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IMPROVING ESTIMATES OF BIRD DENSITY USING MULTIPLE-COVARIATE DISTANCE SAMPLING

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Abstract.—Inferences based on counts adjusted for detectability represent a marked improvement over unadjusted counts, which provide no information about true population density and rely on untestable and unrealistic assumptions about constant detectability for inferring differences in density over time or space. Distance sampling is a widely used method to estimate detectability and therefore density. In the standard method, we model the probability of detecting a bird as a function of distance alone. Here, we describe methods that allow us to model probability of detection as a function of additional covariates—an approach available in DISTANCE, version 5.0 (Thomas et al. 2005) but still not widely applied. The main use of these methods is to increase the reliability of density estimates made on subsets of the whole data (e.g., estimates for different habitats, treatments, periods, or species), to increase precision of density estimates or to allow inferences about the covariates themselves. We present a case study of the use of multiple covariates in an analysis of a point-transect survey of Hawaii Amakihi (*Hemignathus virens*). *Received 2 June 2006, accepted 2 November 2006.*

Key words: covariates, detectability, detection function, distance sampling, line transects, point transects.

Amélioration des estimations de densité d'oiseaux par l'utilisation de l'échantillonnage par la distance avec covariables multiples

Résumé.—L'inférence basée sur des comptages ajustés pour la détectabilité représentent un progrès marqué par rapport aux comptages non ajustés, ces derniers ne fournissant pas d'information sur la densité réelle d'une population et reposant sur des hypothèses non testables et non réalistes d'une détectabilité constante pour inférer des différences de densité dans le temps ou dans l'espace. L'échantillonnage par la distance est une méthode largement utilisée pour estimer la détectabilité et donc la densité. Dans la méthode standard, la probabilité de détecter un oiseau est modélisée comme une fonction de la distance seulement. Ici, nous décrivons des méthodes qui permettent de modéliser la probabilité de détection comme une fonction de covariables supplémentaires—une approche disponible dans le logiciel DISTANCE mais encore peu appliquée. Les avantages principaux de ces méthodes sont d'augmenter la fiabilité des estimations de densité faites sur des sous-ensembles de données complètes (par exemple des estimations pour différents habitats, traitements, périodes de temps ou espèces), d'augmenter la précision des

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estimations de densité ou de permettre l'inférence sur les covariables elles-mêmes. Nous présentons un cas d'étude de l'utilisation de covariables multiples : une analyse de données obtenues via un échantillonnage par transects ponctuels de *Hemignathus virens*.

UNADJUSTED COUNTS OF birds detected during a survey are often used to make inferences about the relative density or abundance of bird populations. However, their general use has been criticized. It is widely recognized that adjusting for detectability provides the basis for stronger inferences by removing the need to rely on untestable and unrealistic assumptions of constant detectability (e.g., Rosenstock et al. 2002, Thompson 2002, Diefenbach et al. 2003). Distance sampling is one of the most widely used methods for adjusting counts for detectability, which allows the estimation of absolute density and abundance of wild animals, including birds. Over the past decade, several new developments have made the methods more widely applicable, leading to increased precision and reducing the bias under specific settings. The methods are discussed in detail in Buckland et al. (2001, 2004), and descriptions oriented toward bird studies are given in a recent book (Bibby et al. 2000) and several papers (Rosenstock et al. 2002, Buckland 2006).

There are two main varieties of distance-sampling survey: line transects and point transects. In the former, the survey is performed from a set of randomly located lines, in the latter, from a set of randomly located points. In both, the basic idea is the same. Observers record the distance from the line or point to all birds detected within some truncation distance, w (which in practice may be infinity, i.e., all detections are recorded). Not all the birds within distance w will be detected, but a fundamental assumption of the standard methods is that all birds at zero distance are detected. Intuitively, one would expect that birds become harder to detect, on average, with increasing distance from the line or point. The key to distance sampling is to use the distribution of the observed distances to estimate the "detection function," $g(y)$, the probability of detecting a bird at distance y. This function can then be used to estimate the average probability of detecting a bird given that it is within w of the line or point, denoted P_a. Given an estimate of P_a, bird density can be estimated as

$$\hat{D} = \frac{n}{a\hat{P}_a} \qquad (1)$$

where n is the number of birds detected and a is the size of the covered region. For line transects, a is the total length of the transect multiplied by twice the half-width w of the strip. For point transects, it is equal to the number of points multiplied by the area of the circle around the point, πw^2. Abundance, if required, is simply density multiplied by the size of the study area.

In reality, in addition to its distance from the line or point, the probability of detecting a bird depends on many factors, including the habitat, weather conditions, observer, bird behavior, etc. (Diefenbach et al. 2003 and references therein). Perhaps surprisingly, ignoring all these other factors besides distance usually causes little or no bias in the estimate of P_a and therefore density, because the standard models used for the detection function are "pooling robust" (Burnham et al. 1980, 2004; Buckland et al. 2001). Nevertheless, there are some circumstances in which it may be advantageous to include some of these other factors as additional covariates in the detection function model—either to reduce bias in situations where pooling robustness does not apply or to increase precision. Extending previous work in this area (Ramsey et al. 1987, Fancy 1997, Beavers and Ramsey 1998), new multiple-covariates distance sampling (MCDS) methods have been developed (Marques and Buckland 2003, 2004) and are now available in DISTANCE, version 5.0 (Thomas et al. 2005). However, they have yet to see widespread use in the ornithological community, perhaps because of the lack of an accessible description of the methods and their uses. The purpose of the present paper is to (1) provide a clear outline of the theory and assumptions behind the multiple-covariate methods; (2) describe when these methods are useful; and (3) provide an example of their use, including guidelines for analysis of similar distance data with multiple covariates.

Conventional Distance Sampling

To help understand the new methods, we begin with a partial overview of standard distance sampling, often called conventional distance sampling (CDS), as described in detail by Buckland et al. (2001). We focus on explaining the detection function and how it is modeled, but, for brevity, we omit many important aspects of the methods, such as a complete statement of assumptions (Buckland et al. 2001) and how these can be accommodated or relaxed in bird studies (e.g., Buckland 2006, Kissling and Garton 2006).

Estimation of density.—We define the detection function, $g(y)$, as the probability of detecting a bird at a distance y. For line transects, y is the perpendicular distance from the line; for point transects, it is the radial distance from the point. In both cases, we assume that all birds at zero distance are detected with certainty, that is, that $g(0) = 1$. We specify a flexible, semiparametric model for $g(y)$ (see below) and aim to estimate the parameters of this model. If transects are located at random, then for line transects, the true number of birds will be the same, on average, at all distances from the line. Thus, changes in the number of birds observed with increasing distance from the line can be interpreted as changes in $g(y)$. This enables us to construct a statistical likelihood for the observed distances in terms of the parameters of $g(y)$, and this likelihood can be maximized to obtain parameter estimates. Similarly, for point transects, we expect the true number of birds in concentric "doughnuts" of a given width to increase linearly with distance from the point, because the area surveyed increases linearly (Buckland et al. 2001), and this can be used to construct the corresponding likelihood.

Given an estimate of the detection function, $\hat{g}(y)$, we can estimate the average probability of detection as

$$\hat{P}_a = \frac{1}{w}\int_0^w \hat{g}(y)dy \tag{2}$$

for line transects and

$$\hat{P}_a = \frac{2}{w^2}\int_0^w y\hat{g}(y)dy \tag{3}$$

for point transects. The result can then be used in Equation (1) to estimate density.

Formulas for estimating variance and confidence limits of the density estimate are given in Buckland et al. (2001). However, more robust estimates can be obtained using a nonparametric bootstrap, with resamples generated by sampling with replacement from the lines or points (Buckland et al. 2001).

Flexible models of the detection function.—For robust estimates of density, we require flexible models for the detection function (Buckland et al. 2001). Buckland et al. (2001) propose models of the form

$$g(y) = \frac{k(y)\left[1+s(y)\right]}{k(0)\left[1+s(0)\right]} \tag{4}$$

where $k(y)$ is a parametric key function and $s(y)$ is a series expansion that can be used to improve the fit of the models if required. The denominator ensures that $g(0) = 1$. Three key functions are suggested: uniform, half-normal, and hazard-rate (Table 1). The half-normal and hazard-rate functions both have a scale parameter, σ, which determines the rate at which the function decreases with increasing y. The hazard-rate

Table 1. Commonly used key functions and series expansions for the detection function (see fig. 2.6 in Buckland et al. [2001] for the shape of the key functions).

Key		Series expansion	
Uniform [a]	$1/w$	Cosine	$\sum_{j=2}^{m} a_j \cos(j\pi y_s)$
Half-normal	$\exp(-y^2/2\sigma^2)$	Simple polynomial	$\sum_{j=2}^{m} a_j (y_s)^{2j}$
Hazard-rate	$1 - \exp[-(y/\sigma)^{-b}]$	Hermite [b]	$\sum_{j=2}^{m} a_j H_{2j}(y_s)$

[a] If a series expansion is included with the uniform, then $j = 1, \ldots, m$ instead of $2, \ldots, m$.
[b] $H(x)$ denotes a Hermite function (see Kotz and Johnson [1982] for details).

function also has a shape parameter, b (see fig. 2.6 in Buckland et al. 2001). Simple functional forms such as these key functions may often not describe $g(y)$ adequately. Therefore, the shape of $g(y)$ can also be modified by adding one or more series expansion terms (also called adjustment terms), chosen from three suggested forms: cosine, simple polynomial, and Hermite polynomial (Table 1). This is illustrated for the example of a half-normal key function and cosine series expansion in Figure 1. Note from Table 1 that the adjustment terms are not functions of y directly—rather they depend on a scaled value of y, denoted y_s, where $y_s = y/w$ (or, if the default is overridden, $y_s = y/\sigma$). This makes the shape of the series expansion independent of the units used for y. Selection of the appropriate key function and series expansion for a given data set usually relies heavily on model-selection criteria such as Akaike's Information Criterion (AIC), but other considerations also play a role and there is no "cookbook" solution (Buckland et al. 2001).

MULTIPLE-COVARIATE DISTANCE SAMPLING

Multiple-covariate models.—We now extend the methods of the previous section so that the detection function is modeled as a function of both distance, y, and one or more additional covariates, represented by the vector $\mathbf{z}$. The probability of detection at a given distance and set of covariate values is therefore denoted $g(y, \mathbf{z})$. The covariates may be factor covariates (i.e., discrete classes such as habitat, observer, etc.), or nonfactor (numerical) covariates such as group (e.g., flock) size or percentage of canopy closure. They may be associated with the transects (e.g., habitat, time of day, weather, observer) or the birds (e.g., sex, group size).

There are many potential ways in which the covariates could affect the detection function (see Otto and Pollock 1990, Marques and Buckland 2004 for a review). One plausible and parsimonious approach is to assume that the covariates affect the scale but not the shape of the function (Fig. 2A). Both the half-normal and the hazard-rate key functions of the previous section have a scale parameter (σ), so we can make this parameter a function of the covariate values by writing

$$\sigma = \exp\left(\beta_0 + \sum_{j=1}^{J} \beta_j z_j\right) \qquad (5)$$

where z_j and β_j are the values of the jth covariate and parameter, respectively, and J is the number of covariates. The exponent ensures that σ

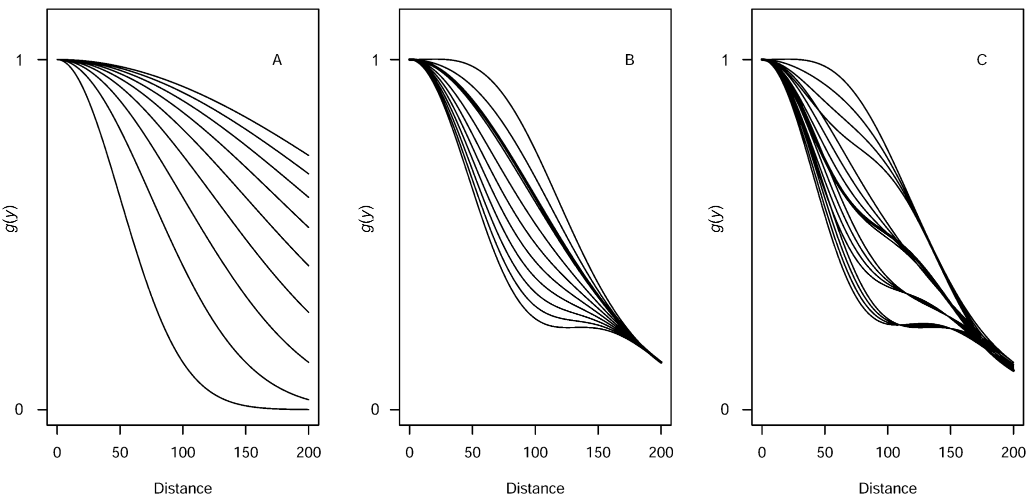

FIG. 1. Illustration of detection-function model formulation and the added flexibility provided by adjustment terms. (A) Half-normal detection function, with different scale parameters (σ = 50, 75, …, 225, 250). (B) Half-normal with σ = 100 and several different values of a single cosine adjustment term (j = 2 in Table 1). (C) Half-normal with σ = 100 and several different values of two cosine adjustment terms (j = 2, 3 in Table 1).

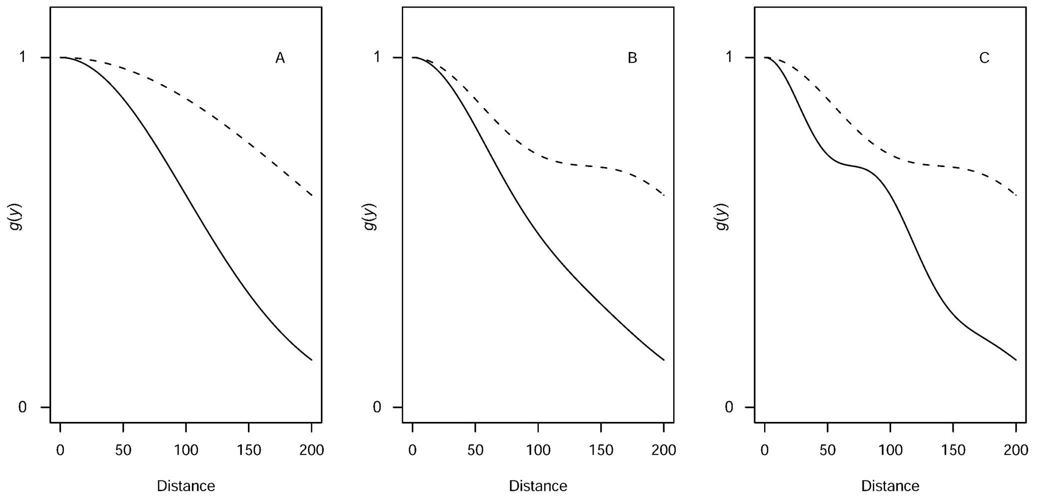

FIG. 2. Illustration of the effect of a factor covariate with two levels (z = 1, 2) on the key function (half-normal) with or without adjustment. (A) Key function without adjustment, with a scale term σ incorporating covariates: $\sigma = \exp[\log(50) + z \log(100/50)]$. (B) Key function with one cosine adjustment (a_2 = 0.1) in which distances are scaled by truncation distance ($y_s = y/w$). In this case, shape of overall detection function changes depending on covariate values. (C) Key function and one adjustment term as in (B) but with distances in adjustment term scaled by covariate scale parameter ($y_s = y/\sigma$). In this case, shape of overall composite detection-function is constant at all covariate values and only the scale varies.

is always positive. The uniform key function does not have a scale parameter, and so is not included in MCDS.

As with CDS, when the detection function includes series adjustment terms, we use scaled distances, y_s, in the adjustment terms, and the scaling can be either $y_s = y/w$ (the default for CDS) or $y_s = y/\sigma$ (Fig. 2B and C). Using the latter ensures that the overall detection-function shape is constant at all covariate values and only the scale varies—some evidence suggests that this is a more likely scenario (e.g., Otto and Pollock 1990), but see the example data set for a counter-example. Using the former means that the key function is affected by the covariates but the adjustment terms are not, so the shape of the overall composite detection-function changes depending on the covariate values. The two alternatives are different models, and the best can be chosen using model selection criteria such as AIC in the same way that the appropriate key function or adjustment terms are chosen. In practice, there is often little difference between them.

Estimation of the parameters of the extended multiple-covariate detection function is again via maximum likelihood. To derive the likelihood, Marques and Buckland (2004) use a statistical approach called "conditioning"—they condition on the observed values of the covariates (see Marques and Buckland 2004 for details). The advantage of this approach is that we do not need to specify a distribution for each covariate in the population. They also assume that the distribution of distances of all birds (as distinct from detected birds) from the line or point is independent of the distribution of the covariates. This will usually be true, provided that the lines or points are located at random, though see below for an example where this is not the case: the type of cue leading to a detection (visual vs. aural).

Estimation of density.—Given fitted values for the detection function, Marques and Buckland (2004) estimated density using the formula

$$\hat{D} = \frac{1}{a} \sum_{i=1}^{n} \frac{1}{\hat{P}_a(\mathbf{z}_i)} \qquad (6)$$

where a is the size of the covered region, n is the number of birds seen, and $\hat{P}_a(\mathbf{z}_i)$ is the estimated probability of detecting the ith bird given that it is within w of the line or point and has the covariate values $\mathbf{z}_i$. For line transects,

$$\hat{P}_a(\mathbf{z}_i) = \frac{1}{w}\int_0^w \hat{g}(y, \mathbf{z}_i)\,dy \tag{7}$$

while for point transects,

$$\hat{P}_a(\mathbf{z}_i) = \frac{2}{w^2}\int_0^w y\hat{g}(y, \mathbf{z}_i)\,dy \tag{8}$$

Marques and Buckland (2004) give formulas for estimating variance and confidence intervals using the above approach, but as with CDS, a more robust approach is to use a nonparametric bootstrap, resampling the lines or points.

Uses of multiple-covariate methods.—There are four situations in which the new MCDS methods offer the potential for improved inference relative to CDS.

The first situation is when we wish to estimate density using a subset of the data. An example is estimation of density by geographic stratum. If there are "sufficient" observations in each stratum (see Buckland et al. 2001 for a discussion of what is "sufficient"), a CDS strategy for this scenario is to estimate a separate detection function for each stratum and use the stratum-level estimates of P_a to obtain independent estimates of density by stratum using

$$\hat{D}_v = \frac{n_v}{a_v \hat{P}_{av}} \tag{9}$$

where, for stratum v, $\hat{D}_v$ is the estimated density, n_v is the number of observations, a_v is the size of the covered region, and $\hat{P}_{av}$ is the average probability of detection estimated from the observations. An alternative is to use all the observations to estimate a global detection function and use the global estimate of P_a to estimate density in each stratum:

$$\hat{D}_v = \frac{n_v}{a_v \hat{P}_a} \tag{10}$$

Using a global detection function introduces bias into the estimate of D_v if the true detection function is different by stratum. For example, if there are two strata and birds are easier to detect in the first than the second, then using the global $\hat{P}_a$ will overestimate density in the first stratum and underestimate it in the second. Nevertheless, it may be the only option available using CDS if there are not enough observations to fit a separate detection function by stratum. Even when there are sufficient observations in each stratum, using the pooled detection function will increase precision, so the choice of pooled versus stratified detection function can be seen as a model-selection problem, and selection criteria such as AIC can be used to determine which alternative gives the best trade-off between bias and precision.

The MCDS methods offer a third option—to include stratum as a factor covariate in a global multiple-covariate detection function, and then to estimate density by applying this detection function to the observations within each stratum:

$$\hat{D}_v = \frac{1}{a_v}\sum_{i=1}^{n_v} \frac{1}{\hat{P}_a(\mathbf{z}_{iv})} \tag{11}$$

where $\hat{P}_a(\mathbf{z}_{iv})$ is the probability of detecting the ith bird in stratum v given the observed covariates $\mathbf{z}_i$. The advantage of this approach is that it uses fewer parameters than a fully stratified detection-function model: the whole data set is used to provide information about the shape of the detection function, whereas the stratum-level data are used only to fit the scale. Thus, this option is viable when one or more strata contain too few observations for a fully stratified analysis. When sample sizes are larger, it may also be preferred over a fully stratified analysis using model-selection criteria because fewer parameters are used. We demonstrate this in the example analysis (see below).

Note that it may be appropriate to try covariates other than (or in addition to) stratum in such an analysis. For example, if there are many geographic strata for which we want density estimates, but it is believed that the main determinant of variation in detection probability is forest-stand age, then this may be a more appropriate covariate, and it requires only one extra parameter (if stand age is a nonfactor covariate). The estimate of $\hat{P}_a(\mathbf{z}_{iv})$ for each geographic stratum would then depend on the forest-stand age in that stratum. Similar examples are habitat, observer, etc. Model-selection criteria can be useful in selecting appropriate covariates. Note also that the strata need not be geographic—for example, we may wish to estimate density by time (see the example analysis), group size, species, etc. For an example of the use of MCDS methods to estimate density by species, see Alldredge et al. (2007).

The second situation where MCDS methods are useful is in cases where pooling robustness does not hold for CDS analyses. One example is where greater levels of survey intensity have been assigned to strata with higher densities of animals to increase efficiency (Buckland et al. 2001). In this case, pooling robustness does not apply (Burnham et al. 1980), and the only options are to estimate a separate detection function in each stratum or to use stratum as one of the covariates in an MCDS analysis. A second example is where there is extreme heterogeneity in detection probability between animals, perhaps because of different animal behaviors (males being showy vs. females cryptic), habitats, or observer behavior (e.g., guarding the trackline; Buckland et al. 2001). In this case, the composite detection function may have a very narrow shoulder (Fig. 3), which leads to unreliable estimates by CDS. Separating the different detection functions, either by stratification or by MCDS, may lead to more reliable inferences. Note, however, that this approach cannot be applied when the variable causing heterogeneity influences the distribution of distances from the transect in the population. For example, in many bird studies, detections may be either aural or visual. The visual detection function tends to decrease more rapidly than the aural one and, in extreme cases, can lead to a composite detection function like that of Figure 3. Where this is caused by a difference in detectability between singing males and other birds (mostly females), it is better to estimate abundance of singing males only (e.g., Buckland 2006), which may force the assumption that the number of territories corresponds with the number of singing males in the population. If nonsinging birds are sufficiently detectable, there may be sufficient data to include these in an MCDS analysis, with whether a bird is singing or not entered as a factor. Whether or not a bird was seen should not be used as a factor in an MCDS analysis, because if a bird is seen, it is excluded from the other category, and so those birds not seen will have a nonuniform distribution with respect to distance from the line.

A third use of MCDS is to reduce variance of the density estimate, by modeling heterogeneity in the detection function that is ignored in CDS methods. Thus, it may be worth using model-selection criteria to evaluate some MCDS models routinely, even when pooling robustness is believed to hold. However, the proportion of the overall variance estimate that comes from estimating the detection function is usually small for line transects in relation to point transects, so this strategy is more likely to be useful in reducing the variance for the latter type of survey, and even then might not result in a large reduction in most cases.

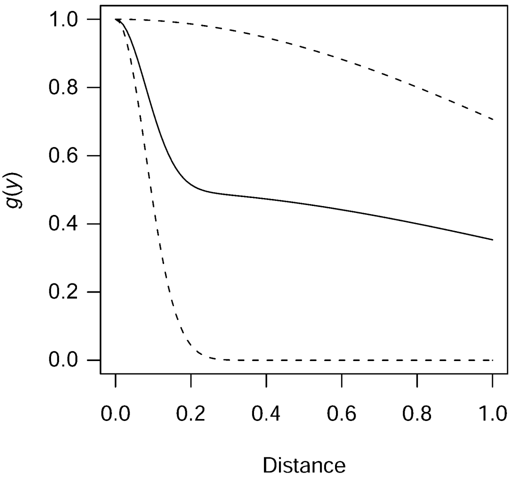

Fig. 3. A hypothetical example of a composite detection function, with males (upper dashed line) much more detectable than females (lower dashed line). Pooling robustness will not apply well in this case, because the composite detection function (solid line) has a strong "spike" close to zero distance; however, analysis using sex as covariate will produce much more reliable inferences.

Lastly, MCDS methods are useful where the covariates are of interest in their own right. Given a fitted detection function, the population distribution of any covariate in that function can be estimated. For example, if birds occur in groups and large groups are easier to detect than small ones, a multiple-covariate model containing group size allows the true distribution of group sizes in the population to be estimated. Obtaining unbiased estimates of mean group size is an essential component of estimating the density of individuals in flocking birds (Marques and Buckland 2004).

Multiple-covariate distance sampling analysis guidelines.—The MCDS analyses present some additional challenges as compared with CDS. We therefore supplement the CDS analysis guidelines given by Buckland et al. (2001) with some additional recommendations for MCDS analyses.

We recommend starting with extensive exploratory data analysis, partly outside of DISTANCE. Just as for CDS analyses, the data should be checked for evidence of violation of the assumptions. A few covariates should be selected for modeling, if there is good *a priori* reason to expect that they affect the detection-function scale and that the MCDS approach will be of use (see above). As with any multiple-regression model, strongly correlated covariates should be avoided. An initial impression of the effect of potential covariates should be obtained, perhaps by plotting distance-frequency histograms at different factor levels and scatterplots of distances versus nonfactor covariates, or by plotting mean- or median-detection distance or number of encounters per survey unit against the covariate values.

Because of the extra parameters, maximization of the MCDS likelihood takes longer and is more prone to failure. It is, therefore, prudent to begin with models with few covariates and build complexity incrementally. Where analyses fail, it may be helpful to enter starting values for parameters manually, on the basis of parameter estimates from previous analyses. Factor covariates may be harder to fit than nonfactor covariates because they require more parameters (one per factor level). In many cases, more parsimonious models can be constructed by combining one or more factor levels together, using *a priori* knowledge about which are likely to have similar detection functions. Experience has shown that fewer problems are encountered with the half-normal key function than with the hazard-rate function (which has one more parameter).

DISTANCE has the capacity to select automatically the number of adjustment terms using a model-selection criterion. We recommend that, at least initially, the maximum number of terms be limited to two. (Note that, unlike in CDS, the default for MCDS analyses in DISTANCE is not to fit any adjustment terms.) Another reason to limit the number of adjustment terms is that DISTANCE does not currently constrain $\hat{g}(y, z)$ to be monotonically nonincreasing as it does for $\hat{g}(y)$. The chance of obtaining an implausible fitted function is decreased with fewer adjustment terms, but in any case it is important to check that the estimated function corresponds with the surveyor's intuition about what is reasonable. If an implausible, nonmonotonic function results from an analysis that includes adjustment terms, the analysis should be repeated with fewer or no adjustment terms.

The density estimator of Equation (6) may be badly biased if the estimated detection probabilities $\hat{P}_a(\mathbf{z}_i)$ are small, especially if their precision is poor. The distribution of $\hat{P}_a(\mathbf{z}_i)$ appears in the output of DISTANCE. If some probabilities are small with poor precision, the truncation distance w can be reduced. This will have the effect of increasing the estimates of $\hat{P}_a(\mathbf{z}_i)$, though it will also result in loss of precision in relation to a CDS analysis using the more liberal truncation point. There will also be less chance of AIC selecting a covariate analysis over the simpler CDS analysis, which is a disadvantage if the relationship between detectability and covariates is of intrinsic interest. More truncation is typically needed for point transects than for line transects, because more detections are generated from the tail of the detection function, given the substantial area that is covered at larger distances from a point than when surveying from a line.

Example Analysis

The example data were collected as part of a larger study to assess a Palila (*Loxioides bailleuli*) translocation experiment on the island of Hawaii (Fancy et al. 1997). Multispecies point-transect surveys were performed at seven survey periods between July 1992 and April 1995. There were 41 point-count stations, though they were not all surveyed in some survey periods.

To illustrate the use of MCDS methods, we selected the most commonly recorded species, the Hawaii Amakihi (*Hemignathus virens*), a generalist Hawaiian honeycreeper. The main goal of the analysis was to estimate Amakihi density during each of the survey periods, which are considered temporal strata. We selected a common species because we wanted to be able to compare a CDS analysis in which a separate detection function was fit to each survey period with an MCDS analysis, and the former is feasible only when there are sufficient observations. For the Amakihi, there were 1,485 observations in total, with the minimum in one survey period being 148. The distances to all birds detected were recorded, with no distinction made between males and females.

In modeling the detection function using MCDS, the additional covariates available for analysis were observer (OBS, factor covariate with three levels: SGF, TGS, or TKP) and time of day. Time was entered into the models either as a nonfactor covariate (TIME, in minutes after sunrise) or as a factor covariate (HOUR, in integer hours after sunrise). Both observer and time were assumed *a priori* to affect the detection probability. The multiple-covariate detection function was fit to all data pooled, but when estimating density by stratum, we calculated stratum-specific detection probabilities based on the covariate values of the birds observed in each stratum. All analyses were done in DISTANCE, though plots for publication were produced with R, version 2.1.1 (R Development Core Team 2005). A DISTANCE project containing the data and analyses is available from the authors.

Exploratory analysis.—Preliminary exploratory analysis indicated no major problems with the data (Fig. 4). Maximum detection distance was 250 m but, as with most studies, there was a long tail of larger distances, and the median distance was 45 m. There was some evidence of rounding of distances to favored values (e.g., nearest 5 and 10 m) but, after initial inspection, it was not believed that this would influence the analysis results (except for reducing the goodness-of-fit of detection functions), and the data were not grouped into distance intervals for analysis. Notice that the histogram of detected distances shows few detections close to the point, because the proportion of the covered area that is close to a point is small. Hence, the histogram frequencies initially increase with distance, until the decline in detectability at larger distances outweighs the increase in area surveyed (Buckland et al. 2001).

The exploratory analysis of the covariates revealed, perhaps not surprisingly, different distance distributions by observer, with TJS tending to detect birds at larger distances (Fig. 5A), a decrease in the mean distance with TIME (Fig. 5B), and a less clear pattern when the time was considered as a factor, HOUR (Fig. 5C).

Several exploratory analyses with different truncation values indicated that 82.5 m was an adequate truncation point, which we used in all subsequent models. This was a compromise: with larger truncation distances, more adjustment terms tend to be required to fit the detection functions, and estimated detection probabilities in the MCDS analysis may often be small, increasing bias; with smaller truncation distances, a substantial proportion of the data may be discarded, reducing precision and decreasing the chance of detecting covariate effects on detectability. After truncation at 82.5 m

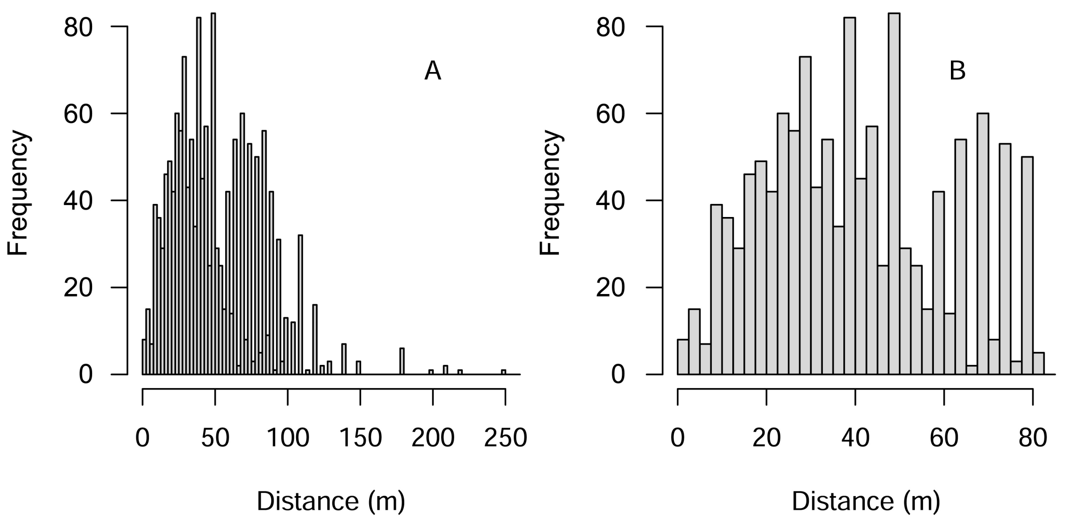

Fig. 4. Frequency histograms of distance data for Hawaii Amakihi: (A) all distances at which singing males were detected during surveys and (B) within the truncation distance selected for analysis distances (82.5 m).

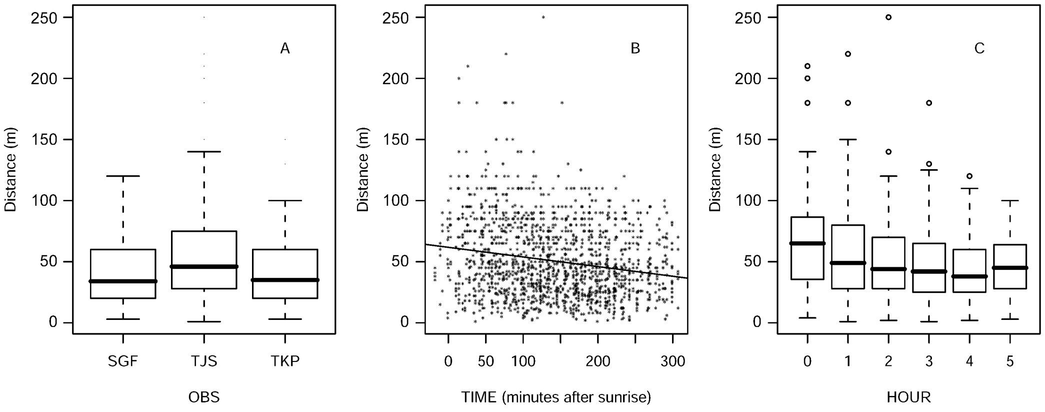

FIG. 5. Exploratory analysis of the effects of covariates on distances at which Hawaii Amakihi were detected during surveys. (A) Boxplots of distance by observer (OBS). (B) Scatterplot of distance as a function of time of day (TIME). (C) Boxplots of distance by hours after sunrise as a factor covariate (HOUR). In boxplots, solid line denotes median, rectangle boundaries are at first and third quartiles, and whiskers are at 1.5 inter-quartile range.

(16% truncation), there were 1,243 observations, with a minimum in any one period of 140.

For the half-normal and hazard-rate models, we tried scaling distances in the adjustment terms by both truncation distance $y_s = y/w$ and scale parameter $y_s = y/\sigma$. For all the models considered, either (1) adjustment terms were not selected, in which case scaling was irrelevant; or (2) AIC values were much higher for σ scaling, with corresponding implausible (nonmonotonic) detection functions. Hence, in the following, if adjustment terms are used, we report only results for w scaling (though we always also tried the corresponding σ scaling).

Conventional distance-sampling detection-function models.—We fit the following detection-function models to all observations pooled: half-normal and uniform with up to five cosine series expansion terms and hazard rate with up to five simple polynomial series. Of these models, the half-normal with four cosine series terms had the lowest AIC (Table 2), with the unusually large number of adjustment terms being needed to fit the tail of the distribution. We also fit the same models independently to data from each survey period (i.e., detection function stratified by time). This time, a uniform with one or two cosine adjustments (depending on the stratum) had the lowest AIC (Table 2). The stratified analyses had considerably lower AICs than the pooled ones, indicating strong support for the notion that detection probability varied among survey periods.

Multiple-covariate distance sampling detection-function models.—We fit the half-normal and hazard-rate models to the pooled data, using OBS and either TIME or HOUR as potential covariates (see Table 2 for a full list of models). We limited the maximum number of adjustment terms to two. No adjustment terms were selected for the best three models according to AIC, so the scaling of adjustment terms was immaterial. For models with only one covariate, including OBS resulted in the largest drop in AIC, whereas TIME produced a smaller decrease but was preferred over HOUR. The best model overall had both OBS and TIME as covariates, and a hazard-rate key function with no adjustment terms. This had a much lower AIC than any of the CDS models.

Figure 6A shows the fitted detection function, averaged over the observed covariate levels for the hazard-rate OBS + TIME model. In this plot, the histogram bars are scaled to account for the fact that there are more birds present at larger distances from the point because of the increasing area surveyed. This means that small discrepancies between the number of observed and expected distances close to the point are amplified, as can be seen in the first bar of the histograms (Fig. 6A). Figure 6B shows the corresponding fitted probability

Table 2. Results from fitting different models to survey data for Hawaii Amakihi using three analytical approaches: conventional distance sampling (CDS) with a pooled detection function, CDS with detection function stratified across seasonal survey periods, and multiple-covariates distance sampling (MCDS). Within each analysis, models are sorted by differences in Akaike's Information Criterion (ΔAIC) between each candidate model and the model with the lowest AIC value. Key functions are uniform (Uni), half normal (HN), or hazard-rate (HR). Adjustment terms are cosine (Cos) or simple polynomial (SP); (0) means that no adjustment terms were selected by AIC. Covariates for MCDS models include observer (OBS) and either time of day (TIME, in minutes after sunrise) as a continuous variable or hours after sunrise (HOUR) as a factor. Number of parameters is shown for each model.

Key	Adjustment terms	Covariates	Number of parameters	ΔAIC
		CDS *f*(0) pooled		
HN	Cos	–	5	21.40
Uni	Cos	–	2	25.11
HR	SP (0)	–	2	29.90
		CDS *f*(0) by strata (survey period)		
Uni	Cos	–	12	13.50
HR	SP (0)	–	14	18.59
HN	Cos	–	15	22.87
		MCDS		
HR	SP (0)	OBS TIME	5	0.00
HR	SP (0)	OBS	4	1.73
HN	Cos	OBS HOUR	10	3.61
HN	Cos	OBS TIME	6	5.53
HR	SP (0)	OBS HOUR	9	5.62
HN	Cos	OBS	6	7.12
HN	Cos	TIME	4	24.56
HN	Cos	HOUR	8	24.57
HR	SP (0)	TIME	3	29.18
HR	SP (0)	HOUR	7	31.62

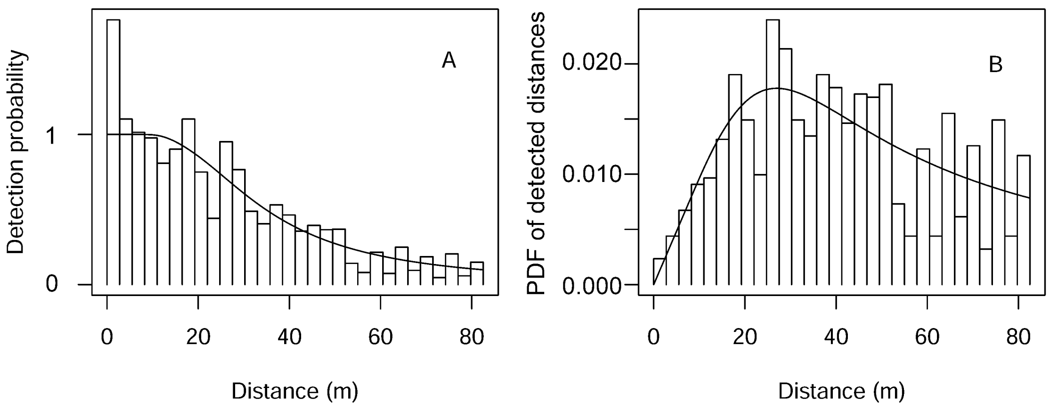

Fig. 6. (A) The estimated MCDS detection function for Hawaii Amakihi, based on the best model (lowest AIC value) and averaged over the observed covariate values for observer (OBS) and time of day (TIME). The detection function is superimposed over the histogram of observed distances, which have been scaled to adjust for increasing area surveyed at increasing distances from the survey point. (B) The corresponding estimated probability density function (PDF) of detected distances, superimposed over the histogram of actual distance data.

density function (PDF) of observed distances (i.e., the expected distribution of the observed distances if the model is correct). The PDF plot accounts for the fact that, for point transects, there are more birds present at large distances from the point (for line transects, the expected number of birds by distance does not increase with distance, and so both plots have the same shape). This plot gives a better indication of the fit, because one can superimpose a histogram of the observed distances and look for a pattern in the discrepancies.

Although the PDF plot shows no systematic departures between the fitted model and the data, the Kolmogorov-Smirnov goodness-of-fit statistic indicates a reasonably poor fit (D_n = 0.042, P = 0.02). This statistic is a function of the largest discrepancy between the observed and expected distances, and the poor result is likely caused by the rounding of observed distances in the data. The Cramér-von Mises goodness-of-fit statistic, which uses the overall departure between data and fitted model, shows no significant problems ($W^2 = 0.187$, $0.2 < P \leq 0.3$). DISTANCE also produces a version of the Cramér-von Mises statistic that weights lack of fit closer to the point or line more heavily (Burnham et al. 2004), and this is also not significant ($W^2_{cos} = 0.105$, $0.3 < P \leq 0.4$). A quantile-quantile plot (not shown) is also a useful way to diagnose systematic lack of fit (Burnham et al. 2004). Using this plot, no serious problems in the fit of the best MCDS model were detected.

DISTANCE also provides detection-function plots for each combination of covariate levels (for factor covariates) or at three levels of the covariate values (nonfactor covariates), which can be useful in interpreting the results. For the MCDS model selected, detection probability shows considerable variation between observers (Fig. 7A) and decreases with time of day (Fig. 7B), as expected given the lower bird activity later in the day.

Density and variance estimates.—Density and probability of detection estimates, with corresponding confidence intervals for the best CDS models (both pooled and detection function stratified by time) and MCDS model, are shown in Figure 8. Both the CDS stratified and the MCDS models estimate that there was considerable variation in detection probability between periods, something that is ignored by the CDS pooled analysis. The CDS stratified and MCDS estimates of detection probability (and therefore density) are reasonably similar, which suggests that observer and time of day probably account for most of the variation in detection probability between periods. However, the MCDS estimates are considerably more precise (narrower confidence limits).

DISCUSSION

The example illustrates one of the advantages of the MCDS approach: the potential to parsimoniously model major causes of variation in detection probability with relatively few parameters.

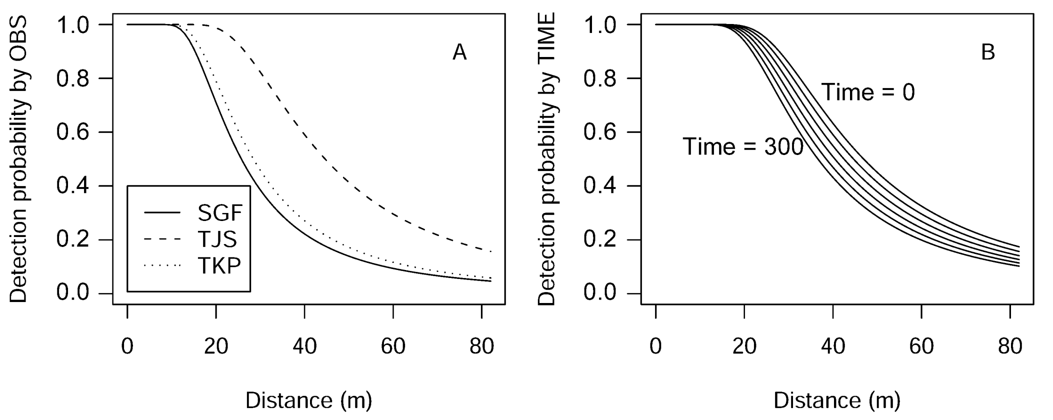

FIG. 7. Marginal detection functions for Hawaii Amakihi plotted for different values of (A) observer and (B) time of day (minutes after sunrise). (A) Time is fixed at 0900 HST. (B) Detection probabilities are shown for observer TJS at hourly intervals between 0 and 300 min after sunrise.

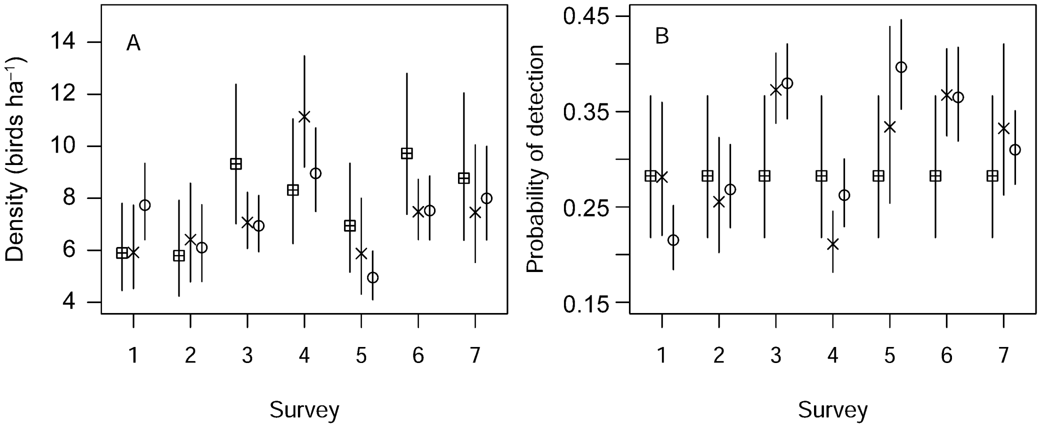

Fig. 8. Estimates and corresponding 95% confidence intervals for (A) density of Hawaii Amakihi (all birds) and (B) probability of detection for three models: best CDS model with pooled detection function (squares), best CDS model with a stratified detection function (crosses), and best MCDS model with covariates for observer (OBS) and time of day (TIME) (circles). See Table 2 for details about models.

The CDS analysis stratified by survey period will produce unbiased estimates of detection probability for each survey period (given that all of the assumptions of the methods have been met), but in the example, the best CDS stratified model contained 12 parameters. By contrast, the best MCDS model required only five parameters, and yet produced similar estimates of detection probability by survey period with greater precision. Note that the differences in surveys 1 and 4 could be from the effect of an unavailable covariate. The MCDS estimates will be slightly biased, because the model cannot include all variables that cause variation in detection probability between survey periods, but according to the AIC statistic, it was the best trade-off between bias and precision. The best pooled CDS model had even fewer parameters (two), but clearly the bias caused by assuming that detection function was constant between all the survey periods outweighed any potential gain in precision, and this model had a far higher AIC.

In our example, we had enough data that we were able to generate a model with detection functions fit separately to each stratum, even if this model was not selected. In many cases, however, there are too few observations by stratum for this. In such cases, MCDS models offer a useful alternative that allows variation in detection probability between strata (through covariates in the scale parameter of the detection function) while at the same time pooling information between strata about the shape of the detection function.

Multiple-covariate distance sampling is no different from other types of multiple-regression analysis, in that it is best to consider only covariates believed *a priori* to influence the response variable—in this case, detection probability. In our example, we were not surprised to find that both observer and time of day were selected in the best MCDS model. Observer differences are well documented in bird surveys (e.g., Diefenbach et al. 2003, Norvell et al. 2003), and our example has once again demonstrated the importance of accounting for such differences if comparisons are to be made between estimates collected by different field teams. It is well known that many species become increasingly harder to detect in the hours following sunrise, and this is indeed what the TIME covariate showed (Fig. 6). Care is needed in the interpretation of the estimated change in detection over the TIME covariate, and (as usual for fixed-effect regression models) we should not extrapolate our findings to unobserved covariate values. We found a drop in detectability with time of day, but for unbiased estimates we still require that all birds at zero distance were detected. If surveys are done at a time of day in which the birds are so inactive that some at zero distance can be missed, MCDS (as CDS) methods will be negatively biased. We also tried HOUR as a factor covariate in case the relationship between time of day and the detection function was nonlinear, but this latter model (which had four more parameters) was not selected by AIC. Another strategy if a nonlinear relationship was suspected might be to include power terms of the original covariate (e.g., TIME and $TIME^2$). Transformations of the original variable could also be considered. For example, for species occurring in groups that vary widely in size, the log of group size might be a better covariate than group size untransformed.

The need to account for undetected birds should not be understated if reliable inferences on bird density are to be made. With that objective in mind, MCDS provides a useful improvement over CDS, avoiding the need for separate detection functions to be estimated for each desired density estimate, of special relevance when sample size is small. It also relaxes the need to rely on pooling robustness and helps to increase precision of density estimates, by modeling heterogeneity in detection probability because of covariates other than distance. Additionally, if there is interest in estimating the distribution of population characteristics such as group size, sex ratio, or age structure and these characteristics also affect detectability, the distribution of observed values will be a biased sample of the distribution of values in the population. By using the observed values as covariates in an MCDS analysis, we can obtain an unbiased estimate of the covariate's distribution in the population. We hope that the present study, combined with the availability of DISTANCE, helps to promote better and more reliable inferences based on MCDS methods.

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