Journal of Field Ornithology

J. Field Ornithol. 80(1):64–78, 2009 DOI: 10.1111/j.1557-9263.2009.00206.x

Using soundscape recordings to estimate bird species abundance, richness, and composition

Antonio Celis-Murillo,[1,2] Jill L. Deppe,[2] and Michael F. Allen

Center for Conservation Biology, University of California, Riverside, California 92521, USA

Received 22 August 2008; accepted 3 November 2008

ABSTRACT. Point counts are the most frequently used technique for sampling bird populations and communities, but have well-known limitations such as inter- and intraobserver errors and limited availability of expert field observers. The use of acoustic recordings to survey birds offers solutions to these limitations. We designed a Soundscape Recording System (SRS) that combines a four-channel, discrete microphone system with a quadraphonic playback system for surveying bird communities. We compared the effectiveness of SRS and point counts for estimating species abundance, richness, and composition of riparian breeding birds in California by comparing data collected simultaneously using both methods. We used the temporal-removal method to estimate individual bird detection probabilities and species abundances using the program MARK. Akaike's Information Criterion provided strong evidence that detection probabilities differed between the two survey methods and among the 10 most common species. The probability of detecting birds was higher when listening to SRS recordings in the laboratory than during the field survey. Additionally, SRS data demonstrated a better fit to the temporal-removal model assumptions and yielded more reliable estimates of detection probability and abundance than point-count data. Our results demonstrate how the perceptual constraints of observers can affect temporal detection patterns during point counts and thus influence abundance estimates derived from time-of-detection approaches. We used a closed-population capture–recapture approach to calculate jackknife estimates of species richness and average species detection probabilities for SRS and point counts using the program CAPTURE. SRS and point counts had similar species richness and detection probabilities. However, the methods differed in the composition of species detected based on Jaccard's similarity index. Most individuals (83%) detected during point counts vocalized at least once during the survey period and were available for detection using a purely acoustic technique, such as SRS. SRS provides an effective method for surveying bird communities, particularly when most species are detected by sound. SRS can eliminate or minimize observer biases, produce permanent records of surveys, and resolve problems associated with the limited availability of expert field observers.

RESUMEN. **Uso de grabaciones de paisaje sonoro para estimar abundancia, riqueza y composición de especies de aves**
Los conteos por punto son la técnica más utilizada para muestrear poblaciones y comunidades de aves, pero tienen limitaciones tales como los errores intra- e inter-observador y la escasa disponibilidad de observadores expertos. Una solución a estas limitaciones es el uso de grabaciones en el campo para censar aves. Diseñamos un sistema de grabación de paisajes sonoros, SRS (por sus siglas en inglés), que combina un sistema de grabación de cuatro canales discretos con un sistema de reproducción cuadrafónica para el censado de comunidades de aves. Comparamos la efectividad del SRS y la de los conteos por punto para estimar la abundancia, riqueza y composición de comunidades de aves en hábitats riparios en California, comparando los datos colectados simultáneamente con ambas técnicas. Utilizamos el método de remoción-temporal para estimar la probabilidad de detección de individuos y abundancia de especies utilizando el programa MARK. El Criterio de Información Akaike proveyó evidencia sustancial de que existen diferencias en la probabilidad de detección entre ambos métodos y entre las 10 especies más comunes de aves. La probabilidad de detección de aves resultó mayor cuando se escucharon las grabaciones del SRS en el laboratorio que durante los conteos por punto en el campo. Además, los datos tomados con la técnica SRS demostraron estar mejor adaptados a los supuestos del modelo de remoción-temporal y ofrecieron estimados más confiables de abundancia y de probabilidad de detección que los datos de conteos por puntos. Nuestros resultados demuestran cómo la percepción de los observadores puede afectar los patrones de detección temporal durante los conteos por punto, influyendo en las estimaciones de abundancia derivadas de procedimientos de tiempo de detección. Utilizamos el método de captura-recaptura de población cerrada para calcular las estimaciones de jackknife de riqueza de especies y la probabilidad de detección de especies para SRS y conteos por punto, utilizando el programa CAPTURE. Ambos tuvieron índices de riqueza de especies y probabilidades de detección similares. Sin embargo, los métodos difirieron en la composición de especies detectadas basados en el índice de similitud de Jaccard. La mayoría de los individuos

[1]Corresponding author. Email: celismu1@illinois.edu

[2]Current address: Illinois Natural History Survey, University of Illinois at Urbana-Champaign, 1816 South Oak Street, Champaign, IL 61820

detectados durante los conteos por punto (83%) vocalizaron al menos una vez durante el periodo de censado, y estuvieron disponibles para ser detectados utilizando una técnica acústica, como SRS. La técnica SRS provee un método efectivo para censar comunidades de aves, particularmente cuando la mayoría de las especies son detectadas por sus sonidos. El SRS puede eliminar o minimizar los sesgos del observador, producir registros permanentes de los censos, y resolver problemas asociados a la limitada disponibilidad de expertos en el campo.

Key words: abundance estimation, acoustic recordings, detection probability, sampling techniques, soundscape, species richness, temporal removal method

Point counts are the most frequently used technique for estimating avian species abundance, richness, and composition (Ralph et al. 1995, Rosenstock et al. 2002, Simons et al. 2007). Point counts allow researchers to survey broad areas and many locations in a relatively economical manner. However, larger sample sizes require more observers, and the availability of highly skilled observers, particularly during the breeding season, is often limited (Hobson et al. 2002). In addition, data quality may be compromised by observer biases. Differences in the ability of observers to detect, identify, and record birds due to variation in visual and auditory acuity, training, and experience manifest themselves as interobserver differences (Cyr 1981, Kepler and Scott 1981, Bart 1985, Emlen and DeJong 1992, Alldredge et al. 2007c). Intraobserver biases arise from variation in the ability of different individuals to detect and identify birds over time due to learning or changes in their physical and emotional state (Sauer et al. 1994, Kendall et al. 1996, McLaren and Cadman 1999).

Technological advances have provided new tools for monitoring natural systems. One approach is the use of audio recordings to survey bird communities (Haselmayer and Quinn 2000, Hobson et al. 2002, Rempel et al. 2005, Scott et al. 2005). Acoustic recordings can minimize observer errors by using a single interpreter, allowing recordings to be replayed, and permitting the cross-validation of detections and identifications by having multiple observers listen to each recording. In addition, recordings provide a potentially permanent record of surveys and resolve logistical problems often encountered in field studies, such as the limited availability of expert observers. Hobson et al. (2002) provide a detailed description of the advantages of using audio recordings rather than trained field observers during point counts.

Although the use of acoustic recordings for surveying birds has gained popularity, few investigators have empirically tested the effectiveness of acoustic recording systems (Haselmayer and Quinn 2000, Hobson et al. 2002). Haselmayer and Quinn (2000) demonstrated that a monodirectional acoustic recording system performed better than point counts at estimating species richness in areas with a high number of bird species. Hobson et al. (2002) tested two commercial recording systems, the CVX-360 omnidirectional system and the CZM-180 stereo system (formerly CVX-180, River Forks Research Corporation; Rempel et al. 2005), by comparing data collected by field observers during point counts and interpreters listening to recordings in the laboratory. Both systems performed well at detecting the presence or absence of species, and the stereo-recording system generated abundance estimates similar to those of field counts for most bird species. These studies show great promise for acoustic recording survey methods, but further evaluation of different types of recording systems or configurations in different ecosystems and seasons is needed.

In this paper, we describe a Soundscape Recording System (SRS) that combines a discrete four-channel microphone/recording unit with a quadraphonic playback system. SRS is a generic recording system with a specific microphone and playback configuration and, if effective, could provide researchers with a flexible, multifunctional alternative to commercial systems.

We tested the effectiveness of our SRS for estimating species abundance, richness, and composition relative to a trained observer conducting point counts in the field. We compared data collected simultaneously using both methods in riparian corridors in southern California. Our objectives were to determine: (1) if individual bird detection probabilities differed between the two survey methods and among species, (2) if SRS and point counts perform equally well at estimating species richness, (3) similarities in species composition between the two methods, and (4) the percentage of individual birds detected during point-count observations that vocalize at least once during the survey period and can be detected by acoustic surveys.

METHODS

Technological description of SRS. SRS, designed by A. Celis-Murillo, consists of a four-microphone/four-channel discrete recording system combined with a quadraphonic playback system. Four Sennheiser ME62/K6 omnidirectional microphones were mounted on a specially designed tripod support (Fig. 1). We selected Sennheiser microphones because of their frequency response, sensitivity, durability, reliability, low self-noise, and high consistency in quality among microphones. Microphones were positioned 1.0 m above the ground and at 90° angles to each other to capture sounds in all directions (360°), and each microphone was positioned at a 30° angle relative to the horizontal plane. Four plastic dividers separated the microphones, creating four directional microphones. Sounds captured by each microphone were recorded to discrete channels. We used two Sony DAT TCD-D8 recorders, each with the capacity to record two channels, and used Logic Pro 6 (Emagic 2004) to synchronize the two recordings (i.e., 4 channels) and produce a single digital file for each survey. In a subsequent study, the two Sony DAT recorders were replaced by an Edirol 4-channel recorder (Roland Corporation, Los Angeles, California; A. Celis-Murillo, unpubl. data). In the lab, we transferred the recordings from the DAT recorders to a PowerBook G4 1.5 MHz Macintosh Computer using an external USB-Edirol UA5 drive (Roland Corporation). We digitized recordings using Logic Pro 6 software and saved sound files in WAV format at 44.1 KHz and 16 bit resolution.

Fig. 1. Photograph of SRS four-microphone recording system.

Recordings were played back in a quadraphonic playback room. Four loudspeakers with the capacity to reproduce sounds between 20 Hz and 20 kHz were placed in the four corners of a square room and connected to a M-Audio Firewire 410 multichannel playback interface (Avid Technology Inc., Tewksbury, Massachusetts) connected to the PowerBook. We selected this frequency range because it encompasses essentially the full range of bird vocalization frequencies. We conducted playback sessions using Logic Pro 6. A single interpreter (ACM) listened to all recordings to eliminate interobserver bias. The interpreter (i.e., listener) sat in a swivel chair at the center of the room and was able to rotate while listening to recordings to better judge and map the relative location of each bird vocalization.

The use of four microphones and four discrete channels to record the soundscape coupled with a four-loudspeaker playback system creates a three-dimensional, high-resolution "image" of the original 360° soundscape. This combination of recording and playback configurations provides a listener with both the interaural intensity (IID) and interaural time difference (ITD) cues needed to localize sound sources and allows a listener to distinguish between two or more individuals vocalizing simultaneously, making it possible to accurately estimate species abundance, composition, and richness. By rotating in the SRS playback room, the interpreter can determine the relative direction of a bird anywhere in the 360° reproduced soundscape using IID and ITD localization cues. Thus, the interpreter in the lab has the same acoustic signals as an observer in the field.

Study site. We used SRS (purely auditory survey) and point counts (audiovisual survey) to sample breeding bird communities along 15 riparian corridors in western Riverside County, California (Allen et al. 2005). The vegetation was classified as Cottonwood-Willow Riparian Forest and Southern Willow Scrub, and riparian corridors were generally bordered by Coastal Sage Scrub and exotic grasslands (see Allen et al. [2005] for a description of vegetation types and study area).

Point counts and SRS recordings in the field. From 1 April to 31 July 2004, a single observer (ACM) conducted 314 point counts in the Western Riverside County Multispecies Habitat Conservation Plan area (Allen et al. 2005). At 42 survey locations, birds were simultaneously surveyed using SRS and unlimited-radius point counts. Prior to initiating the point count, the observer placed the SRS recording system at the point with a specified microphone always directed toward magnetic north. For each survey, the observer recorded the UTM coordinates, site name, location number, date, time, and meteorological data (wind direction and velocity, temperature, and humidity). The point count and recording were initiated and terminated at the same time, and both lasted 10 min.

We followed the point count method of Ralph et al. (1993, 1995) with some modifications (Allen et al. 2005). In the field, the observer mapped each bird's location (distance and direction from the point center) on a bulls-eye type data sheet. For each bird detected, the observer recorded (1) the approximate or exact distance to the bird using a laser rangefinder, (2) the time of first detection (min and s ranging from 0:00 to 10:00), and (3) how the bird was first detected (sight, song, or call). Birds initially detected by sight were followed during the survey period to determine if they subsequently vocalized. If a bird did not vocalize during the survey, it was marked as sight only. This information was used to estimate the proportion of birds detected during a point count that did not vocalize and, therefore, would go undetected using an auditory survey technique such as SRS.

Interpretation of recordings in the laboratory. Each soundscape recording was digitized and labeled with the site name, location number, and date. To avoid confounding observer and survey method by having different persons perform the point counts in the field and the interpretations of SRS recordings in the lab (Hobson et al. 2002), a single observer (ACM) conducted the point counts and interpreted the recordings. However, we wanted data collected from recordings to be independent of data collected during point counts. Therefore, we created a set of recordings that eliminated all identifying information associated with the location and timing of the survey. A second person (JLD) copied the master set of recordings and removed all identifying information (e.g., site name, location number, date, and time). Additionally, recordings were not interpreted until winter 2005, with the lapse of time minimizing the likelihood of confounding experience and survey method. The large number of point counts performed by the observer/interpreter during the 2004 field season (300+) further reduced the likelihood of recalling a particular survey.

For interpretation of recordings in the playback room, the interpreter sat in a swivel chair in the center of the room, listened to the 10-min recordings, and mapped birds onto a bull's-eye data sheet noting the exact time individuals were first detected, just as was done in the field. Each recording was listened to once and, in some cases, a recording or parts of it were replayed to check the abundance estimate or to confirm the identification of a species. When a call or song was difficult to identify, the observer viewed the spectrogram using either Raven 1.2.1 (Cornell Laboratory of Ornithology 2003) or Audacity 1.2.4 (Audacity 2005), compared it to a reference collection and, if necessary, verified its identification with regional experts. Up to 30 min were required to interpret some 10-min recordings in the laboratory, including playback time, but most recordings were interpreted in less time. We allowed the interpreter to relisten to recordings, evaluate spectrograms, compare vocalizations to reference collections, and cross-validate identifications to perform a complete evaluation of SRS, including its potential advantages relative to point counts. In addition, we also included both aural and visual detections made during point counts because visual detection represents the main advantage of field surveys over recordings, and are included in most analyses of count data.

Species abundance. To evaluate the ability of SRS to detect birds and estimate abundance relative to point counts, we estimated detection probabilities for the 10 most common bird species for the two survey methods using the temporal-removal model approach (Farnsworth et al. 2002). The 10 most common species were the most abundant based on raw field counts. We divided each of our 10-min SRS and point-count surveys into four 2.5-min intervals and calculated the total number of individuals of each species counted during each of the four intervals. Data from point-count surveys included aural and visual detections. We used program MARK (White and Burnham 1999) to fit our data to four models: (1) Model M_{sm} estimated separate detection probabilities, $\hat{p}$, for the two survey methods and the 10 species, (2) Model M_m estimated a separate $\hat{p}$ for each survey method, (3) Model M_s estimated a separate $\hat{p}$ for each species, and (4) Model M did not distinguish among species or methods and fit a single estimate of $\hat{p}$ to the data. We used Akaike's Information Criterion (AIC, Burnham and Anderson 2002) to select the most parsimonious model for our data by evaluating ΔAIC values and model weights. We evaluated the effectiveness of SRS relative to point counts by comparing estimated detection probabilities based on this model.

The temporal-removal method is based on the notion that the population of birds within the detection radius during the survey is closed, so that as birds are detected they are "removed" from the population and fewer individuals are left to be initially detected during subsequent time intervals. This phenomenon is apparent in the data as a decline in the number of initial detections over time during the survey. To determine how well SRS and point-count data satisfied this assumption, we examined the number of detections during each of the four time intervals for the 10 common species.

We did not calibrate SRS to detect birds out to a distance comparable to the effective hearing distance of a human observer, a challenging exercise because detection distances vary among species, among human observers, and with environmental conditions. To assess potential differences in the detection radius and sampling area between SRS and point-count surveys, we calculated the ratio of abundance estimates from SRS recordings and point counts ($\frac{\hat{N}_{SRS}}{\hat{N}_{field}}$). We used the abundance estimates ($\hat{N}$) from MARK for each species for the two survey techniques based on the most parsimonious model, where $\hat{N} = \frac{x.}{\hat{p}}$, $\hat{p}$ is the probability of detecting an individual at least once during the 10-min count, and $x.$ is the total number of birds counted (i.e., the raw count; Farnsworth et al. 2002). Although detection probabilities may differ between the two survey methods, the temporal-removal model should yield comparable estimates of abundance, provided the area sampled is similar (J. D. Nichols, pers. comm.). If population estimates derived from SRS are much larger than those derived from point counts, it suggests that SRS is sampling birds over a larger area. If so, the ratio will be larger than 1.0 and will provide an approximation of how much larger of an area is sampled by SRS than point counts. On the other hand, if estimates derived from SRS are smaller (i.e., ratio <1.0), this indicates that point counts sampled a larger area. To evaluate the significance of deviations from 1.0, we calculated approximate 95% confidence intervals for the ratios; if the CI for the estimate included 1, we concluded that both survey methods likely sampled equal areas. Confidence intervals were calculated using values for $\hat{N}$ and SE from MARK, and variance of the ratio was approximated according to the following equation (e.g., Mood et al. 1974):

$$\mathrm{Var}\left(\frac{\hat{N}_{SRS}}{\hat{N}_{field}}\right) \approx \left(\frac{\hat{N}_{SRS}}{\hat{N}_{field}}\right)^2 \left\{\frac{\mathrm{var}\left(\hat{N}_{SRS}\right)}{\hat{N}^2_{SRS}} + \frac{\mathrm{var}\left(\hat{N}_{field}\right)}{\hat{N}^2_{field}}\right\}. \quad (1)$$

We also performed a test for each species by calculating its z-score (z_i) using the following equation:

$$z_i = \left\{\frac{\left(\hat{N}_{SRS} - \hat{N}_{field}\right)}{\sqrt{\left[\mathrm{var}\left(\hat{N}_{SRS}\right) + \mathrm{var}\left(\hat{N}_{field}\right)\right]}}\right\}. \quad (2)$$

This statistic is normally distributed (0, 1) under the null hypothesis of no difference between abundance estimates of the two survey techniques. For an overall approximate test, we summed the z-scores over the species and divided by the square root of the number of species (Nichols and Hines 1987); this statistic is also normal (0, 1) under the overall null hypothesis of no difference between areas sampled by the two methods across all species.

Species richness. Survey methods do not detect all individuals during a sampling period and may also fail to detect all species present in the area at the time of the survey. To compare the ability of SRS and point counts to estimate species richness, we used a closed-population capture–recapture approach to estimate species richness and the probability of detecting an average species for the two survey techniques (Boulinier et al. 1998, Nichols et al. 1998). We used the program CAPTURE (Rexstad and Burnham 1991) to estimate species richness for SRS and point counts. We used a jackknife estimator (Burnham and Overton 1979) and computed interpolated estimates of species richness, SE, and 95% confidence intervals. We expected detection probabilities to vary among species, so we used a model that incorporated heterogeneity in species' detection probabilities (Boulinier et al. 1998). CAPTURE uses information on the frequencies, f_h, or numbers of species detected on exactly $h = 1, 2, \ldots,$ K sample locations to estimate species richness. We estimated the average species detection probability, $\hat{p}_s$, for each survey method for the entire 10-min point count as the number of species detected divided by estimated richness (equation 2, Nichols et al. 1998), where average species detection probability is the probability that at least one individual of an "average" species is detected on at least one of our 42 sampling locations. We compared $\hat{p}_s$ between SRS and point counts with and without visually detected birds. To determine if the detection probability of an "average species" was equal between SRS and point counts, we performed a 2 X K contingency table test using the raw frequency data, f_h, to test the null hypothesis that the proportions of species found on $h = 1, 2, \ldots, K$ sampling locations were similar for the two survey methods (Nichols et al. 1998).

Throughout the results, we use $\hat{p}$ to denote the probability of detecting an individual bird at least once during a 10-min period; this detection probability for individual birds was used to estimate species abundance. We use $\hat{p}_s$ to refer to the probability of detecting at least one individual of an "average" species during a survey. This species-level detection probability was used to estimate species richness.

Species composition. We used Jaccard's similarity index, based on species detection/nondetection data, to determine if the two survey methods detected the same species, that is, similar species composition (Magurran 1988). For each survey location, we calculated Jaccard's index using point-count data with and without visual detections. To test the hypothesis that the absence of visual cues during purely acoustic (SRS) surveys contributes to differences between the two survey methods, we used a General Linear Model to compare mean similarity between SRS and point-count surveys with and without visually detected birds. Values presented in the text are mean values for Jaccard's index ± SE. GLMs were performed using SPSS (Version 11.0.1, SPSS 2002).

RESULTS

Individual detection probabilities and bird abundance estimates. Model M_{sm} was the most appropriate model fit to our data based on ΔAIC values and AIC model weights (Table 1). There was strong evidence that detection probabilities differed between the two survey methods and among the 10 most common species (Fig. 2). There was substantially less support for model M_m and essentially no support

Table 1. Akaike's Information Criterion (AIC) values for four removal models evaluating differences in detection probability ($\hat{p}$) between the two survey methods (SRS and point counts) and among the 10 most common bird species at our site.

Model[a]	Number of parameters	ΔAIC_c	AIC_c model weight
M_{sm}	20	0.00	0.96
M_m	2	6.28	0.04
M_s	10	89.56	0.00
M	1	107.84	0.00

[a] Model M_{sm} estimated separate detection probabilities for the two survey methods and the 10 species, M_m estimated a separate $\hat{p}$ for each survey method, M_s fit a different $\hat{p}$ for each species, and M did not distinguish among species or methods and fit a single estimate of $\hat{p}$.

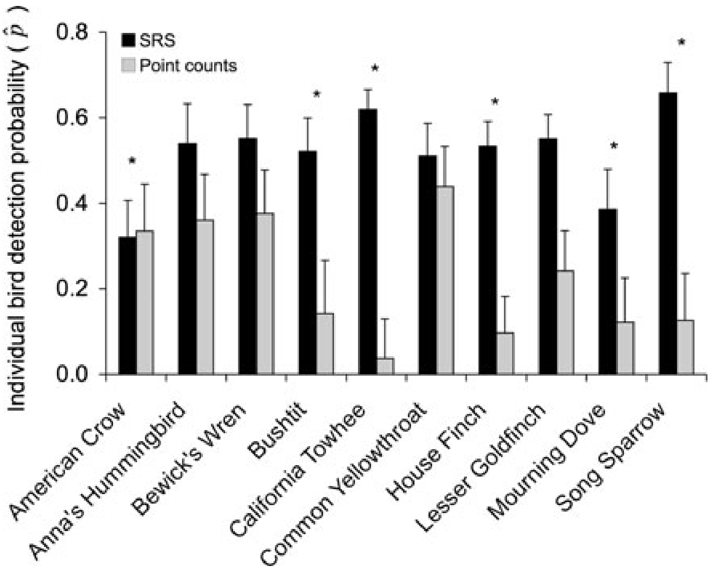

Fig. 2. Estimated individual bird detection probabilities ($\hat{p}$) $\pm$ SE for the 10 most common bird species during 10-min SRS and point-count surveys. Detection probabilities for six species calculated from point-count data (marked with an *) are not reliable because data violate the assumption of the temporal-removal approach that the number of initial detections declines over time during the survey period (see Fig. 3). Scientific names are provided in Table 3.

for models M_s and M (Burnham and Anderson 2002). All species for which we could calculate reliable detection probabilities had higher $\hat{p}$ values using SRS surveys than point counts (Fig. 2).

Point-count data for six species (American Crow, *Corvus brachyrhynchos*; Bushtit, *Psaltriparus minimus*; California Towhee, *Pipilo crissalis*; House Finch, *Carpodacus mexicanus*; Mourning Dove, *Zenaida macroura*; and Song Sparrow, *Melospiza melodia*) were illconditioned and did not satisfy the assumption of the removal model that the frequency of initial detections declines over time during the survey period (Fig. 3). Consequently, detection probabilities and derived estimates of abundance for these species based on point-count data were not reliable. In contrast, SRS data for all 10 species were well conditioned as the number of initial detections decreased over successive intervals, satisfying the assumption of the removal model (Fig. 3).

We compared the areas sampled by SRS and point counts for the four species where data from both survey methods satisfied the assumption of the removal model and where we were able to calculate reliable detection probabilities and abundance estimates. The two survey methods sampled similar areas for Bewick's Wrens (*Thryomanes bewickii*) and Lesser Goldfinches (*Carduelis psaltria*), as indicated by their ratio of abundance estimates approximately equal to 1.0 and *z*-scores close to 0 (Table 2). For Anna's Hummingbirds (*Calypte anna*), SRS sampled an area estimated to be 21% smaller than point counts. Thus, for these three species, the higher detection probability using SRS (Fig. 2) was not due to a larger sample area. On the other hand, for Common Yellowthroats (*Geothlypis trichas*), SRS appeared to sample an area 27% larger than that sampled by point counts, so the species' greater detection probability using SRS may be due to the larger area surveyed. The 95% confidence interval for this species did not contain 1.0 and the *z*-score was more than two standard deviations away from the mean (0), indicating that the areas sampled by the two methods were different (Table 2). The overall *z*-score for this group of four species was 0.62, suggesting no difference in the areas sampled by SRS and point counts. Finally, we note that possible differences in areas sampled by the two

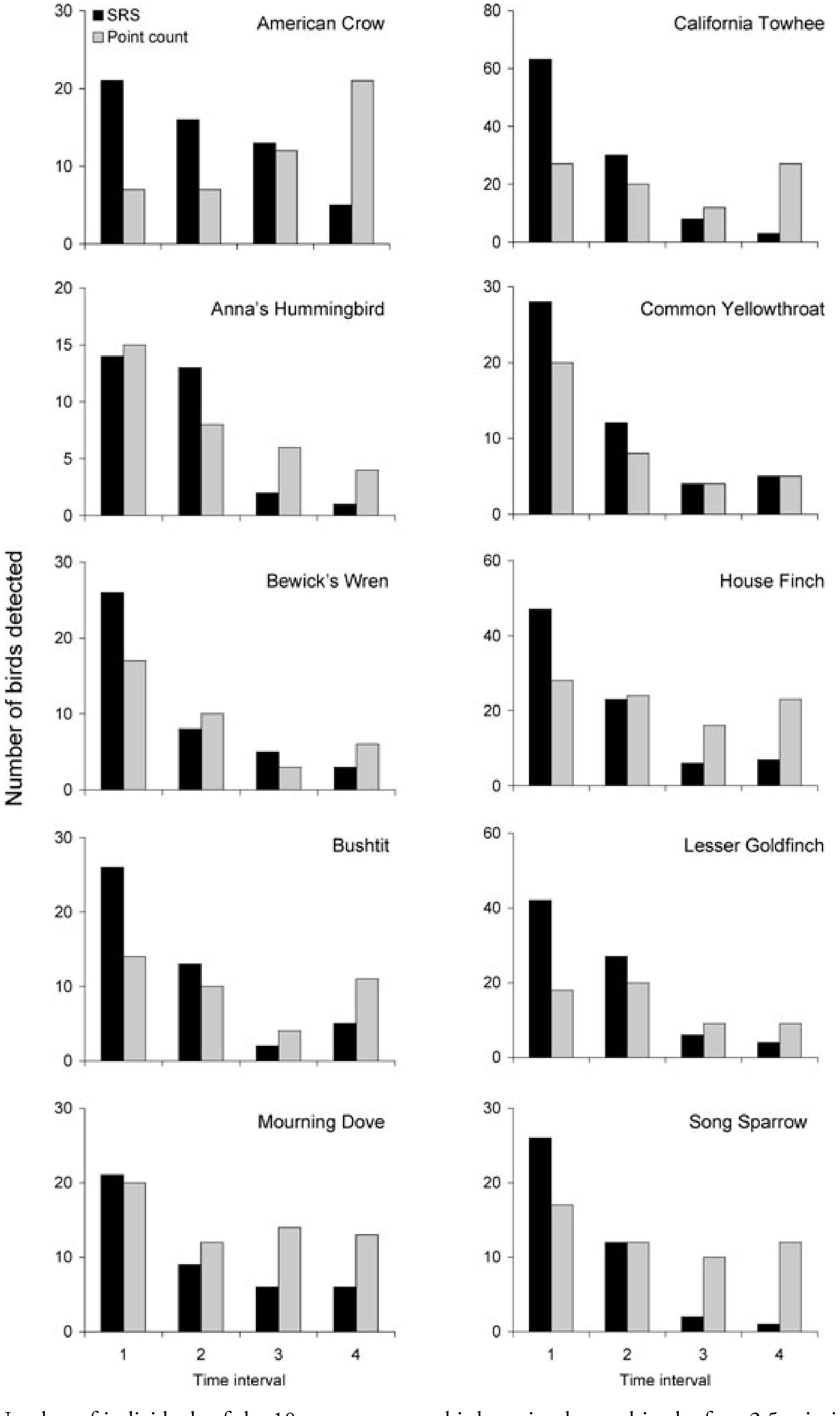

Fig. 3. Number of individuals of the 10 most common bird species detected in the four 2.5-min intervals during SRS and point-count surveys. Scientific names are provided in Table 3.

Table 2. Ratio of abundance estimates for the SRS and point counts (field surveys) to evaluate differences in the area sampled by the two survey methods.

Species[a]	$(\frac{\hat{N}_{SRS}}{\hat{N}_{field}})$	Lower 95% CI[c]	Upper 95% CI[c]	z-score[d]
Anna's Hummingbird	0.79	0.54	1.05	−1.30
Bewick's Wren	1.03	0.75	1.31	0.22
Common Yellowthroat	1.27	1.01	1.52	2.39
Lesser Goldfinch	0.99	0.49	1.48	−0.06

[a]Only species with data from both survey methods that satisfied the assumption of the removal model (i.e., a decline in the number of detections over time throughout the survey) and for which we were able to calculate reliable detection probabilities and abundance estimates are considered. Scientific names are provided in Table 3.

[b]Values for $\hat{N}_{SRS}$ and $\hat{N}_{field}$ were calculated by program MARK.

[c]95% Confidence intervals (CI) were calculated using equation (1) for the approximate variance of $(\frac{\hat{N}_{SRS}}{\hat{N}_{field}})$ (see Species abundance section in the Methods section).

[d]z-scores for each species were calculated using equation (2) (see Species abundance section in the Methods section).

methods should not necessarily lead to different detection probabilities.

"Average" species detection probabilities and species richness estimates. The "average" species detection probability, $\hat{p}_s$, tended to be higher for SRS than point counts regardless of whether visually detected birds were included. Estimated richness over the 42 survey points was 72.7 ± 5.5 for SRS, 73.0 ± 5.2 for point counts with aural and visual detections, and 69.7 ± 5.0 for point counts with aural detections only. The results of our Contingency table test for similar distribution of detection frequencies provided little evidence of a difference in detection probabilities between the two survey methods (SRS vs. point counts with auditory and visual detections: $\chi^2_{26} = 27.50$, $P = 0.30$; SRS vs. point counts with auditory detections only: $\chi^2_{26} = 32.67$, $P = 0.17$). Raw counts of species richness over the 42 points were 64 for SRS, 64 for point counts with aural and visual detections, and 62 for point counts with aural detections only.

Similarity in species composition between SRS and point counts. Jaccard's index ranges from 0.0 to 1.0, with an index of 1.0 indicating 100% similarity in species composition detected by the two survey methods. Mean Jaccard's index for the 42 sample locations was 0.59 ± 0.11 and 0.60 ± 0.13 with and without visual point-count detections, respectively, indicating that, of all the species detected by one or both methods, only 59–60% of species were detected by both SRS and point counts. The inclusion/omission of birds detected visually during point-count surveys had little effect on the pattern of similarity in species composition between SRS and point counts ($F_{1,82} = 0.2$, $P = 0.64$). Rather, the modest overlap appeared to be due to differences in the identification of species in the field and laboratory.

Proportion of vocalizing individuals during point counts. Data collected during point-count surveys revealed that 83% ± 3% of all individuals detected during the 10-min survey period vocalized at least once. Species varied in the percent of individuals that vocalized, but, for 29 of 38 species detected at 10% or more of the 42 sampling locations, over 70% of the individuals vocalized at least once during the survey period, suggesting that a purely auditory survey technique would detect most individuals of these species (Table 3, last column). Eight species of conservation concern were all detected at as many or more sampling locations using SRS than point counts.

DISCUSSION

The value of raw survey data for estimating avian abundance, richness, and composition depends on detection of a bird given it is present at the sampling location during the survey period (Farnsworth et al. 2002, Simons et al. 2007), accurate identification, and proper documentation (Robbins and Stallcup 1981,

Table 3. Frequency of species' detections at 42 locations surveyed using the SRS and point counts (10-min field surveys) and the percent of individuals of each species that vocalized at least once during 10-min point counts.

Species common name[a]	Scientific name	Number of survey locations where species was detected: SRS	Number of survey locations where species was detected: Point counts[b]	Percentage of individuals that vocalizing during point counts (Total number of individuals detected)[c]
California Quail	*Callipepla californica*	15	11	100 (20)
White-tailed Kite*	*Elanus leucurus*	5	1	50 (2)
Red-shouldered Hawk	*Buteo lineatus*	8	3	67 (3)
Red-tailed Hawk	*Buteo jamaicensis*	6	5	80 (5)
American Kestrel	*Falco sparverius*	5	4	100 (4)
Mourning Dove	*Zenaida macroura*	23	24	63 (60)
Common-ground Dove	*Columbina passerina*	4	5	86 (7)
Long-eared Owl*	*Asio otus*	1	0	–
Anna's Hummingbird	*Calypte anna*	24	21	64 (33)
Nuttall's Woodpecker	*Picoides nutallii*	27	18	100 (23)
Downy Woodpecker	*Picoides pubescens*	7	6	100 (9)
Black Phoebe	*Sayornis nigricans*	7	7	88 (8)
Willow Flycatcher*	*Empidonax traillii*	2	0	–
Ash-throated Flycatcher	*Myiarchus cinerascens*	17	11	95 (19)
Western Kingbird	*Tyrannus verticalis*	5	2	75 (4)
Least Bell's Vireo*	*Vireo bellii*	12	9	100 (15)
Western-scrub Jay	*Aphelocoma californica*	9	6	86 (7)
American Crow	*Corvus brachyrhynchos*	22	18	83 (46)
Common Raven	*Corvus corax*	6	6	71 (7)
Northern Rough-winged Swallow	*Stelgidopteryx serripennis*	14	10	64 (25)
Cliff Swallow	*Petrochelidon pyrrhonota*	3	6	23 (13)
Barn Swallow	*Hirundo rustica*	1	5	43 (23)
Oak Titmouse	*Baeolophus inornatus*	9	3	100 (5)
Bushtit	*Psaltriparus minimus*	17	12	69 (39)
Bewick's Wren	*Thryomanes bewickii*	28	22	100 (36)
House Wren	*Troglodytes aedon*	6	2	100 (3)
California Gnatcatcher*	*Polioptila californica*	2	2	100 (2)
Wrentit	*Chamaea fasciata*	12	12	100 (14)
European Starling	*Sturnus vulgaris*	6	6	75 (8)
Yellow Warbler*	*Dendroica petechia*	12	10	100 (17)
Common Yellowthroat	*Geothlypis trichas*	18	15	95 (37)
Yellow-breasted Chat*	*Icteria virens*	9	7	93 (15)
Spotted Towhee	*Pipilo maculatus*	21	20	97 (30)
California Towhee	*Pipilo crissalis*	38	32	74 (87)
Rufous-crowned Sparrow*	*Aimophila ruficeps*	6	6	100 (10)
Song Sparrow	*Melospiza melodia*	25	25	87 (52)
Blue Grosbeak	*Passerina caerulea*	12	12	84 (19)
Brown-headed Cowbird	*Molothrus ater*	8	7	53 (17)
House Finch	*Carpodacus mexicanus*	27	24	81 (78)
Lesser Goldfinch	*Carduelis psaltria*	28	18	94 (53)
American Goldfinch	*Carduelis tristis*	13	12	82 (28)

[a]Only species detected at 10% or more of the survey locations based on the Soundscape Recording System or point-count data are listed in the table as well as eight species of conservation concern for western Riverside County (denoted by *), including California Gnatcatcher and Rufous-crowned Sparrow that were detected from surrounding scrub habitat. Species are listed in taxonomic order.

[b]Includes auditory and visual detections.

[c]Percentage of birds that vocalized during point-count surveys, including individuals that were initially observed visually but subsequently vocalized during the 10-min survey period; – indicates that species was not detected during point-count surveys.

Bart and Schoultz 1984, Bart 1985). Nondetection, although pervasive, can be dealt with by using one of a variety of possible estimation methods (Nichols et al. 2000, Buckland et al. 2001, Farnsworth et al. 2002, Alldredge et al. 2006, 2007a). Misidentification and improper documentation of birds are more problematic because they cannot be corrected without ancillary data and, therefore, result in biased estimates of abundance, richness, and composition. The use of recordings enhances our ability to detect, identify, and properly document birds because recordings may be replayed or listened to by multiple interpreters, vocalizations can be cross-validated with published recordings or other experts, and sonograms can be viewed.

The advantages of using acoustic recordings in our study included higher detection probabilities of individual birds and earlier detection. An assumption of the closed-population temporal removal model is that the frequency of initial detections declines over time during the survey. In point-count data for six of the 10 common species, the frequency of initial detections did not decline through the survey, suggesting a possible violation of the closed-population assumption (Farnsworth et al. 2002). However, SRS data for those same species showed a decrease in the number of initial detections during the survey period, indicating that the patterns observed in our point-count data likely were not due to a violation of the closed-population assumption, but rather a bias in the timing of initial detections once individuals vocalized and could be detected (Alldredge et al. 2007a, b).

Differences in temporal detection patterns between SRS and point counts and the poor fit of point-count data to the assumption that initial detections decline over time during the survey could also be due to the inclusion of visually detected individuals during field surveys. In the field, an observer may spend more time searching visually later in the survey once most of the aural detections have been accounted for. To assess this, we examined temporal patterns using aural detections only. Two species, Bushtits and Song Sparrows, demonstrated an improved fit to the assumption of the temporal removal model when visual detections were removed, whereas Mourning Doves showed a poorer fit to the model assumption. The remaining seven species demonstrated similar temporal patterns with and without visual detections. Thus, the inclusion of visually detected birds in the field could not completely explain the differences in temporal patterns of detection between SRS and point-count data.

The temporal patterns observed in our point-count data are cause for concern in light of the frequent use of methods for estimating detection probabilities based on time of detection. The first several minutes of a point-count survey, particularly in productive ecosystems or early in the morning (Bystrak 1981, Bart and Schoultz 1984, Haselmayer and Quinn 2000), can present a challenge to observers because many birds are active simultaneously and observers need to make quick decisions. Consequently, some birds may not be immediately detected, identified, or documented by the observer once they have vocalized. Often, these individuals are detected or documented later in the point-count survey and ultimately are included in the data, as our study demonstrates. However, this pattern of detection, observed in 6 of 10 species, yields unreliable estimates of detection probability and species abundance using temporal removal models. The use of recordings that can be replayed increases the likelihood that the listener detects, identifies, and documents birds when they first vocalize. Although SRS is restricted to vocalizing birds, all 10 species considered here demonstrated temporal detection patterns that permitted reliable estimation of abundance when based on SRS data. The ability to detect available birds earlier using SRS represents a key advantage to investigators interested in estimating detection probabilities and evaluating patterns in species abundance, particularly when other methods of estimating detection probabilities cannot be used, for example, distance sampling (Buckland et al. 2001) and multiple observer methods (Nichols et al. 2000, Alldredge et al. 2006). The delay in detecting available birds during point counts is also expected to bias abundance estimates derived from the full time-of-detection model (Alldredge et al. 2007a, b) by introducing errors in detection histories. Our results demonstrate how observers' perceptual constraints can influence temporal detection patterns during point counts and abundance estimates derived from time-of-detection approaches.

With the possible exception of Common Yellowthroats, there was no evidence that the higher detection probabilities derived from SRS were due to sampling a larger area than point counts. Differences in the ratios of SRS- and point-count-derived abundance estimates among the four bird species highlight the difficulty in calibrating recording systems to detect birds to a given distance, particularly if the goal is to examine community-level parameters. In our study, we evaluated relative sampling area between the two survey methods. However, to compare bird density among habitats, seasons, geographic locations, or species, it will be necessary to estimate absolute sampling area. Future research to develop standards and protocols for estimating absolute sampling area are required before acoustic recording methods can be appropriately incorporated into such studies.

SRS and point counts detected a similar number of species, but the two methods differed in the composition of species they detected. Omitting visual detections during point counts had no discernable impact on similarity/dissimilarity in species composition between SRS and point counts. Rather, differences in the identification of species are likely primarily responsible for the differences between methods. Species with vocalizations, particularly call notes that are difficult to identify may be underrepresented on point counts because they are misidentified or recorded as unknown (Bart 1985). Our ability to replay recordings, view sonograms, and verify identifications presumably enhances the accuracy of species' identifications. However, detection and identification in the laboratory are not perfect and, for some species, the combination of auditory and visual cues in the field may increase the accuracy of identification.

SRS tended to be better at detecting rare species of conservation concern, likely because their infrequent vocalizations increased their probability of going undetected or being misidentified in the field. Although differences in frequency of occurrence between the two methods were small, such differences may be meaningful for rare species. For example, detections of Yellow-breasted Chats (*Icteria virens*) and Least Bell's Vireos (*Vireo bellii*) were 29% and 33% higher, respectively, using SRS than point counts for the 42 survey locations. In contrast, Haselmayer and Quinn (2000) found that rare species in Peru were detected more frequently by point counts than acoustic surveys. These differences may be due to their use of a single directional microphone or characteristics of their listening environment.

An advantage of using SRS in combination with a single interpreter in the laboratory, as in our study, is the elimination of interobserver error and minimization of intraobserver error (the interpreter may listen to the recordings multiple times during the same or different days; Hobson et al. 2002). Approaches to abundance estimation other than the temporal removal model are also possible, such as having multiple interpreters listen to each recording (Nichols et al. 2000, Alldredge et al. 2006). SRS and other acoustic recording systems will be particularly effective in long-term studies, where turnover in field assistants is likely to be high, and in large-scale studies that require many observers. The decision to use audio-visual field surveys (e.g., point counts or transects) or purely auditory surveys (e.g., SRS or CZM-180; Hobson et al. 2002, Rempel et al. 2005) depends on many factors, including vocal characteristics of the species to be surveyed, for example, vocalization frequency (Hz), vocalization rates, and ease and accuracy of detecting and identifying vocalizations in the field and laboratory (Wiley and Richards 1982, Alldredge et al. 2006, 2007b), period of the annual cycle (Wilson and Bart 1985, Selmi and Boulinier 2003), vegetation type(s) surveyed (Scott et al. 1981, DeJong and Emlen 1985, Sauer et al. 1994, Schieck 1997), the diversity and productivity of communities to be surveyed (Bart and Schoultz 1984, Parker 1991, Haselmayer and Quinn 2000, Simons et al. 2007), and logistical constraints. Those considering the use of acoustic recording methods to sample bird populations or communities should conduct an assessment of their recording system prior to using it in a study, even if it has been used successfully in other vegetation types, during other seasons, or for other species.

Although seemingly more complex than other recording systems, our four-channel SRS system has several important benefits. First, the combination of four discrete channels played back through four speakers presumably creates a more realistic simulation of the natural soundscape because the listener receives acoustic signals in three dimensions. As part of an on-going experiment, we asked volunteers to interpret recordings made by SRS and two different stereo recording systems and most indicated that the SRS interpretation room felt more natural than the stereo interpretation setup that involved listening through headphones. In addition, they felt more confident at distinguishing among individuals in the SRS playback room because they received cues from four directions instead of two (A. Celis-Murillo, unpubl. data).

Second, despite its additional components, SRS is not necessarily more expensive than stereo recording systems and it provides a level of flexibility and multifunctionality not afforded by other commercial recording units. SRS is a generic recording system with a specific configuration, that is, number, type, and position of microphones, but investigators can use any one of many different brands of components. For example, many different omnidirectional microphones or recorders are available that range widely in cost, but satisfy the characteristics outlined in our description of the system. Thus, investigators can custom build SRS units to meet their particular needs and budgets. For studies requiring multiple systems, however, they should use the same components to standardize the quality of data across space and time.

The cost of a single SRS system, assuming no equipment is already available, ranges from $1550 to 3400 (US), including the recorder, microphone, tripod, microphone mount, and cables. This estimate is well within the price range for commercially available stereo recording systems, ranging from $1250 to 2250 for the microphone/tripod unit and $4250–6580 for the microphone/tripod unit plus recorder (EARS©). The cost of the sound interpretation room, excluding the computer is about $800, but costs can be reduced by using free software. In our study, we performed interpretations in a standard office space. For a small additional cost, steps can be taken to enhance the listening environment by addressing the reflective nature of the space. Despite additional time required for the interpretation of the SRS recordings in the laboratory, labor costs comparable to those incurred using point counts may be achieved by using inexperienced personnel or volunteers in the field in combination with one or more experts in the lab outside of the breeding season when trained experts are in reduced demand.

Although SRS may require a greater effort, particularly more time, than point counts, the quality and types of data obtained by the different survey methods must be considered. Depending on the research question, investigators may face tradeoffs between time, effort, and financial cost versus the type or quality of data required. In addition to SRS's potential to minimize observer biases and provide reliable estimates of abundance and richness, SRS and other acoustic recording systems provide a permanent record of the survey that can be used for training and to quantify bird vocalization frequencies, measure the precise timing of vocalizations, and quantify environmental noise, for example, vehicles, people, wind, or other animals.

Further study to quantify the benefits of successive playbacks and to determine how many times a recording should be reviewed to maximize effort is needed. When the objective of a study is to compare abundance estimates among habitat types, seasons, or other treatments, the amount of interpretation time should be standardized or factored into the analysis, for example, as a covariate. Finally, as adaptations to our SRS system and other acoustic recording units are implemented, there is a need to establish standards for testing and calibrating systems (e.g., using test tones, Hobson et al. 2002), estimate absolute sampling area, identify relevant covariates, and standardize the recording and reporting of metadata so that data from different recording units are comparable.

In summary, SRS offers an alternative method for surveying bird communities. We emphasize that the proper and effective application of SRS, or any other acoustic recording system, requires assessment of the study objectives, species, study location, vegetation type(s), season, and logistical constraints. In some cases, a combination of survey techniques with complementary biases may be needed. Furthermore, although we have developed and used SRS to survey temperate breeding bird communities, this acoustic system should be effective for surveying tropical bird communities throughout the year.

ACKNOWLEDGMENTS

We thank J. Nichols and J. Hines for direction and assistance with the statistical analyses. Early discussions with T. Scott regarding audio recording and survey techniques were insightful. R. Trubbit, J. Storm, L. Elliott, and G. Weddig offered technical comments and suggestions on the design of SRS. J. Nichols, J. Rotenberry, K. Preston, M. Ward, A. Farnsworth, G. Ritchison, C. Handel and three anonymous reviewers provided valuable comments on the manuscript. This research was funded by the Center for Conservation Biology-University of California Riverside, NSF (AMARSS Project No.NSF-EF0410408), Western Riverside County, California Department of Fish and Game, and the California Department of Transportation (CalTrans).

LITERATURE CITED

ALLDREDGE, M. W., K. H. POLLOCK, AND T. R. SIMONS. 2006. Estimating detection probabilities from multiple-observer point counts. Auk 123: 1172–1182.

ALLDREDGE, M. W., K. H. POLLOCK, T. R. SIMONS, J. A. COLLAZO, AND S. A. SHRINER. 2007a. Time-of-detection method for estimating abundance from point-count surveys. Auk 124: 653–664.

ALLDREDGE, M. W., K. H. POLLOCK, T. R. SIMONS, AND K. PACIFICI. 2007b. A field evaluation of the time-of-detection method to estimate population size and density for aural avian point counts. Avian Conservation and Ecology 2:13. Available at: http://www.ace-eco.org/vol2/iss2/art13/ (6 June 2008)

ALLDREDGE, M. W., T. R. SIMONS, AND K. H. POLLOCK. 2007c. Factors affecting aural detections of songbirds. Ecological Applications 17: 948–955.

ALLEN, M. F., J. T. ROTENBERRY, K. L. PRESTON, K. J. HALAMA, T. TENNANT, C. W. BARROWS, V. RIVERA DEL RIO, A. CELIS-MURILLO, X. CHEN, AND V. M. RORIVE. 2005. Towards developing a monitoring framework for Multiple Species Habitat Conservation Plans. Part I. Center for Conservation Biology, University of California – Riverside, Riverside, CA.Available at: http://repositories.cdlib.org/ccb/CCB2005 (30 May 2008)

AUDACITY [ONLINE]. 2005. Audacity for Macintosh OSX, version 1. 3. 5. Free Digital Audio Editor. Available at: http://audacity.sourceforge.net/ (11 June 2008)

BART, J. 1985. Causes of recording errors in singing bird surveys. Wilson Bulletin 97: 161–172.

BART, J., AND J. D. SCHOULTZ. 1984. Reliability of singing bird surveys: changes in observer efficiency with avian density. Auk 101: 307–318.

BOULINIER, T., J. D. NICHOLS, J. R. SAUER, J. E. HINES, AND K. H. POLLOCK. 1998. Estimating species richness: the importance of heterogeneity in species detectability. Ecology 79: 1018–1028.

BUCKLAND, S. T., D. R. ANDERSON, K. P. BURNHAM, J. L. LAAKE, D. L. BORCHERS, AND L. THOMAS. 2001. Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, New York.

BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach, second edition. Springer-Verlag, New York.

BURNHAM, K. P., AND W. S. OVERTON. 1979. Robust estimation of population size when capture probabilities vary among individuals. Ecology 60: 927–936.

BYSTRAK, D. 1981. The North American Breeding Bird Survey. Studies in Avian Biology 6: 34–41.

CORNELL LABORATORY OF ORNITHOLOGY. 2003. Raven, version 1.2.1. Cornell Laboratory of Ornithology, Ithaca, NY.

CYR, A. 1981. Limitation and variability in hearing ability in censusing birds. Studies in Avian Biology 6: 327–333.

DEJONG, M. J., AND J. T. EMLEN. 1985. The shape of the auditory detection function and its implication for songbird censusing. Journal of Field Ornithology 56: 26–31.

EMAGIC. 2004. Logic Pro 6: Music and Audio Production. Reference Manual, version 6.4. Emagic USA, Grass Valley, CA.

EMLEN, J. T., AND M. J. DEJONG. 1992. Counting birds: the problem of variable hearing abilities. Journal of Field Ornithology 63: 26–31.

FARNSWORTH, G. L., K. H. POLLOCK, J. D. NICHOLS, T. R. SIMONS, J. E. HINES, AND J. R. SAUER. 2002. A removal model for estimating detection probabilities from point-count surveys. Auk 119: 414–425.

HASELMAYER, J., AND J. S. QUINN. 2000. A comparison of point counts and sound recording as bird survey methods in Amazonian southeast Peru. Condor 102: 887–893.

HOBSON, K. A., R. S. REMPEL, H. GREENWOOD, B. TURNBULL, AND S. VAN WILGENBURG. 2002. Acoustic surveys of birds using electronic recordings: new potential from an omni- directional microphone system. Wildlife Society Bulletin 30: 709–720.

KENDALL, W. L., B. G. PETERJOHN, AND J. R. SAUER. 1996. First-time observer effects in the North American Breeding Bird Survey. Auk 113: 823–829.

KEPLER, C. B., AND J. M. SCOTT. 1981. Reducing bird count variability by training observers. Studies in Avian Biology 6: 366–371.

MAGURRAN, A. E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, NJ.

MCLAREN, M. A., AND M. D. CADMAN. 1999. Can novice volunteers provide credible data for bird surveys requiring song identification? Journal of Field Ornithology 70: 481–490.

MOOD, A. M., F. A. GRAYBILL, AND D. C. BOES. 1974. Introduction to the theory of statistics, 3rd edition. McGraw Hill, New York.

NICHOLS, J. D., T. BOULINIER, J. E. HINES, K. H. POLLOCK, AND J. R. SAUER. 1998. Inference methods for spatial variation in species richness and community composition when not all species are detected. Conservation Biology 12: 1390–1398.

NICHOLS, J. D., J. E. HINES, J. R. SAUER, F. W. FALLON, J. E. FALLON, AND P. J. HEGLUND. 2000. A double-observer approach for estimating detection probability and abundance from point counts. Auk 117: 393–408.

———, AND ———. 1987. Population ecology of the Mallard. VIII. Winter distribution patterns and survival rates of winter-banded Mallards. United States Department of the Interior, Fish and Wildlife Service, Resource Publication, Issue 162, Washington, D. C.

PARKER, T. A. 1991. On the use of tape recorders in avifaunal surveys. Auk 108: 443–444.

RALPH, C. J., S. DROEGE, AND J. R. SAUER. 1995. Managing and monitoring birds using point counts: standards and applications. In: Monitoring bird populations by point counts (C. J. Ralph, J. R. Sauer, and S. Droege, eds.), pp. 161–168. U.S. Department of Agriculture Forest Service, General Technical Report PSW-GTR-149, Albany, CA.

Ralph, C. J., G. R. Geupel, P. Pyle, T. E. Martin, and D. F. DeSante. 1993. Handbook of field methods for monitoring landbirds. U. S. Department of Agriculture Forest Service, General Technical Report PSW-GTR-144, Albany, CA.

Rempel, R. S., K. A. Hobson, G. Holborn, S. L. Van Wilgenburg, and J. Elliott. 2005. Bioacoustic monitoring of forest songbirds: interpreter variability and effects of configuration and digital processing methods in the laboratory. Journal of Field Ornithology 76: 1–108.

Rexstad, E., and K. P. Burnham. 1991. User's guide for interactive program CAPTURE. Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, CO.

Robbins, C. S., and R. W. Stallcup. 1981. Problems in separating species with similar habits and vocalizations. Studies in Avian Biology 6: 360–365.

Rosenstock, S., D. R. Anderson, K. M. Giesen, T. Leukering, and M. F. Carter. 2002. Landbird counting techniques: current practices and an alternative. Auk 119: 46–53.

Sauer, J. R., B. G. Peterjohn, and W. A. Link. 1994. Observer differences in the North American breeding bird survey. Auk 111: 50–62.

Schieck, J. 1997. Biased detection of bird vocalizations affects comparisons of bird abundance among forested habitats. Condor 99: 179–190.

Scott, J. M., F. L. Ramsey, and C. B. Kepler. 1981. Distance estimation as a variable in estimating bird numbers from vocalizations. Studies in Avian Biology 6: 334–340.

Scott, T. A., P. Lee, G. C. Greene, and D. A. McCallum. 2005. Singing rate and detection probability: an example from the Least Bell's Vireo (*Vireo belli pusillus*). In: Bird conservation implementation and integration in the Americas: proceedings of the third international Partners in Flight Conference (C. J. Ralph, and T. D. Rich, eds.), pp. 845–853. U.S D.A. Forest Service, General Technical Report PSW-GTR-191, Albany, CA.

Selmi, S., and T. Boulinier. 2003. Does time of season influence bird species number determined from point-count data? A capture-recapture approach. Journal of Field Ornithology 74: 349–356.

Simons, T. R., M. W. Alldredge, K. H. Pollock, and J. M. Wettroth. 2007. Experimental analysis of the auditory detection process on avian point counts. Auk. 124: 986–999.

SPSS Inc. 2002. SPSS 11.0 for Macintosh Brief Guide, version 11.0. SPSS, Chicago, IL.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46: 120–138.

Wiley, R. H., and D. G. Richards. 1982. Adaptations for acoustic communication in birds: sound transmission and signal detection. In: Acoustic communication in birds, vol. 1 (D. E. Kroodsma, and E. H. Miller, eds.), pp. 131–181. Academic Press, New York.

Wilson, D. M., and J. Bart. 1985. Reliability of singing bird surveys: effects of song phenology during the breeding season. Condor 87: 69–73.