, simulations demonstrated diminishing variability and bias in occupancy estimates with increasing sample size. However, the degree to which the accuracy of estimates was affected differed between simulations that varied the number of visits and sites. In general, occupancy was positively biased (overestimated) when the number of sites sampled was relatively low (≤ 10) but was unaffected by a comparable number of visits for a given p and Ψ (Figs. 1 and 2, top panels). The overall levels of variance were usually greater in site versus visit simulations, particularly in high p conditions and at low sample sizes (site number ≤ 15; Figs. 1 and 2, lower panels). The results indicated that the number of sites sampled often had a greater effect than number of visits in correctly approximating actual p and Ψ.

Simulations of number of visits showed that overall variance was greater for observations with low versus high initial values of Ψ, particularly at low sample sizes (Fig. 1, lower panel; compare parts a and c to parts b and d). Further, when the probability of detection is low, a survey may require at least 15 visits to fully minimize variance.

In contrast, the precision of simulations that varied site number did not differ as a function of p. Instead, the effects of varying site number were most apparent between low versus high values of Ψ, particularly when site number ≤ 15 (Fig. 2, lower panel; compare parts a and c to parts b and d). Therefore,

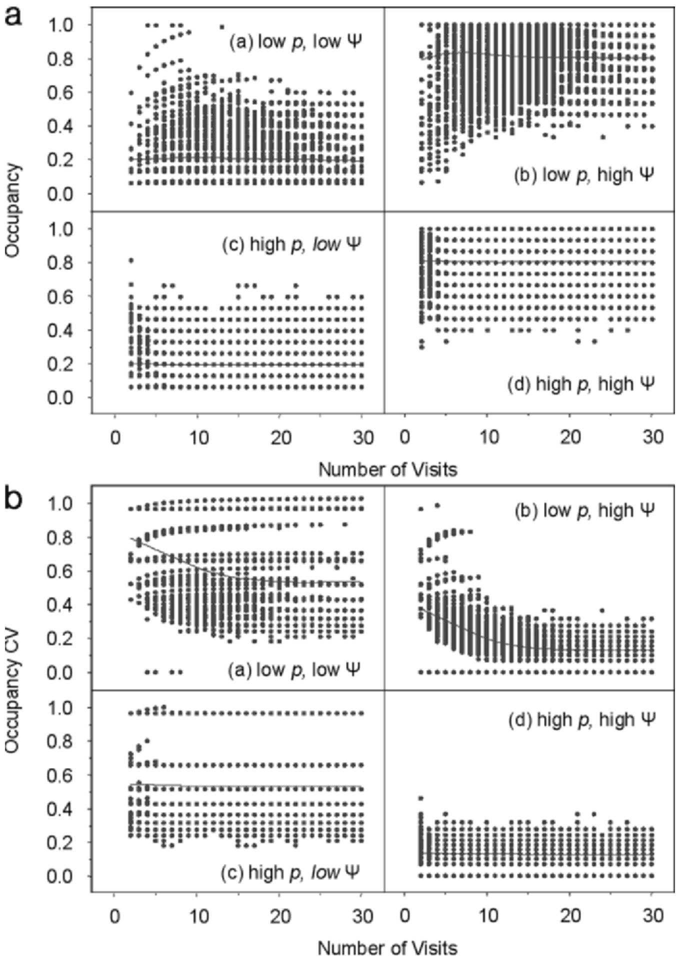

Fig. 1.—Estimated occupancy (top panel) and coefficient of variation (bottom panel) as a function of the number of visits conducted for each of 4 hypothetical combinations of detection probability (*p*) and occupancy (Ψ; i.e., low–low, low–high, high–low, and high–high shown in parts a–d). Smoothing splines qualitatively identify the direction of bias in parameter estimates.

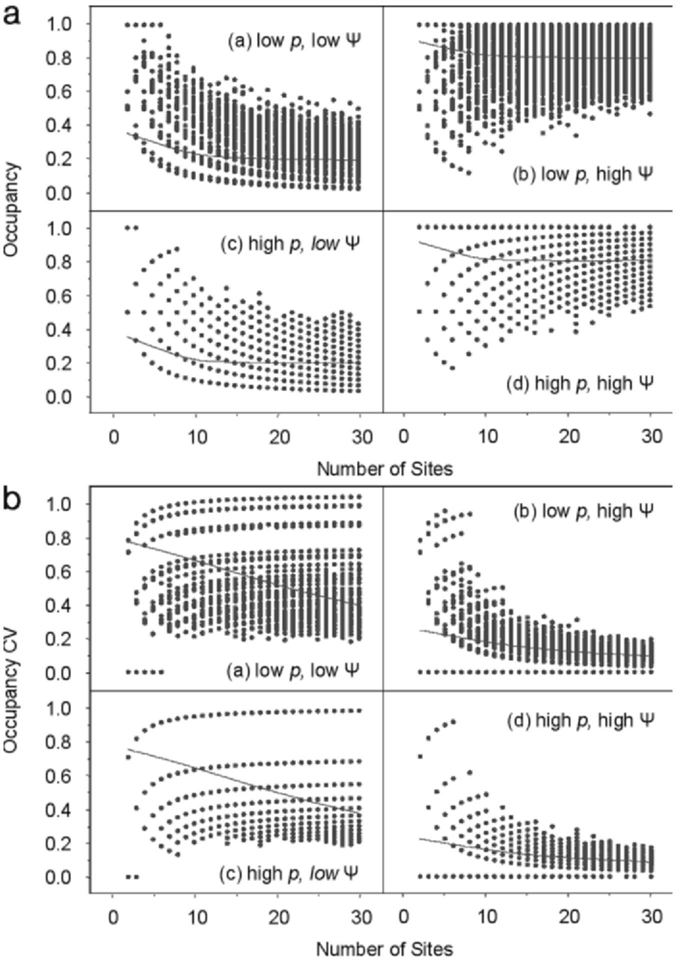

Fig. 2.—Estimated occupancy (top panel) and coefficient of variation (bottom panel) as a function of the number of sites sampled for each of 4 hypothetical combinations of detection probability (*p*) and occupancy (Ψ; i.e., low–low, low–high, high–low, and high–high shown in parts a–d). Smoothing splines qualitatively identify the direction of bias in parameter estimates.

in areas where occupancy is expected to be low, sampling more sites will likely improve precision.

DISCUSSION

The potential bias of unknown and variable detection probabilities is widely recognized as a problem for studies in which echolocation is used as a measure of bat occurrence and activity (Crampton and Barclay 1998; Duchamp et al. 2006; Hayes 2000; O'Shea et al. 2003; Patriquin and Barclay 2003; Yates and Muzika 2006). Correcting this bias in occurrence data should permit the standardization and direct comparison of detection-based indices among regions, habitats, or time periods.

We showed that bat detection probabilities can be generated by repeated sampling over a series of nightly visits. The method relies on automated echolocation recording to acquire encounter histories across a spatially extensive array of sites. Yates and Muzika (2006) also employed repeated sampling to assess bat occurrence; however, an important difference between the 2 approaches is that they used several time periods within a night from which to parse detections and estimate *p*, whereas we estimated this parameter based on observations over a series of nights. An advantage to their approach is that survey-specific models where *p* varies by time period (MacKenzie et al. 2006) allows Ψ to be estimated for a single night. Alternatively, estimates of *p* also may be derived in a single night using the double-observer approach employed by Duchamp et al. (2006) with paired detectors. These methods are advantageous when the cost of survey duration is a primary consideration or *p* is expected to change rapidly and must be calculated for a relatively brief time period. However, because bat activity at a site can be highly variable across nights (Hayes 2000), our method likely produces a more reliable estimate of *p* because it is based on a series of nightly encounter histories that averages out this source of variability (although the parameters may not be directly comparable because the sample periods differ among each of our methods). Despite the greater sampling duration needed to acquire an adequate encounter history, repeatedly sampling occurrence on a series of nights also has the advantage of requiring one-half as many detectors per site as the double-observer approach. Given the ease with which automated recordings of echolocation calls can be made, the trade-off between number of detectors (sites) and number of nights (visits) may favor repeated sampling over multiple nights.

Detection probabilities can be applied in a number of ways to correct for bias in occurrence data depending on whether the question of interest is specific to a site or a region. For example, estimates of p can be used to calculate false-negative error rates and the probability of absence given that a species was not detected (e.g., MacKenzie 2005; MacKenzie et al. 2006; Tyre et al. 2003). These parameters may be treated as distinct observations for each site or pooled to produce region-wide estimates (e.g., Wintle et al. 2005). The occupancy modeling described by MacKenzie et al. (2002) that we used is area-based and uses site samples to derive estimates of the proportion of locations at which a species occurs. Estimates of p and Ψ generated from the encounter histories of multiple sites probably provide a better approximation of actual occupancy than do single sites because variability due to microhabitat conditions is averaged.

We used the median number of pulses per 1-min period as a threshold to identify peak echolocation events indicative of high-use areas. Although the threshold we applied was arbitrary, the approach provides an example of how bat call data may be subsampled to obtain activity-specific estimates of p and Ψ. Moreover, thresholds can be adjusted to assess lesser or greater levels of activity. For example, if no threshold is used or a threshold is set relatively low, brief commuting passes and calls of bats searching for prey will be included with bouts of active feeding. This may be appropriate for investigations measuring any and all echolocation calls produced by bats. Higher thresholds can be used to infer periods of peak activity indicative of high-quality habitat. Alternatively, encounter histories may be generated based on a predetermined threshold for the number of consecutive minutes during which echolocation activity was recorded. A combination of methods may be used to identify periods of sustained high activity.

Conventionally, terminal-phase calls (i.e., feeding buzzes—Griffin et al. 1960) have been used to infer increased importance of a site relative to sites where only search-phase calls were recorded. We used an alternate measure of high activity for 2 reasons. First, in preliminary tests, we found that detectors with the reflector-type microphone assembly underestimated the number of feeding buzzes recorded when compared to paired detectors without reflector plates aimed upward. Second, the only practical means of handling the large number of calls generated by remotely deployed bat detectors is via automated recognition of echolocation pulses using filters. However, it is difficult for filters to distinguish between nonbat noise and the short, rapid series of pulses characteristic of feeding buzzes. As a result, many fragmentary feeding buzzes were discarded from the pool of automatically recognized echolocation pulses. Increased microphone sensitivity, improvements in the design of the automated detector assembly (e.g., upwardly aimed waterproof microphones that preclude use of reflector plates), and software tailored to distinguish terminal phase calls may eventually permit direct detection of foraging events and success of prey capture (e.g., Surlykke et al. 2003). Such developments would free researchers from merely conjecturing about levels of bat activity based on numbers of call files or pulses and allow direct inferences about habitat use and quality.

Tyre et al. (2003:1799) and MacKenzie (2005:850) discuss the interpretation of detection probability and occurrence in the context of movements of organisms and sample area. When the neighborhood of movement is small relative to sample area, p is the probability of detecting a species given that it is actually present within a surveyed landscape unit and Ψ is the proportion of the sampled sites that are occupied (i.e., occupancy). If the extent of movement is large compared to the sample area, parameter p will include a random component representing the probability that individuals were actually present in a landscape unit during the time at which it was surveyed. In this circumstance, Ψ is interpreted as use of the landscape unit. Given the extent of movement shown by the Hawaiian hoary bat (e.g., mean and maximum of the most distant locations within the home ranges of 18 radiotagged bats were 4.4 and 17.9 km, respectively; United States Geological Survey, in litt.), estimated Ψ describes the species' relative use of native forest habitat at each study area.

Our simulation exercise indicated that the likelihood of correctly estimating occupancy depends on applying a sample effort appropriate to the actual values of p and Ψ for a target population. For instance, the high bat occurrence observed in native forests during late fall on Hawai‘i indicates that we could have sampled using 8–10 detectors deployed for as few as 5 or 6 nights. However, because p and Ψ are usually unknown for a target population, it may often be necessary to oversample to ensure that variance is minimized where p or Ψ turns out to be low. In general, we found that, given similar levels of p and Ψ, estimates were more influenced by the number of sites sampled than the number of visits. In practice this means that when species occurrence is low, survey design should emphasize sampling a greater number of sites at the expense of repeat visits. This is consistent with MacKenzie and Royle (2005:1110), who concluded that the "optimal strategy for rare species is to conduct fewer surveys at more sites, while for common species . . . conduct more surveys at fewer sites." MacKenzie and Royle (2005) provide a table of analytically derived values for recommended survey effort at various levels of p and Ψ. However, although their estimation methods are asymptotically unbiased when model assumptions are met (e.g., appropriately denoting constant or survey-specific p), the design recommendations are based on large-sample solutions that may underestimate the parameter variance and bias encountered in small-sample situations. Our results complement theirs by demonstrating how the precision and bias of occupancy estimates varies in relation to the limited survey effort common to field studies.

We should note that sampling effort considerations related to the number of sites can be addressed by moving detectors to additional locations. In such cases, the model assumption that the occupancy state does not change during the sampling period (MacKenzie et al. 2006) needs to be evaluated based on known or expected patterns of distribution or behavior (e.g., migration). Where the number of sites surveyed is augmented by relocating detectors and the sampling period covers a long timescale, study designs may employ multiple-season occupancy models. Studies spanning shorter timescales may use covariates (e.g., week 1, week 2, etc.) to accommodate sampling at different periods within a season.

Our analysis of occurrence data collected with multiple automated echolocation detectors may be applicable to a variety of research objectives. This passive, noninvasive method could be used to compare the likelihood of detecting bats (e.g., Duchamp et al. 2006) or bat occupancy among habitats or regions (e.g., Yates and Muzika 2006). Local and regional measures of occupancy also could be compiled to provide a large-scale picture of bat distribution across seasons. Furthermore, the subsetting of occurrence data to identify peak activity levels could be used to track occupancy as a function of the time of night. Such information may aid in improving management practices that avoid or minimize adverse impacts to bats (e.g., timing wind-turbine operations to reduce bat mortality).

Occupancy analysis has another important application related to the delisting of the Hawaiian hoary bat as an endangered species. Because of the difficulty of assessing the status of bat populations, particularly those consisting of solitary individuals occurring at low densities, a key recovery objective—the development and implementation of a survey and monitoring program for the Hawaiian hoary bat (United States Fish and Wildlife Service 1998)—remains unmet. The methods described in this study could potentially be used to provide the quantitative measures necessary for monitoring population trends in this and other species for which calls can be unambiguously identified.

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