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ESTIMATING DETECTION PROBABILITY AND DENSITY FROM POINT-COUNT SURVEYS: A COMBINATION OF DISTANCE AND DOUBLE-OBSERVER SAMPLING

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Abstract.—Point counts are the method most commonly used to estimate abundance of birds, but they often fail to account properly for incomplete and variable detection probabilities. We developed a technique that combines distance and double-observer sampling to estimate detection probabilities and effective area surveyed. We applied this paired-observer, variable circular-plot (POVCP) technique to point-count surveys (n = 753) conducted in closed-canopy forests of southeast Alaska. Distance data were analyzed for each species to model a detection probability for each observer and calculate an estimate of density. We then multiplied each observer's density estimates by a correction factor to adjust for detection probabilities <1 at plot center. We compared analytical results from four survey methods: single-observer fixed-radius (50-m) plot; single-observer, variable circular-plot (SOVCP); double-observer fixed-radius (50-m) plot; and POVCP. We examined differences in detection probabilities at plot center, effective area surveyed, and densities for five bird species: Pacific-slope Flycatcher (*Empidonax difficilis*), Winter Wren (*Troglodytes troglodytes*), Golden-crowned Kinglet (*Regulus satrapa*), Hermit Thrush (*Catharus guttatus*), and Townsend's Warbler (*Dendroica townsendi*). Average detection probabilities for paired observers increased ~8% (SE = 2.9) for all species once estimates were corrected for birds missed at plot center. Density estimators of fixed-radius survey methods were likely negatively biased, because the key assumption of perfect detection was not met. Density estimates generated using SOVCP and POVCP were similar, but standard errors were much lower for the POVCP survey method. We recommend using POVCP when study objectives require precise estimates of density. Failure to account for differences in detection probabilities and effective area surveyed results in biased population estimators and, therefore, faulty inferences about the population in question. *Received 14 October 2003, accepted 28 September 2005.*

Key words: density estimator, detection probability, distance sampling, double-observer sampling, effective area surveyed, point count.

Estimaciones de la Densidad y de las Probabilidades de Detección a Partir de Muestreos Utilizando Conteos en Puntos: Una Combinación de Muestreos de Distancia y de Doble Observador

Resumen.—El método de conteo en puntos es comúnmente el más usado para estimar la abundancia de aves. Sin embargo, este método generalmente no da cuenta de una forma apropiada de que las probabilidades de detección pueden ser variables e incompletas. Desarrollamos una técnica que combina muestreos de distancia con

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muestreo de doble observador para estimar las probabilidades de detección y las áreas efectivas de muestreo. Aplicamos esta técnica de parcela circular variable con observador doble (PCVOD) en muestreos utilizando conteos en puntos (n = 753) realizados en bosques de dosel cerrado en el sureste de Alaska. Los datos de distancia fueron analizados para cada especie para modelar una probabilidad de detección para cada observador y para calcular una estimación de la densidad. Luego, multiplicamos la estimación de densidad de cada observador por un factor de corrección para ajustar por probabilidades de detección < 1 en el centro de la parcela. Comparamos los resultados analíticos de cuatro métodos de muestreo: parcelas de radio fijo (50 m) con un observador único, parcelas de radio variable con un observador único (PCVOU); parcelas de radio fijo (50 m) con dos observadores; y PCVOD. Examinamos las diferencias en las probabilidades de detección en el centro de la parcela, el área efectiva muestreada y las densidades para cinco especies de aves: *Empidonax difficilis*, *Troglodytes troglodytes*, *Regulus satrapa*, *Catharus guttatus* y *Dendroica townsendi*. Las probabilidades de detección promedio de los muestreos con dos observadores aumentaron en un ~8% (EE = 2.9) para todas las especies, una vez que las estimaciones fueron corregidas por las aves no detectadas en el centro de la parcela. Las estimaciones de densidad utilizando el método de radio fijo estuvieron probablemente sesgadas de manera negativa, debido a que el supuesto de detección perfecta no se cumplió. Las estimaciones de densidad generadas utilizando los métodos de PCVOU y PCVOD fueron similares, aunque los errores estándar fueron mucho menor para el método de muestreo de PCVOD. Recomendamos utilizar el método de PCVOD cuando se requieren estimaciones precisas de densidad. No considerar las diferencias en las probabilidades de detección y en las áreas de muestreo efectivas genera estimaciones poblacionales sesgadas y, por lo tanto, inferencias erradas sobre la población estudiada.

Comparisons of avian populations across space or time often require estimates of abundance. All measures of abundance are at best indices, because the number of birds counted is a proportion of the true population (Lancia et al. 1994), and true abundance is rarely known. The goal when estimating abundance is to reduce sources of bias by using standardized survey protocols and by estimating detection probabilities and area surveyed, which can vary among observers, species, habitat types, environmental conditions, and distances (McCracken 1994, Nelson and Fancy 1999, Buckland et al. 2001). If counts are not adjusted for differences in detection probability and in area effectively surveyed, point counts can result in a biased density estimator and, therefore, faulty inferences about the population in question (Diefenbach et al. 2003, Norvell et al. 2003, Farnsworth et al. 2005). Improved understanding of problems associated with unadjusted point-count data has stimulated the development of more sophisticated sampling methods that are practical and realistic for use in the field (Reynolds et al. 1980; Buckland et al. 1993, 2001; Farnsworth et al. 2002, 2005). However, these methods require additional observer skills and data collection, slightly more complicated analyses, and compliance with several key assumptions; therefore, such methods are not commonly used by the ornithological community. Distance sampling and double-observer sampling are two techniques that can be used to estimate detection probabilities and effective area sampled, but assumptions of these techniques can be difficult to meet in the field.

Distance-sampling theory is well developed and permits estimation of detection probabilities and effective area surveyed by species, observer, and habitat type (Roeder et al. 1987; Buckland et al. 1993, 2001; Thomas et al. 2002). Although the merits of distance sampling methods used at point-count stations are apparent, analysis relies on the validity of several key assumptions (Gates 1969, Seber 1973, Reynolds et al. 1980, Buckland et al. 1993). (1) Detection probability at the plot center is 1 (or a known value). (2) Birds do not move in response to the observer prior to detection. (3) Distance to each detected bird is recorded accurately (Buckland et al. 1993, 2001; Thomas et al. 2002). These assumptions can be difficult to satisfy (Thompson 2002). For example, in dense forests with high canopies where most birds are detected aurally, perfect detection at plot center—that is, $g(0) = 1$, where $g(r)$ is the probability of detecting a bird at radial distance r—most likely is not achieved (DeSante 1981, 1986). Movements of birds within the count period can also be problematic, leading to density estimators that are biased either low or high depending on the type of movement and behavior of the bird. Although simulation models have demonstrated that several methods used to estimate density are robust to bird disturbance (Roeder et al. 1987), precaution must be taken to minimize responsive movement in the field. Distance-sampling methods used at point counts are sensitive to accurate measurements of distance, particularly those near the count station, because area of a circle increases with the square of the distance. These key assumptions and results of field tests conducted early in development of variable circular plots have deterred many biologists from implementing distance sampling during point-count studies in the field (DeSante 1981, 1986). However, rigorous training programs and experienced observers can greatly reduce the likelihood of violating assumptions of distance-sampling techniques (Kepler and Scott 1981).

Some research has focused on relaxing key assumptions of distance sampling, particularly the assumption that $g(0) = 1$. Researchers conducting line-transect surveys for marine mammals have performed most of the research (Buckland et al. 1993; Laake et al. 1997; Borchers et al. 1998a, b), because this assumption is particularly problematic for species that spend a significant proportion of time underwater, where they are undetectable. The general approach has been extended to aerial surveys (Alpizar-Jara and Pollock 1996, Manly et al. 1996) and other boat-based surveys (Evans Mack et al. 2002).

Another survey technique recently proposed to address simple differences in detection probabilities involves sampling with two observers. Nichols et al. (2000) modified methods developed for aerial surveys (Cook and Jacobson 1979) to accommodate standard point-count surveys. This procedure uses capture–recapture theory and Cook-Jacobson estimators to estimate detection probabilities and variances (Nichols et al. 2000). Advantages of using the double-observer approach include the ability to detect simple differences in detection probabilities, increased possibility of detecting rare species, and the simplicity of the method. A major advantage of this approach is that it uses both observers' data to provide information about each observer's probability of detection. A drawback to the double-observer approach is the failure to account for differences in distance at which different observers detect birds. The double-observer approach assumes that the same bird is potentially detectable by both observers; in reality, this is probably not always true (Nichols et al. 2000) and potentially introduces a serious bias in estimating detection probabilities. This availability bias is present in all methods involving two or more observers, but it is impossible to address or quantify without a known benchmark of density (see below for further details). Nichols et al. (2000) suggested combining the double-observer approach with other methods for additional modeling of the detection probability (as we do below), because the double-observer approach does not allow for an empirical measure of the area effectively sampled.

We developed a new survey method, the paired-observer, variable circular-plot (POVCP) technique, which combines double-observer and distance-sampling methods to estimate densities of breeding landbirds. This technique combines the advantages of both sampling methods by empirically estimating the effective area sampled using distance sampling and by using information collected by paired observers to estimate and increase detection probabilities. The combination method relaxes the critical assumption of distance sampling that detection probability at plot center is 1, that is, $g(0) = 1$.

Here, we describe the field and analytical methods required for the POVCP technique. We then compare detection probabilities at plot center, density estimates, and associated variances obtained from a field test of four survey methods: single-observer with 50-m fixed-radius plot; single-observer, variable circular-plot (SOVCP); double-observer with 50-m fixed-radius plot; and POVCP. Without a known benchmark of true density, we compare results of each technique with those of all other survey methods examined here, none of which adjusts for availability bias (see below for details). Because we do not know how our results compare to true densities, we rigorously evaluate how closely key assumptions of each survey method were met. We discuss strengths and weaknesses of the combination method, and provide recommendations for studies.

METHODS

STUDY AREA AND SURVEY METHODS

We conducted field trials in forested stands on the Tongass National Forest in southeast Alaska. The forests of southeast Alaska are part of the continuous coastal, temperate rainforest that extends along the Pacific Coast from northern California to Cook Inlet in Alaska. These forests are characterized by western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*), with western red cedar (*Thuja plicata*) and Alaska yellow cedar (*Chamaecyparis nootkatensis*) more common to the south (Alaback 1982). The forest understory is dominated by blueberry (*Vaccinium* spp.), devilsclub (*Oplopanax horridus*), and salmonberry (*Rubus* spp.). Mosses (*Hylocomium splendens*, *Rhytidiadelphus loreus*, *Sphagnum* spp.), ferns (*Dryopteris* spp., *Gymnocarpium dryopteris*), and lichens (*Cladonia* spp.) cover the forest floor, and downed logs and root wads are scattered throughout the forest understory.

Admiralty, Baranof, and Chichagof islands were surveyed in 2001; Kuiu, Kupreanof, Mitkof, Zarembo, Etolin, and Wrangell islands were surveyed in 2002. We selected study sites that consisted only of old-growth forest, defined as a forest stand where trees average ≥23 cm diameter at breast height (DBH) and the stand is ≥150 years old (Caouette et al. 2000). We established 3–12 count stations at each of 47 randomly selected sites (for details, see Kissling 2003). Stations were ≥150 m apart to avoid counting the same birds at multiple stations (Reynolds et al. 1980) and to ensure independence. Before sampling started, all observers participated in a two-week field training session to improve bird identification and distance-estimation skills. We sampled from 29 May to 3 July in 2001 and 2002. Surveys commenced 30 min before sunrise (0230–0300 hours AST) and continued for 5–6 h, until not later than 0900 hours. We surveyed 753 point-count stations in 2001 (n = 355) and 2002 (n = 398), visiting each station twice during the breeding season, for a total of 1,506 point counts over the two-year period.

At each count station, two observers simultaneously and independently conducted a point count using the variable circular-plot method (Reynolds et al. 1980). For each bird detected, each observer recorded on a map the species, radial distance to location of first detection, time of detection (in 2002 only), number in group, mode of detection (i.e., song, call note, visual, or a combination), and direction of any movements. A laser rangefinder was used to improve estimates of distance, which were rounded to the nearest meter. Flyovers were recorded separately and were not used for density estimation. Duration of count was 8 min to be consistent with other landbird studies conducted in southeast Alaska (Dellasala et al. 1996). At the end of each count, observers discussed the results, making notes of birds detected by both observers and those detected by only one observer. At the end of the day, observers combined maps on a final data sheet, noting which observer(s) detected each bird, and averaging estimated distances to birds detected by both observers. If an observer detected a bird and the bird moved to a new location, where it was detected by the other observer, both observers recorded the bird on the final data sheet, but only the estimated distance to the initial location was retained.

ANALYTICAL METHODS

We used four techniques to analyze data collected on singing males for five species: Pacific-slope Flycatcher, Winter Wren, Golden-crowned Kinglet, Hermit Thrush, and Townsend's Warbler (see Appendix 1 for scientific names). Analyses included all count stations in forested habitat.

Single-observer fixed-radius.—We randomly selected one observer at each count station, truncated the data at 50 m, and used that observer's data in the single-observer fixed-radius approach to estimate density of the five selected species. Individual distance estimates were used to determine whether a bird was inside the 50-m radius. For each species, we calculated the mean number of detections for each observer, converted these to estimates, and then calculated a weighted mean density across all observers (n = 7; Cochran 1977). We computed a weighted sum of variances across all observers to obtain estimates of standard errors (Cochran 1977).

Single-observer, variable circular-plot.—We randomly selected one observer at each count station and used the SOVCP technique with that observer's data to estimate density of the five selected species. For data from each observer (n = 7), we followed steps of analysis recommended by Buckland et al. (2001) to develop models of detection probability and estimate density; we then calculated a weighted mean and variance of density across observers for each species.

We used DISTANCE, version 4.1, release 2 (Research Unit for Wildlife Population Assessment, University of St. Andrews, Fife, United Kingdom; see Acknowledgments), to model the probability of detection and effective area sampled, assuming that $g(0) = 1$. Before model selection in DISTANCE, we fitted a plausible model to the data and truncated the data at a distance where detection probability fell below 10% (Buckland et al. 2001). Individual distance estimates, not averaged estimates, were used for estimating density. To improve model fit, we grouped data into distance intervals for each species. We used Akaike's Information Criterion (AIC) to select the hazard rate detection function with a cosine series expansion term to model $g_{ij}(\pi r^2)$ for each observer (i) and each species (j) (Buckland et al. 2001). This model provided an estimate of $\hat{h}_{ij}(0)$, defined as the slope of the probability density function of detection distances evaluated at distance zero (Buckland et al. 1993, 2001), which we later used to calculate density of birds and associated variances.

Double-observer fixed-radius.—Following double-observer fixed-radius analysis methods described by Nichols et al. (2000), we estimated density for each species and each observer pair (n = 12 pairs). We truncated all detections beyond 50 m and used DOBSERV (U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland; see Acknowledgments) to calculate the probability of detection and to estimate density. Primary and secondary observers were randomly assigned, and individual distance estimates were used for calculating density (as opposed to the averaged estimate). Density and associated variance estimates for each species were weighted across all observer pairs (Cochran 1977).

Combination method: Paired-observer, variable circular-plot.—We combined distance-sampling theory with the double-observer technique to model the probability of detection and effective area sampled, applying a correction factor, $\hat{\theta}$, to relax the assumption of perfect detection (p = 1.0) at plot center. We estimated $\hat{h}_{ij}(0)$ using the same steps outlined above, except that averaged distance estimates were used instead of individual estimates. Additionally, to account for birds missed at or near the plot center, we used a logistic function to model a correction factor, $\hat{\theta}_{ijz}$, for each observer (i) and each species (j), given environmental conditions (z) (Borchers et al. 1998a).

To estimate $\hat{\theta}_{ijz}$, for each observer and species, we first used DISTANCE to determine the radius of "perfect" detection, that is, $g(r) = 1$. Distance-sampling theory states that detection should remain certain or nearly certain at small distances from the point (Buckland et al. 2001). We use the "shoulder" of the detection function to determine the radius of "perfect" detection for each observer and species. We then used data within this radius to model $\hat{\theta}_{ijz}$ using logistic regression (Proc LOGISTIC; SAS Institute 1999). To remove bias introduced by the regression, we used a bias-corrected logistic model proposed by Steinhorst and Samuel (1989) (Proc LOGISTIC). The modified logistic function is

$$\theta_{ijz} = 1 + e^{-x'\hat{\beta} - x'\hat{\Sigma}x/2}$$

where θ = correction factor for observer i, species j, and covariates z; x = covariate vector; $\hat{\beta}$ = logistic regression coefficients; and $\hat{\Sigma}$ = variance–covariance matrix of regression coefficients. Response variables were successes (detected) and failures (not detected) for each observer and species within the determined area of "perfect" detection (Borchers et al. 1998a). We considered the following covariates (z) to help explain the variability in detection probabilities at plot center: percentage of canopy cover (CC), percentage of shrub cover (SC), percentage of slope (SLP), wind (WIND), precipitation (PREC), and noise level (NSE). Covariates CC and SC were estimated visually in the field within a 50-m radius of each count station, and SLP was measured using a clinometer over a distance of 30 m. Covariates WIND and PRECIP were recorded using the Beaufort scale, and NSE (e.g., stream and surf noise) was recorded on a scale from 0 to 5. All covariates were evaluated as continuous variables.

On the basis of our field experience and knowledge of southeast Alaska, we developed a set of five candidate models that we used to model $\hat{\theta}_{ijz}$. Candidate models (G) included: G_{FULL} = CC, SC, SLP, WIND, PREC, NSE; G_{SITE} = CC, SC, SLP; G_{ENV} = WIND, PREC, NSE; and G_{CANOPY} = CC;

$G_{\text{INTERCEPT}}$ = intercept-only model. We used the information-theoretic approach, based on AIC corrected for small sample sizes (AIC_c), to select the most parsimonious model (Burnham and Anderson 2002). We ranked the fitted models from best to worst, based on ΔAIC_c values, and calculated the weight of evidence (w_u) to interpret the relative likelihood of each model (u) given the set of candidate models. If empirical evidence for selecting one "best" model was weak (ΔAIC_c < 2 and $w_u \leq 0.9$), we used multimodel inference to estimate parameters and associated unconditional standard errors (Burnham and Anderson 2002). We then used this estimated correction factor, $\hat{\theta}_{ijz}$, to estimate the density of birds.

We also used individual estimates of theta to illustrate differences in detection probabilities among survey methods. For each individual observer, we estimated the probability of detecting each species at or near the point by averaging the reciprocal of theta over all count stations where observer i was successful in detecting species j, given the set of covariates. To estimate the probability of detection at or near the point for paired observers (i.e., probability that a bird is observed by at least one observer), we assumed that the probability of detection by each observer was independent (Borchers et al. 1998a):

$$g_{jk}\left[\pi(r=0)^2\right] = \theta^{-1}_{i=1jkz} + \theta^{-1}_{i=2jkz} - \left(\theta^{-1}_{i=1jkz} \times \theta^{-1}_{i=2jkz}\right)$$

Density estimates were obtained at each point k for each observer i and species j as follows:

$$\hat{D}_{ijk} = \frac{\hat{h}_{ij}(0)\sum_{k_i}^{q_i}\hat{M}_{ijkz}}{2\pi q}$$

where $\hat{D}_{ijk}$ = estimated bird density for observer i and species j at point k; $\hat{h}_{ij}(0)$ = estimate of the slope of the probability density function, estimated at $r = 0$; q = total number of points k; and

$$\hat{M}_{ijkz} = n_{ijkz} \times \hat{\theta}_{ijkz}$$

the corrected number of birds for observer i, species j, point k, and covariates z.

Density estimates $\hat{D}_{ijk}$ were then averaged over both observers to estimate $\hat{D}_{jk}$, the density of species j at point k, and then overall density was computed by averaging $\hat{D}_{jk}$ across all points.

Estimates of density have four sources of error that were evaluated as variance components: sampling error (S^2_{sampling}), error associated with estimating the effective area ($S^2_{\text{effective area per point}}$), visibility bias ($S^2_{\text{visibility}}$), and error associated with estimating the correction factors ($S^2_{\text{logistic model}}$) (Steinhorst and Samuel 1989). Variance was calculated generally as follows: $S^2_{\text{density}} = S^2_{\text{sampling}} + S^2_{\text{effective area per point}} + S^2_{\text{visibility}} + S^2_{\text{logistic model}}$. Each component was estimated separately. Sampling variance was calculated as follows:

$$S^2_{\text{sampling}} = \frac{1}{q}\left[\frac{\sum_{k=1}^{q}\left(\hat{M}_k - \overline{M}\right)^2}{q-1}\right]$$

A weighted sampling variance by different strata also could be calculated if a stratified sampling design was used.

Variance associated with the effective area per point was estimated in DISTANCE as follows:

$$S^2_{\text{effective area per point}} = \frac{\text{var}(\hat{h}(0))}{2\pi}$$

Variance associated with visibility bias was estimated from the correction factors for each observation (Steinhorst and Samuel 1989):

$$S^2_{\text{visibility}} = \frac{1}{q^2}\sum_{k=1}^{q}\sum_{i=1}^{7}(\hat{\theta}_{ik} - 1) \times \hat{\theta}_{ik}$$

The model component of variance was estimated by including model selection uncertainty (Burnham and Anderson 2002), with the model component of variance estimated from the regression coefficients and the variance-covariance matrix (Steinhorst and Samuel 1989):

$$S^2_{\text{logistic model}} = \sum_{i=1}^{7}\left\{\sum_{u=1}^{R}W_u\sqrt{\left\langle \frac{1}{q^2}\sum_{k_i}^{q_i}\left[\begin{array}{l}\left(e^{-2x'\hat{\beta}-2x'\hat{\sum}x}\right)\\ \times\left(e^{x'\sum x}-1\right)\end{array}\right]\middle| G_u\right\rangle + \left(\hat{\theta}_{ijzu} - \overline{\theta}\right)^2}\right\}^2$$

where R = number of models u in the selection set; w_u = AIC weight of model u; G_u = model u; and $\overline{\theta}$ = model averaged correction factor for probability of detection across all models in the selection set.

Results

Estimates of effective area surveyed.—Estimates of effective area surveyed, ν, differed among observers and species, and clearly showed that detectability declined with distance even within 50 m of an observer. Estimates ranged from a low of 0.12 ha for Golden-crowned Kinglets detected by observer 2 to a high of 2.05 for Hermit Thrushes detected by the same observer (Table 1). Averaged across all seven observers, estimates of effective area surveyed ($\bar{\nu}$ ± SE) were most similar for Winter Wren (0.68 ± 0.18) and Townsend's Warbler (0.66 ± 0.15), and least similar for Hermit Thrush (1.78 ± 0.24) and Golden-crowned Kinglet (0.18 ± 0.05). Variability among observers' estimates, as measured by the coefficient of variation (Table 1), was greatest for Golden-crowned Kinglet (31%) and Pacific-slope Flycatcher (30%); estimates were most consistent among observers for Hermit Thrush (14%).

Estimates of detection probabilities for single observers at plot center.—Variability among observers in detection probabilities, as measured by coefficient of variation, was greatest (17%) for Hermit Thrush, with detection probabilities ranging from 0.60 to 1.00, and least (6%) for Winter Wren, which had much more consistent detection probabilities (range: 0.82–0.99; Table 2). Variability of detection probabilities among observers for Hermit Thrush was notable, because we suspected that this species would be easily detectable near the point. Relative variability among observers was inconsistent: one observer did not consistently perform better than the others.

Averaged across all seven observers, detection probabilities at or near plot center for SOVCP counts were <0.92 for all five species, violating the assumption that $g(0) = 1$ (Table 2 and Fig. 1). Survey methods in which two observers counted simultaneously (i.e., double-observer and POVCP) had detection probabilities >0.93 for all five species, resulting in an average increase of 8% (SE = 2.9) over estimates of detection probabilities of a single observer. Detection probabilities generated with the double-observer and POVCP methods were comparable (e.g., $\left|\bar{p}_{\mathrm{POVCP}} - \bar{p}_{\mathrm{double\ observer}}\right| < 0.02$) for all five species; but generally, estimates were more precise using the double-observer method (Fig. 1). Perfect detection at the plot center was never achieved for all observers, however, by any method.

Estimates of correction factors.—We developed logistic regression models to estimate correction factors ($\hat{\theta}_{ijz}$) to account for incomplete detection at the plot center for 32 of 35 combinations of observers and species (Appendix 2). In six cases (19%), the intercept-only model ($G_{\mathrm{INTERCEPT}}$) was selected as the single most-parsimonious model, indicating that none of the covariates we tested helped explain variability in detection of birds at the plot center for that observer. In one case (3%), a single model (G_{SITE}) with the covariate for site characteristics was supported. In most (78%) of the cases, more than one model received substantial support ($\Delta AIC_c < 2$) and model-averaging was necessary. The model

Table 1. Estimates of effective area surveyed (ha) for five species by seven observers in old-growth forests in southeast Alaska, 2001–2002. Estimates were modeled using a hazard rate function and cosine series expansion term in DISTANCE. Note that a 50-m radius circle is ~0.78 ha. Number of detections is in parentheses. Mean ($\bar{\nu}$), standard error (SE), and coefficient of variation (CV) of the seven observers' estimates are summarized below the individual estimates.

Observer	Pacific-slope Flycatcher	Winter Wren	Golden-crowned Kinglet	Hermit Thrush	Townsend's Warbler
1	0.25 (208)	0.40 (255)	0.15 (81)	1.81 (99)	0.47 (138)
2	0.27 (217)	0.47 (250)	0.12 (70)	2.05 (105)	0.60 (137)
3	0.57 (212)	0.86 (231)	0.12 (94)	1.63 (121)	0.89 (142)
4	0.38 (452)	0.83 (336)	0.17 (131)	1.98 (181)	0.71 (251)
5	0.41 (229)	0.77 (199)	0.25 (56)	1.91 (111)	0.71 (162)
6	0.35 (217)	0.76 (149)	0.25 (60)	1.73 (98)	0.77 (113)
7	0.29 (209)	0.67 (149)	0.18 (38)	1.34 (109)	0.50 (104)
$\bar{\nu}$ ± SE	0.36 ± 0.11	0.68 ± 0.18	0.18 ± 0.05	1.78 ± 0.24	0.66 ± 0.15
CV (%)	30	26	31	14	23

TABLE 2. Estimates of detection probabilities at or near the plot center for single observers and five species in southeast Alaska, 2001–2002. Number of detections is in parentheses. Mean ($\overline{p}$), standard error (SE), and coefficient of variation (CV) of the seven observers' estimates are summarized below the individual estimates. See Appendix 1 for sample sizes.

Observer	Pacific-slope Flycatcher	Winter Wren	Golden-crowned Kinglet	Hermit Thrush	Townsend's Warbler
1	0.92 (119)	0.96 (152)	0.98 (48)	0.99 (65)	1.00 (83)
2	0.87 (119)	0.85 (129)	0.88 (37)	0.74 (57)	0.74 (72)
3	0.77 (138)	0.92 (154)	1.00 (57)	1.00 (90)	0.73 (92)
4	0.93 (250)	0.83 (211)	0.81 (71)	0.60 (107)	0.91 (139)
5	0.97 (128)	0.99 (120)	0.87 (36)	0.89 (62)	0.98 (98)
6	0.97 (117)	0.92 (92)	0.78 (32)	0.85 (60)	0.71 (59)
7	0.91 (115)	0.94 (92)	0.68 (18)	0.93 (70)	0.89 (64)
$\overline{p}$ ± SE	0.91 ± 0.07	0.92 ± 0.06	0.86 ± 0.11	0.86 ± 0.14	0.85 ± 0.12
CV (%)	7	6	13	17	13

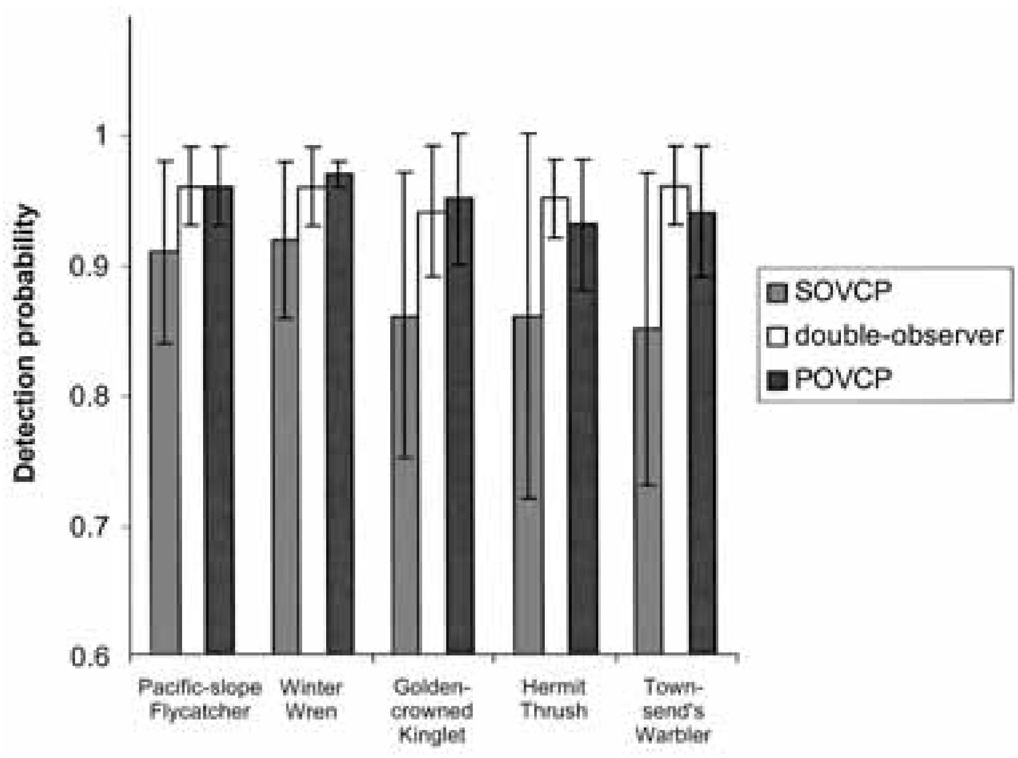

FIG. 1. Average detection probabilities ($\overline{p}$ ± SE) at or near the point (r = 0) derived from SOVCP, double-observer, and POVCP methods for five bird species in old-growth forests in southeast Alaska during 2001 and 2002. See Appendix 1 for sample sizes.

including CC (G_{CC}) was the most consistently supported model (72% of 32 cases). Generally, as CC increased, detectability increased. In southeast Alaska, thick canopy cover in old-growth forests can form an impenetrable sound barrier, creating excellent acoustics and allowing sounds to resonate throughout the forest. The more heavily parameterized models, G_{ENV} and G_{SITE}, were seldom supported by the data (13% each of 32 cases). Not surprisingly, all covariates included in the environmental condition model, G_{ENV}, had a negative relationship with detectability. Under the site condition model, G_{SITE}, probability of detection increased with increasing CC and SLP, but decreased with increasing SC. The full model, G_{FULL}, was never selected as the most parsimonious model.

Density estimates.—Density estimates for all species were highest using the POVCP method and lowest using the single-observer fixed-radius approach (Table 3). POVCP estimates averaged 237% (range: 68–676%) more than single-observer fixed-radius estimates, 7% (range: 1–12%) more than SOVCP estimates, and 94% (range: 3–310%) more than the double-observer estimates.

Density estimates varied considerably but consistently among analytical methods (Table 3). Survey techniques that did not include distance sampling resulted in much lower density estimates unless the effective detection radius for a species, such as the Hermit Thrush, was >50 m (Tables 1 and 3). Estimates were most variable for species with small areas effectively surveyed, like Pacific-slope Flycatchers (range: 1.17–3.78 singing males ha^{-1}) and Golden-crowned Kinglets (range: 0.38–2.94 singing males ha^{-1}). Survey techniques that involved two observers generally resulted in more precise estimators of density than the same techniques with single observers. Standard errors of estimates using two observers never exceeded 0.07 singing males ha^{-1} (Table 3).

Discussion

Density estimates are generally calculated by $D = n(p \times a)^{-1}$, with an inverse relationship between the number of birds counted (n) and both the probability of detection (p) and the effective area surveyed (a) (Lancia et al. 1994, Thomas et al. 2002). Failure to include correct estimates of p and a will lead to a biased density estimator. Our study demonstrates that three point-count techniques commonly used for surveying birds, including single-observer fixed-radius counts, SOVCP, and double-observer fixed-radius counts, consistently result in density estimates that are biased low compared with POVCP. All these estimators may be further biased low if some portion of the population is unavailable for detection with these methods (Laake and Borchers 2004), but the magnitude of availability bias could be determined only with some independent measure of true density.

Not surprisingly, single-observer fixed-radius counts, which are not adjusted for either detection probability or effective area surveyed, produced the lowest estimate of density. It is incorrect to assume that probability of detection is 1.0 within a survey radius of 50 m for all observers, species, and habitats. The shortcomings of unadjusted point counts have long been recognized (Barker and Sauer 1995, Rosenstock et al. 2002, Thompson 2002, Diefenbach et al. 2003, Norvell et al. 2003, Farnsworth et al. 2005, and others), and our results further substantiate recommendations to abandon their use for estimating densities of birds.

The SOVCP technique explicitly measures effective area surveyed and includes an estimator of detection probability; however, the assumption that probability of detection at or near the point is equal to 1 was in most cases incorrect for the species we studied in forests of southeast Alaska. The lowest estimate of probability of detection at or near the plot center we recorded was 0.60 for a single observer counting Hermit Thrushes, a severe underestimation. Although the assumption that $g(0) = 1$ was violated in most cases, density estimates generated with the SOVCP approach were comparable to those generated with POVCP, and differences in the relative level of bias were low. We conclude that density estimators using

Table 3. Density estimates for singing males ha^{-1} (mean ± SE) generated from four survey methods (for acronyms, see text) for five bird species in old-growth forests in southeast Alaska, 2001–2002. Coefficient of variation (%) is in parentheses. See Appendix 1 for sample sizes.

Observer	Pacific-slope Flycatcher	Winter Wren	Golden-crowned Kinglet	Hermit Thrush	Townsend's Warbler
Single-observer	1.17 ± 0.03 (3)	0.84 ± 0.12 (14)	0.38 ± 0.04 (11)	0.22 ± 0.03 (14)	0.64 ± 0.04 (6)
SOVCP	3.63 ± 0.33 (6)	1.70 ± 0.41 (24)	2.92 ± 0.86 (29)	0.31 ± 0.03 (10)	1.17 ± 0.13 (11)
Double-observer	1.85 ± 0.01 (1)	1.39 ± 0.01 (1)	0.72 ± 0.01 (1)	0.36 ± 0.01 (3)	1.05 ± 0.01 (1)
POVCP	3.78 ± 0.04 (1)	1.86 ± 0.03 (2)	2.94 ± 0.07 (2)	0.38 ± 0.05 (13)	1.27 ± 0.05 (4)

SOVCP methods were generally robust to violations of the assumption of perfect detection at distance zero. Estimates generated using POVCP were much more precise, however, likely because they estimate the proportion of birds missed by each observer, than those estimated with SOVCP methods.

Differences in $g(0)$ among observers and species that we measured are consistent with findings from other studies (e.g., Laake et al. 1997, Laake 1999, Evans Mack et al. 2002, Farnsworth et al. 2002). Observer experience, attentiveness, and hearing acuity are significant factors affecting the ability to detect birds (Emlen and DeJong 1981). Covariates (other than observer and species) we considered in our study did not help to explain variability in detection probabilities. Modeling of the covariates is the most complicated step in analysis of POVCP data and, therefore, their seemingly insignificant value may not warrant the additional modeling effort. If the effect of covariates is expected to be negligible, the simplest approach to analysis would be to estimate the proportion of birds missed by an observer within the "perfect" detection radius without considering additional explanatory variables. Detection probabilities could then be estimated using methods described in Nichols et al. (2000), but availability bias would remain problematic.

The double-observer fixed-radius approach produced comparable detection probabilities, but we found that it was incorrect to assume that the effective area surveyed was uniform for all observers and species. As a result, this density estimator was biased low except when the effective area surveyed was >50 m, as for the Hermit Thrush. For species that can be detected at long distances, density estimates using the double-observer approach and POVCP will likely be similar, with minor differences resulting from variation in the number of detections used in the two methods. Regardless, few species and observers will likely have perfect detection radii out to 50 m. Although a smaller fixed radius could be used, too small a radius will unnecessarily decrease the number of birds included in the analysis.

Applying the Paired-observer, Variable Circular-plot Technique

A combination of double-observer and distance sampling proved valuable and practical for estimating detection probabilities and obtaining the least-biased density estimator. Survey techniques that involve paired observers offer several advantages. Inexperienced observers receive immediate feedback regarding count results, which improves their field skills. Likewise, observers are motivated to remain attentive and to sharpen bird-identification and distance-estimation skills because they are constantly being evaluated against their partner. Most importantly, estimates of detection probabilities at or near the plot center are relatively high when paired observers independently and simultaneously conduct the point count. By estimating the detection probability at plot center, as opposed to assuming perfect detection, $g(r)$ can be rescaled to be 1 at the point (Williams et al. 2002).

Although compliance with key assumptions can be evaluated to assess potential biases of the estimator, only a known benchmark of density (a virtual impossibility outside of small aviaries) will address all sources of bias, including availability bias. Without knowing true densities in our study area, we evaluated the adequacy of POVCP by measuring how closely key assumptions were satisfied.

Assumption 1: Paired observers collect data independently.—During field application, this assumption may be difficult to achieve; however, with adequate training of observers, we are confident that observer independence can be obtained, and violation of this assumption will be rare. One observer may notice another observer focusing attention in one direction, prompting the former to focus his or her attention in the same direction (Farnsworth et al. 2005). Nichols et al. (2000) suggest encouraging observers to occasionally scribble on their data sheets to discourage observers from following cues provided by their partner. Laser rangefinders are often used to aid in distance estimation, but can also cue observers. We recommend directing observers to estimate distance during the count and verify their distance estimate using a laser rangefinder after the count. In general, if bird density is high, observers will be more focused on recording bird activity during the count and less distracted by the second observer. Therefore, independence between observers may be more difficult to achieve in areas with low densities of birds. Educating observers on the assumptions of the method will improve quality of the data and adequacy of this assumption of independence.

Assumption 2: Birds are detected at their initial location.—Distance-sampling methods assume that there is no random movement of birds during the count period or evasive movement of birds in response to the observer, and point-transect sampling is less robust to object movements than line-transect methods (Buckland et al. 2001). With longer count periods, there is increased potential for positive bias owing to random movement of birds (Buckland et al. 2001), but shorter counts result in fewer detections. Observer disturbance can elicit two different behaviors: (1) birds are flushed from their initial location or (2) birds are motionless and secretive. Flushed birds can move either beyond the range of detectability, which can result in negative bias, or within the area of detectability, which can result in double-counting of birds. Roeder et al. (1987) showed that variable circular-plot methods could provide reasonable results in the presence of moderate (~10 m) amounts of bird disturbance, but results were much more sensitive to hidden birds than to flushed birds. If birds hide from detection by observers, the density estimator will be biased low.

Detection of birds at their initial location is the most difficult assumption to meet when using distance-sampling methods, because it is difficult to measure. Length of counts should be short enough to minimize random movements of birds, but long enough to accumulate a sufficient number of detections. Although length of count (8 min) in the present study was relatively long compared with the "snapshot" approach (Buckland et al. 2001), naturally low densities of birds in our study area allowed observers to concentrate on any major movements made during the count period, and most smaller movements, while undetected, were unlikely to affect estimates of density. A longer waiting period before the count may address issues of responsive movement; but also, observers in the field must be alert and attentive when approaching the point to minimize disturbance of birds. Birds that are flushed by the observer while approaching the count station should be recorded as if they were detected during the count period. Thompson et al. (1998) suggested using distance categories that are large enough to allow for responsive movement, but small enough to have a minimum of five distance categories. We agree with Buckland et al. (2001) to record exact distances and assign distance categories at the analysis stage, at which time intervals can be adjusted to accommodate responsive movements.

Assumption 3: Distance is measured without error.—In the dense forests of southeast Alaska, most birds are detected aurally and distance estimation can be difficult, but extensive training and use of laser rangefinders can help observers meet this assumption. Scott et al. (1981) provided several suggestions for minimizing measurement errors. It should be emphasized to all observers that detections close to the point are most important and their attention should be focused on the immediate surrounding area (Scott et al. 1981). The POVCP technique averages distances to birds detected by both observers, which results in a more precise distance estimate, provided that the estimates are unbiased. Additionally, distance estimation skills for all observers are continually refined and calibrated using the POVCP approach. More experienced observers are better prepared for methods that involve distance sampling, because they are more knowledgeable about bird behavior and song.

In the present study, distance to each bird was estimated to the nearest meter. Although it may seem unreasonable to make such exact estimates, this level of resolution allowed for a more meaningful exploratory analysis. The flexibility in assigning distance categories *a posteriori* maximized model fit. We believe that accurate distance estimation is possible with well-trained observers. To illustrate this point, we examined the variation in distance estimates when both observers detected the same bird. Overall, paired distance estimates were within 8.7 ± 0.3 m (n = 1,070) of each other. We further evaluated the precision of paired distance estimates using six distance categories (0–10, 11–20, 21–30, 31–40, 41–50, ≥51 m). Not surprisingly, precision decreased with increasing distance from plot center (0–10 m: 2.6 ± 0.4, n = 57; 11–20 m: 5.5 ± 0.3, n = 209; 21–30 m: 6.9 ± 0.4, n = 242; 31–40 m: 7.6 ± 0.4, n = 218; 41–50 m: 9.4 ± 0.6, n = 159; ≥51 m: 17.6 ± 1.6, n = 185). Despite the variability in estimates as distance from plot center increased, we suggest that observers record exact distances, allowing for evaluation of assumptions and flexibility during analysis (Norvell et al. 2003). If distance categories are desired, our data show that 10-m intervals are reasonable, at least within 50 m of plot center. Given the high level of agreement between observers' estimates, we would expect that accuracy would be similarly high, though that would need to be tested explicitly for birds at known distances.

Assumption 4: Independent observers' data are correctly combined.—Among the greater challenges when applying the POVCP technique is combining observers' data and correctly identifying birds detected by one observer only and birds detected by both observers. Because birds detected by one observer but not the other provide information about the detection probability of each observer, violation of this assumption could introduce serious difficulties for estimating detection probabilities and densities. To minimize this problem, observers recorded time and movements of birds detected during the count period, were encouraged to discuss detections after the count, and noted any discrepancies between observers. Recording of movements and time of detections allowed observers to determine the bird's location when first detected (Assumption 2).

Although we took precautions, this assumption may have been violated. By far, the birds most difficult for us to reconcile were the Hermit Thrushes. The ventriloqual voice of a Hermit Thrush resonates throughout the forest, making it difficult to determine the direction and distance from which the bird is singing. Occasionally, when the count period ended, both observers agreed on the species and number of birds detected but not on the direction. DeSante (1986) noted the same problem for estimating density of species with ventriloqual voices using distance-sampling methods. We attributed much of the observer variability in Hermit Thrush detection probabilities to this phenomenon. Several measures can be taken to minimize this problem: (1) observers should be encouraged to use techniques to determine directionality, such as covering one ear and carefully listening for birds in the presumed direction; (2) observers should record time of detection for each bird; and (3) at the end of the count period, observers should compare data sheets and resolve any ambiguities related to particular detections.

Bird densities in the forests of southeast Alaska are relatively low compared with regions in lower latitudes of North America, where it may be harder for observers to decide whether the birds detected were the same or different. A shorter count period would likely reduce any problems when combining both observers' data, but would also result in fewer detections. Carefully trained and experienced observers can minimize the likelihood of incorrectly combining data from both observers, but we believe that the POVCP method will be more difficult to implement in areas with a high density of birds unless creative approaches are used.

Assumption 5: An observer's detection probability does not change according to the identity of the other observer conducting the count.—Observers have different abilities to hear birds at different distances. If a bird was detected by one observer and not by the other, we assumed that the bird was detectable by both observers, which may have been a spurious assumption. This problem is not unique to this survey technique; all sampling that involves two observers assumes that all birds used in the analysis were potentially detectable by both observers present at the count station (Nichols et al. 2000). Truncation of the data at a specified distance minimizes this problem but does not eliminate it. To avoid violation of this assumption, alternate observers should be paired with different observers when feasible. This, of course, is possible only if the study is designed to use more than two observers.

Disadvantages of the Paired-observer, Variable Circular-plot Method

Although the density estimator of the POVCP method appeared to be the least biased, there are limitations to this survey technique. Farnsworth et al. (2005) described two components of detection probability: P_a is the probability that a bird vocalizes during a count, and P_b is the probability that this vocalization is detected by an observer. Marsh and Sinclair (1989) used the terms "availability bias" and "perception bias" to describe effects of P_a and P_b, respectively. The POVCP technique addresses P_b but fails to account for P_a, or availability bias, which can be a substantial source of bias that may be much larger than perception bias (Laake and Borchers 2004). Estimation of P_a can be difficult and expensive, usually requiring marked animals (see Laake and Borchers 2004). Farnsworth et al. (2002) suggested the use of temporal removal methods for estimating P_a; however, these methods require longer counts, which may result in a positive bias because of birds moving into the detection radius, violating the assumption that birds are detected at their initial locations. All survey methods examined in our study, including POVCP, fail to account for availability bias; POVCP only estimates P_b, or the probability that—because of environmental conditions, fatigue, or other such factors—an observer overlooks birds that are otherwise detectable.

If the magnitude of availability bias is high, the variance estimator can also be biased. For example, a survey method may effectively detect nearly all the individuals "available" for detection given the survey method, resulting in counts that are very close. However, if availability bias is high, density estimators may be very precise but inaccurate. Again, we are unable to assess the potential bias of the variance estimator of POVCP without a known benchmark of density.

The POVCP technique requires two skilled observers to be present at each count station, which potentially increases survey costs. However, in areas like southeast Alaska, where two people are required to be present because of safety concerns, the POVCP technique offers an improvement over existing methods without adding significant cost. To reduce costs, correction factors can be calculated using a portion of count stations, assuming that an observer's ability does not change over time and that similar habitats are surveyed. If correction factors are reapplied, we suggest occasionally refining the estimates to ensure their accuracy.

Analyzing data collected using the POVCP method is more complex than analyzing data collected with other methods. Modeling correction factors for each species and observer given certain environmental conditions is time-consuming and requires statistical expertise. The major advantage of POVCP over other methods we examined in the present study was a gain in precision of the density estimates, but clearly this method requires the most complicated analysis. Therefore, project objectives should necessitate precise density estimates to warrant the increased complexity and time required to implement POVCP.

Recommendations

Point-count surveys are an efficient, cost-effective technique for estimating abundance of land birds, but a minimally biased estimator is essential for addressing management concerns, providing a basis for monitoring, and testing scientific hypotheses. Survey methods are often driven by the goals and objectives of the project, but quality and reliability of data should be maximized. For point-count surveys, techniques must include ways to estimate both detection probabilities and the effective area sampled.

We recommend using the POVCP technique described here to estimate detection probabilities and density, particularly when precise density estimates are necessitated, such as with species or habitats of concern, threatened or endangered species, or species difficult to detect. This survey method performed well in the dense forests of southeast Alaska, providing precise density estimates of breeding songbirds. The SOVCP method also performed well and appeared to be robust to violations of assumptions. We conclude that either of these methods is an adequate survey method for estimating detection probabilities and density, but if project goals require precise estimates of density, the POVCP method is preferred.

If POVCP is applied, precautions must be taken to meet all assumptions. In general, we recommend the following guidelines for developing new survey protocols that involve distance sampling and double-observer sampling methods. (1) Estimate the exact distance to each bird. If this task is too daunting, we recommend using distance intervals of 10 m. (2) Intensively train observers. A rigorous training program should include field exercises, information about the theory of distance estimation, discussion of potential biases in the field, and a clear explanation of the assumptions (see Kepler and Scott [1981] and Scott et al. [1986] for specific recommendations regarding training programs). Observers should practice distance estimation in all habitats scheduled for survey. A prepared and well-trained observer will have the skills and knowledge to make good decisions.

We strongly agree with others that the use of unadjusted point counts is unacceptable in light of recent methodological advances (Rosenstock et al. 2002, Thompson 2002, Norvell et al. 2003, Farnsworth et al. 2005). Combining SOVCP or POVCP with temporal removal methods (Farnsworth et al. 2002) holds promise for further reducing bias and providing more accurate and repeatable estimates of abundance. By increasing the reliability of density estimates, such model-based techniques will not only improve our scientific knowledge of birds, but will also aid in making more informed decisions about conservation and land management.

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Literature Cited

Alaback, P. B. 1982. Dynamics of understory biomass in Sitka spruce-western hemlock forests of southeast Alaska. Ecology 63: 1932–1948.

Alpizar-Jara, R., and K. H. Pollock. 1996. A combination of line transect and capture–recapture sampling model for multiple observers in aerial surveys. Environmental and Ecological Statistics 3:311–327.

Barker, R. J., and J. R. Sauer. 1995. Statistical aspects of point count sampling. Pages 125–130 *in* Monitoring Bird Populations by Point Counts (C. J. Ralph, J. R. Sauer, and S. Droege, Eds.). U.S. Department of Agriculture, Forest Service General Technical Report PSW-GTR-149.

Borchers, D. L., S. T. Buckland, P. W. Goedhart, E. D. Clarke, and S. L. Hedley. 1998a. Horvitz-Thompson estimators for double-platform line transect surveys. Biometrics 54:1221–1237.

Borchers, D. L., W. Zucchini, and R. M. Fewster. 1998b. Mark–recapture models for line transect surveys. Biometrics 54:1207–1220.

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. Introduction to Distance Sampling. Oxford University Press, Oxford.

Buckland, S. T., K. P. Burnham, D. R. Anderson, and J. L. Laake. 1993. Distance Sampling: Estimation of Abundance of Biological Populations. Chapman and Hall, London.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Inference: A Practical Information-theoretic Approach, 2nd ed. Springer-Verlag, New York.

Caouette, J. P., M. G. Kramer, and G. Nowacki. 2000. Deconstructing the timber volume paradigm in management of the Tongass National Forest. U.S. Department of Agriculture, Forest Service General Technical Report PNW-GTR-482.

Cochran, W. G. 1977. Sampling Techniques. John Wiley and Sons, New York.

Cook, R. D., and J. O. Jacobson. 1979. A design for estimating visibility bias in aerial surveys. Biometrics 35:735–742.

Dellasala, D. A., J. C. Hagar, K. A. Engel, W. C. McComb, R. L. Fairbanks, and E. G. Campbell. 1996. Effects of silvicultural modifications of temperate rainforest on breeding and wintering bird communities, Prince of Wales Island, southeast Alaska. Condor 98:706–721.

DeSante, D. F. 1981. A field test of the variable circular-plot censusing technique in a California coastal scrub breeding bird community. Pages 177–185 *in* Estimating Numbers of Terrestrial Birds (C. J. Ralph and J. M. Scott, Eds.). Studies in Avian Biology, no. 6.

DeSante, D. F. 1986. A field test of the variable circular-plot censusing method in a Sierran subalpine forest habitat. Condor 88:129–142.

Diefenbach, D. R., D. W. Brauning, and J. A. Mattice. 2003. Variability in grassland bird counts related to observer differences and species detection rates. Auk 120:1168–1179.

Emlen, J. T., and M. J. DeJong. 1981. The application of song detection threshold distance to census operations. Pages 346–352 *in*

Estimating Numbers of Terrestrial Birds (C. J. Ralph and J. M. Scott, Eds.). Studies in Avian Biology, no. 6.

Evans Mack, D., M. G. Raphael, and J. L. Laake. 2002. Probability of detecting Marbled Murrelets at sea: Effects of single versus paired observers. Journal of Wildlife Management 66:865–873.

Farnsworth, G. L., J. D. Nichols, J. R. Sauer, S. G. Fancy, K. H. Pollock, S. A. Shriner, and T. R. Simons. 2005. Statistical approaches to the analysis of point count data: A little extra information can go a long way. *In* Bird Conservation, Implementation, and Integration in the Americas: Proceedings of the Third International Partners in Flight Conference 2002 (C. J. Ralph and T. D. Rich, Eds.). U.S. Department of Agriculture, Forest Service General Technical Report GTR-PSW-191.

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.

Gates, C. E. 1969. Simulation study of estimators for the line transect sampling method. Biometrics 25:317–328.

Kepler, C. B., and J. M. Scott. 1981. Reducing bird count variability by training observers. Pages 366–371 *in* Estimating Numbers of Terrestrial Birds (C. J. Ralph and J. M. Scott, Eds.). Studies in Avian Biology, no. 6.

Kissling, M. L. 2003. Effects of forested buffer width on breeding bird communities in coastal forests of southeast Alaska with a comparison of avian sampling techniques. M.S. thesis, University of Idaho, Moscow.

Laake, J. L. 1999. Distance sampling with independent observers: Reducing bias from heterogeneity by weakening the conditional independence assumption. Pages 137–148 *in* Marine Mammal Survey and Assessment Methods (G. W. Garner, S. C. Amstrup, J. L. Laake, B. F. J. Manly, L. L. McDonald, and D. G. Robertson, Eds.). Balkema, Rotterdam, The Netherlands.

Laake, J. L., and D. L. Borchers. 2004. Methods for incomplete detection at distance zero. Pages 108–189 *in* Advanced Distance Sampling (S. T. Buckland, D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas, Eds.). Oxford University Press, Oxford.

Laake, J. L., J. C. Calambokidis, S. D. Osmek, and D. J. Rugh. 1997. Probability of detecting harbor porpoise from aerial surveys: Estimating $g(0)$. Journal of Wildlife Management 61:63–75.

Lancia, R. A., J. D. Nichols, and K. H. Pollock. 1994. Estimating the number of animals in wildlife populations. Pages 215–253 *in* Research and Management Techniques for Wildlife and Habitats (T. A. Bookhout, Ed.). The Wildlife Society, Bethesda, Maryland.

Manly, B. F. J., L. L. McDonald, and G. W. Garner. 1996. Maximum likelihood estimation for the double-count method with independent observers. Journal of Agricultural, Biological, and Environmental Statistics 1: 170–189.

Marsh, H., and D. F. Sinclair. 1989. Correcting for visibility bias in strip transect aerial surveys of aquatic fauna. Journal of Wildlife Management 53:1017–1024.

McCracken, M. L. 1994. Factors affecting bird counts and their influence on density estimates. Ph.D. dissertation, Oregon State University, Corvallis.

Nelson, J. T., and S. G. Fancy. 1999. A test of the variable circular-plot method where exact density of a bird population was known. Pacific Conservation Biology 5:139–143.

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.

Norvell, R. E., F. P. Howe, and J. R. Parrish. 2003. A seven-year comparison of relative-abundance and distance-sampling methods. Auk 120:1013–1028.

Reynolds, R. T., J. M. Scott, and R. A. Nussbaum. 1980. A variable circular-plot method for estimating bird numbers. Condor 82:309–313.

Roeder, K., B. Dennis, and E. O. Garton. 1987. Estimating density from variable circular-plot censuses. Journal of Wildlife Management 51:224–230.

Rosenstock, S. 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.

SAS Institute. 1999. SAS/STAT User's Guide, Release 8.02. SAS Institute, Cary, North Carolina.

Scott, J. M., S. Mountainspring, F. L. Ramsey, and C. B. Kepler. 1986. Forest bird communities of the Hawaiian Islands: Their dynamics, ecology, and conservation. Studies in Avian Biology, no. 9.

Scott, J. M., F. L. Ramsey, and C. B. Kepler. 1981. Distance estimation as a variable in estimating bird numbers from vocalizations. Pages 334–340 *in* Estimating Numbers of Terrestrial Birds (C. J. Ralph and J. M. Scott, Eds.). Studies in Avian Biology, no. 6.

Seber, G. A. F. 1973. The Estimation of Animal Abundance. Hafner, New York.

Steinhorst, R. K., and M. D. Samuel. 1989. Sightability adjustment methods for aerial surveys of wildlife populations. Biometrics 45:415–425.

Thomas, L., S. T. Buckland, K. P. Burnham, D. R. Anderson, J. L. Laake, D. L. Borchers, and S. Strindberg. 2002. Distance sampling. Pages 544–552 *in* Encyclopedia of Environmetrics, vol. 1 (A. H. El-Shaarawi and W. W. Piegorsch, Eds.). John Wiley and Sons, Chichester, United Kingdom.

Thompson, W. L. 2002. Towards reliable bird surveys: Accounting for individuals present but not detected. Auk 119:18–25.

Thompson, W. L., G. C. White, and C. Gowan. 1998. Monitoring Vertebrate Populations. Academic Press, San Diego, California.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and Management of Animal Populations. Academic Press, San Diego, California.

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Appendix 1. Total number of detections by species and survey method.

		Number of detections			
Common name	Scientific name	Single-observer [a]	SOVCP [b]	Double-observer [a]	POVCP [b]
Pacific-slope Flycatcher	*Empidonax difficilis*	883	986	1,129	1,744
Winter Wren	*Troglodytes troglodytes*	631	950	894	1,569
Golden-crowned Kinglet	*Regulus satrapa*	286	299	371	530
Hermit Thrush	*Catharus guttatus*	168	511	240	824
Townsend's Warbler	*Dendroica townsendi*	480	607	649	1,047

[a] 50-m fixed radius.
[b] Unlimited radius.

Appendix 2. Logistic models explaining variation in detectability within the perfect detection radius of five bird species. Models are listed in order of ΔAIC_c, and only those models with strong support ($\Delta AIC_c \leq 2$) are shown.

Species (j)	Observer (i)	"Perfect" detection radius (m)	n [a]	Model (u)	Explanatory variables [b] (z)	ΔAIC_c	AIC_c weight
Pacific-slope Flycatcher	1 [c]	14	42	G_{CANOPY}	CC	0	0.40
				$G_{INTERCEPT}$	–	0.80	0.27
	2 [c]	16	60	G_{ENV}	PREC, WIND, NSE	0	0.42
				$G_{INTERCEPT}$	–	0.18	0.39
	3 [c]	31	152	$G_{INTERCEPT}$	–	0	0.62
				G_{CANOPY}	CC	1.61	0.28
	4 [c]	16	84	$G_{INTERCEPT}$	–	0	0.62
				G_{CANOPY}	CC	1.79	0.25
	5 [c]	17	55	G_{CANOPY}	CC	0	0.52

Appendix 2. Continued.

Species (j)	Observer (i)	"Perfect" detection radius (m)	n [a]	Model (u)	Explanatory variables [b] (z)	ΔAIC_c	AIC_c weight
Pacific-slope Flycatcher				$G_{INTERCEPT}$	–	1.81	0.45
	6 [c]	21	94	$G_{INTERCEPT}$	–	0	0.50
				G_{CANOPY}	CC	0.33	0.45
	7 [c]	15	50	G_{CANOPY}	CC	0	0.62
				$G_{INTERCEPT}$	–	1.67	0.27
Winter Wren	1 [c]	16	39	$G_{INTERCEPT}$	–	0	0.51
				G_{CANOPY}	CC	1.00	0.31
	2 [c]	20	85	G_{CANOPY}	CC	0	0.45
				$G_{INTERCEPT}$	–	0.13	0.42
	3 [c]	19	20	G_{CANOPY}	CC	0	0.44
				$G_{INTERCEPT}$	–	0.09	0.42
	4 [c]	25	96	$G_{INTERCEPT}$	–	0	0.57
				G_{CANOPY}	CC	1.16	0.32
	5	23	56	$G_{INTERCEPT}$	–	0	0.91
	6 [c]	18	18	$G_{INTERCEPT}$	–	0	0.50
				G_{CANOPY}	CC	0.21	0.45
	7	22	41	G_{CANOPY}	CC	0	0.79
Golden-crowned Kinglet	1	12	48	G_{CANOPY}	CC	0	0.74
	2 [c]	12	45	$G_{INTERCEPT}$	–	0	0.66
				G_{CANOPY}	CC	1.93	0.25
	3	1	1		NO MODEL [d]		
	4 [c]	12	111	G_{CANOPY}	CC	0	0.27
				G_{ENV}	PREC, WIND, NSE	0.01	0.27
				$G_{INTERCEPT}$	-	0.33	0.23
	5 [c]	25	101	$G_{INTERCEPT}$	–	0	0.42
				G_{ENV}	PREC, WIND, NSE	0.61	0.31
				G_{CANOPY}	CC	1.63	0.19
	6 [c]	20	80	$G_{INTERCEPT}$	–	0	0.48
				G_{CANOPY}	CC	0.45	0.38
	7 [c]	18	78	G_{CANOPY}	CC	0	0.42
				$G_{INTERCEPT}$	–	0.03	0.41
Hermit Thrush	1	40	33	G_{SITE}	CC, SC, SLP	0	0.83
	2	51	54	G_{CANOPY}	CC	0	0.77
	3	22	14		NO MODEL [d]		
	4 [c]	40	67	$G_{INTERCEPT}$	–	0	0.67
				G_{CANOPY}	CC	1.92	0.26
	5	50	52	G_{CANOPY}	CC	0	0.84
	6	57	72	$G_{INTERCEPT}$	–	0	0.76
	7	40	38	$G_{INTERCEPT}$	–	0	0.84
Townsend's Warbler	1	13	9		NO MODEL [d]		
	2 [c]	23	52	$G_{INTERCEPT}$	–	0	0.50
				G_{CANOPY}	CC	1.23	0.27
	3	19	18	$G_{INTERCEPT}$	–	0	0.74

APPENDIX 2. Continued.

Species (j)	Observer (i)	"Perfect" detection radius (m)	n [a]	Model (u)	Explanatory variables [b] (z)	ΔAIC_c	AIC_c weight
Townsend's Warbler	4 [c]	31	137	$G_{INTERCEPT}$	–	0	0.49
				G_{SITE}	CC, SC, SLP	1.51	0.23
				G_{CANOPY}	CC	1.87	0.19
	5	30	73	G_{CANOPY}	CC	0	0.78
	6 [c]	36	86	G_{ENV}	PREC, WIND, NSE	0	0.62
				$G_{INTERCEPT}$	–	1.95	0.23
	7 [c]	28	66	$G_{INTERCEPT}$	–	0	0.42
				G_{SITE}	CC, SC, SLP	0.70	0.30
				G_{CANOPY}	CC	1.74	0.18

[a] Number of detections within the "perfect" detection radius.

[b] Abbreviations: CC = percentage of canopy cover, SC = percentage of shrub cover, SLP = percentage of slope, WIND = wind intensity, PREC = precipitation level, NSE = noise intensity.

[c] Multimodel inference was used to calculate a model-averaged estimator because $\Delta AIC_c \leq 2$.

[d] Observer detected all birds within the "perfect" detection radius; therefore, a correction factor was not modeled.