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A SEVEN-YEAR COMPARISON OF RELATIVE-ABUNDANCE AND DISTANCE-SAMPLING METHODS

Russell E. Norvell,[1] Frank P. Howe, and Jimmie R. Parrish

Nongame Avian Program, Utah Division of Wildlife Resources, Salt Lake City, Utah 84114-6301, USA

Abstract.—We used data from statewide surveys of riparian birds in Utah, 1992–1998, to compare relative-abundance and distance-sampling methods. By generating relative-abundance indices with point-count methods and density with point-transect sampling methods, we examined whether the assumptions underlying each method were met during field surveys for four bird species (Brown-headed Cowbird [*Molothrus ater*], Bullock's Oriole [*Icterus bullockii*], Warbling Vireo [*Vireo gilvus*], and Yellow Warbler [*Dendroica petechia*]). Point-count methods failed to reasonably meet the fundamental assumption of constant proportionality, with estimated detectability varying 3- to 5-fold despite the use of widely accepted and well-standardized methods. Population trends based on relative abundance were subsequently unstable, often varying in both magnitude and direction with the survey plot radius used (25 m, 50 m, or unlimited distance). Distance-sampling methods appeared to meet critical assumptions, were robust to assumption violations, allowed methodological self-assessment, and were demonstrably efficient in a large-scale, multispecies survey setting. Our data show surveys of birds without estimations of detectability are likely biased because the assumption of constant proportionality is violated to a degree that precludes strict inference and may confound trend analyses. *Received 23 July 2002, accepted 26 May 2003.*

Resumen.—En este estudio utilizamos datos de censos a nivel estatal de aves ribereñas en Utah (1992–1998) para comparar los métodos de abundancia relativa y de muestreo de distancia. Generando índices de abundancia relativa con métodos de conteo de punto y de densidad con muestreos de puntos en transectos, examinamos si los supuestos de cada método se cumplían durante censos de campo realizados para cuatro especies de aves (*Molothrus ater*, *Icterus bullockii*, *Vireo gilvus* y *Dendroica petechia*). Los métodos de conteo de punto no cumplieron de forma razonable el supuesto fundamental de proporcionalidad constante; la detectabilidad estimada varió de 3 a 5 veces a pesar del uso de métodos ampliamente aceptados y bien estandarizados. Las tendencias poblacionales basadas en abundancia relativa fueron subsecuentemente inestables y a menudo variaron tanto en magnitud como en dirección con el radio de la parcela de muestreo utilizado (25 m, 50 m ó distancia ilimitada). Los métodos de muestreo de distancia parecieron cumplir los supuestos críticos, fueron robustos ante violaciones de los supuestos, permitieron hacer autoevaluaciones metodológicas y fueron eficientes de forma demostrable en un escenario de censo de múltiples especies a gran escala. Nuestros datos muestran que los censos de aves sin estimaciones de la detectabilidad son probablemente sesgados porque el supuesto de proporcionalidad constante es violado a un grado que no permite hacer inferencias estrictas y puede confundir los análisis de tendencias.

The estimation of abundance is the foundation on which studies investigating bird population size, habitat associations, and population trends are built. Point-count methods are the most widespread survey methods in use, generating relative abundance indices (Ralph et al. 1995, Rosenstock et al. 2002). Relative abundance indices are frequently used as the basis for further analyses, as in the case of our monitoring of riparian bird populations in Utah (Howe et al. 1999). The validity and utility of relative abundance indices relies upon the assumption of constant proportionality that translates to a constant probability of detection. The method itself, however, does not allow for testing of that assumption, and a large body of data suggests relative abundance derived from point counts may be an unstable base upon which to build (see Thompson 2002 for a recent overview). By estimating the probability of detection directly, distance-sampling methods (point-transect sampling) allowed us to examine the assumption of constant detectability, and only required the additional collection of distance-to-bird data in an otherwise standard relative abundance monitoring study.

[1]E-mail: russellnorvell@utah.gov

Because of incomplete and unequal counts resulting from a less-than-perfect but unknown probability of detection, relative abundance is widely considered an index and not an estimate of density (Pendleton 1995). Even when used as an index, however, relative abundance does not typically have a known or defined relationship to true density (but see Bart and Earnst 2002). Nor is it considered comparable between species because of acknowledged differences in detectability among species (Hutto and Mosconi 1981, Scott and Ramsey 1981a, Gutzwiller 1991, Gates 1995, Wolf et al. 1995, Nichols et al. 2000). Differences in detectability continue to be tacitly ignored, such as in the common presentation of species lists ranked by frequency of observation.

Despite almost two decades of studies indicating that significant variation in detectability commonly occurs (Cyr 1981, Hutto and Mosconi 1981, Kepler and Scott 1981, Ralph and Scott 1981, Robbins 1981, Scott and Ramsey 1981b, Skirvin 1981, Verner 1985, Wilson and Bart 1985, Balph and Romesburg 1986, Bibby and Buckland 1987, Block et al. 1987, Sauer et al. 1994, Nichols et al. 2000), relative-abundance indices are still widely accepted as comparable among surveys within a species, as long as the important classes of variation in detectability (observer, environment, and the bird itself) are controlled for through methodological standardization (e.g. Ralph et al. 1993, 1995). Johnson (1981), however, termed our reliance upon an assumed comparability a "Pollyanna approach" and later cautioned that "if detection probabilities vary markedly from one occasion to another, the comparison of point counts over time can be…hazardous" (1995:119). Nichols et al. (2000:405) have also argued against that assumption, concluding "…we see little justification for the use of standard point counts unaccompanied by some effort to estimate detection probability." But relative abundance derived from point-count sampling continues to be the overwhelming method of choice. In their recent review of papers using avian field sampling techniques, Rosenstock et al. (2002) found 95% of published studies used relative abundance methods. That is likely due to the perception that alternative methods (e.g. distance sampling [Buckland et al. 2001], double-observer [Nichols et al. 2000], or removal [Farnsworth et al. 2002]) are overly difficult, time consuming, and expensive when relative-abundance methods will suffice (Pendleton 1995, Ralph et al. 1995, Verner 1985). Distance-sampling methods, where the distance to each observation is recorded and detection probabilities are directly estimated (see Buckland et al. 2001 for methodological history), are less frequently used because of that perception.

Many studies have compared various incarnations of distance-sampling methods with other methods of estimating bird abundance and with some exceptions (e.g. DeSante 1981, 1986) found distance-sampling methods to work reasonably well in the field (Ralph and Scott 1981, Hamel 1984, Casagrande and Bessinger 1997, Tarvin et al. 1998, Jimenez 2000, Jones et al. 2000; but see discussion in Buckland et al. 2001). However, we are not aware of its paired use with relative-abundance methods over a long time frame and large spatial scale in a multispecies survey setting. Here, we combined relative-abundance and distance-sampling methods as a collateral project to a larger study monitoring statewide populations of birds breeding in the riparian habitats of Utah, 1992–1998 (Howe 1992, Howe et al. 1999, Norvell et al. 2003). Here we present statewide population trends based on relative-abundance indices and distance sampling methods for four species—Brown-headed Cowbird (*Molothrus ater*), Bullock's Oriole (*Icterus bullockii*), Warbling Vireo (*Vireo gilvus*), and Yellow Warbler (*Dendroica petechia*)—and use the results to compare the methods in terms of their robustness to assumption violations, ecological conclusions, and overall utility in the field.

METHODS

Study area and survey methods.—Thirty-two survey sites (Fig. 1) were selected through a stratified random design, with sites distributed to cover the Utah's riparian habitat as completely as possible (for details see Howe 1992, Howe et al. 1999). Point-count methods followed Ralph et al. (1993, 1995). Point-to-observation distances were also measured (Howe 1992) to allow the data to be analyzed as point transects, a form of distance sampling (Buckland et al. 2001). Ten sampling points per site were systematically established in riparian habitat from a random start, each point a minimum of 200 m apart; perpendicular point-to-stream distances were allowed to vary somewhat with habitat patch width. Sites were surveyed twice each breeding season. Count duration at each point was 8 min and surveys were conducted between 15 min before sunrise and 1000 hours. Observers were assigned to site visits with the restriction that no ob-

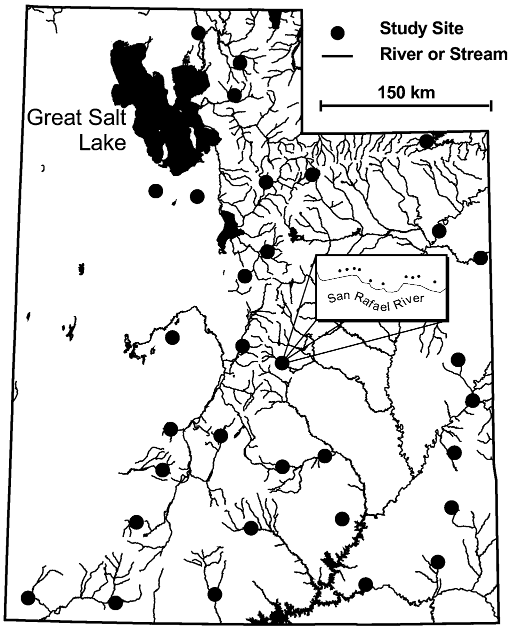

Fig. 1. Riparian study sites in Utah, with major rivers and water bodies shown. The 32 study sites indicated by dots were surveyed from 1992 to 1998; each contains 10 subsample points (as shown in the San Rafael study site inset).

server would survey the same site twice in any given year. Distance to each detection was estimated (calibrated by pacing) to the nearest meter. Experienced observers were hired each season and given a 3–4 day field training in bird identification and survey methods with an emphasis on distance estimation. Observers were also encouraged to frequently recalibrate their distance estimation during the field season by pacing.

Analysis methods.—Both visual and audible observations of nonjuvenile, nonflyover birds were used for that comparison; all analyses were by species. The four species selected for presentation here were chosen for their ease of field identification, relatively high frequency of detection, and widespread distribution; that is, all were species for which both methods should work well (Ralph et al. 1993, Buckland et al. 2001), thus enabling a strong methodological comparison.

Estimation of Annual Abundance

Survey data were used to calculate relative abundances (per Sauer and Droege 1990, Nur et al. 1999) and estimate density (using program DISTANCE version 3.5; Thomas et al. 1998, Buckland et al. 2001). Relative-abundance data were grouped and analyzed according to three commonly used survey plot radii: 25 m, 50 m, and unlimited distance (Hutto et al. 1986, Ralph et al. 1993, 1995). Point and visit data were treated as subsamples and collapsed into annual site means. Statewide averages of the annual site means were used in subsequent relative-abundance trend analyses (i.e. mean number of birds detected statewide per point per visit per site for each year).

Distance-sampling analyses followed Buckland et al. (2001) with modifications to accommodate multiple strata in DISTANCE version 3.5 (L. Thomas pers. comm.). Tests for estimation of a common (global) detection function versus separate detection functions for annual strata (Buckland et al. 2001) indicated that a year-specific detection probability function was warranted for each of those species. Selections of annual detection functions were guided by Akaike's Information Criterion (Akaike 1973, Burnham and Anderson 1998), chi-square model-fit statistics, and visual inspection of detection probability and probability density plots (Buckland et al. 2001; see Appendix). Data were grouped for analysis to compensate for persistent rounding (heaping) errors beyond 25 m noted in preliminary analyses of the audibly detected data (which constituted between 80 and 90% of all detections). Distance-sampling analyses were designed for maximum comparability both between years and between species. Grouping cut points and truncation distances were standardized for each species' analysis. Distance sampling analyses yielded estimates of the annual unconditional probability of detection (P_a)—the probability that a randomly selected object within the survey area is detected. Measures of P_a provide an unbiased means to directly assess the issue of constant detectability, if key assumptions are adequately met (Buckland et al. 2001). Nonparametric runs tests were used to assess statistical significance of temporal trends in P_a (Zar 1984).

Trend Analyses

Population trend was defined as the mean annual change from 1992 to 1998 in the estimated population parameter in question, measured using simple linear regression slope (Allen 1983, Allen et al. 1983, Zar 1984, Neter et al. 1996). Relative-abundance trends (for each species at each plot radius) were measured as the mean annual change in a species' statewide relative abundance. Trends in estimated density (calculated from distance sampling) for each species was similarly measured as the mean annual change in a species' statewide density estimate (because sample sizes were generally inadequate to reliably estimate density at each site in each year). However, comparisons of relative abundance and density trends themselves are made in terms of the percentage change in the mean statewide relative abundance and density respectively. That approach has the advantage of a common scale for comparisons, necessary because relative abundance indices have no absolute scale unless one is willing to assume perfect detectability within the survey plot radius, that is, assuming the sample censused all birds in the defined area and results are expressed as an absolute density: number of birds per unit-area (e.g. Jones et al. 2000).

METHODOLOGICAL ASSUMPTIONS

The assumptions common to both relative-abundance and distance-sampling methods include: (1) the study is well designed, methods are strictly adhered to, and birds are identified correctly; (2) points are randomly located with respect to bird distributions (and although independence of detections is also considered important for both methods, it is necessary primarily for variance estimation and hypothesis testing) (adapted from Bibby et al. 1992, Pendleton 1995, Thompson et al. 1998, Buckland et al. 2001).

Assumptions specific to relative-abundance (index) methods are that (1) counts of birds are a consistent proportion of true population abundance, that is, the assumption of constant proportionality (adapted from Hutto et al. 1986, Barker and Sauer 1995, Pendleton 1995, Thompson et al. 1998). That covers several types of potential biases: double-counting within and between points and responsive movement.

Assumptions specific to distance-sampling methods are that (1) birds directly on the point are always detected with certainty (and ideally, detectability should remain near-perfect for some distance around the observer, to improve the reliability of the estimates); (2) birds are detected at their initial location (i.e. birds are detected prior to movement in response to observer, nor are they double-counted at a point or chased from one point to the next); (3) distances are measured without error, or if data are to be grouped for analysis, detections are placed into the appropriate distance category (adapted from Buckland et al. 2001).

RESULTS

Brown-headed Cowbird (BHCO).—Total detections (n = 370) ranged annually from 26 to 75 ($\bar{x}$ = 52.86 ± 7.82) (Fig. 2A). Annual relative abundance values from point-count sampling and density estimates from point-transect (distance) sampling (Table 1) were highly variable with large magnitude shifts seen between consecutive years for most species examined. Annual estimates of P_a also varied widely (Table 1, Fig. 3A; estimated detection functions for all species are shown in Appendix). Brown-headed Cowbird detectability varied more than 4-fold between years. Proportion of total annual detections captured by 25 and 50 m radius survey plots ranged from 16 to 69%, and from 54 to 92%, respectively (Appendix). All statewide trends (except 25 m plots) indicated Brown-headed Cowbird are increasing statewide (Fig. 4A), but those measures varied widely in magnitude (Table 2). Trend slope for relative-abundance measures also increased notably with increasing plot size indicating a possible systematic bias, in that apparent latter study year increases in observer detection efficiency were disproportionately greater in more distant annuli, thereby biasing relative abundance trends upward with increasing plot radius (a result also typical of all species examined).

Bullock's Oriole (BUOR).—Total detections (n = 330) ranged annually from 24 to 79 ($\bar{x}$ = 47.14 ± 6.76) (Fig. 2B). Proportion of detections captured by survey plots of 25 and 50 m radius varied from 5 to 54% and from 62 to 96%, respectively (Appendix). Like Brown-headed Cowbird, P_a for Bullock's Oriole varied more than 4-fold between years (Table 1, Fig. 3B). Although the small number of years (n = 7) warrants caution, a nonparametric runs test was also significant at α = 0.05 for an increasing P_a with year (P-value ~ 0.0393). Statewide trends in density and in relative abundance were again all increasing except for 25 m plots, and as with Brown-headed Cowbird, relative-abundance trend slopes increased with increasing plot radius (Fig. 4B, Table 2).

Warbling Vireo (WAVI).—Total detections (n = 1760) ranged annually from 153 to 330 ($\bar{x}$ = 251.4 ± 27.64) (Fig. 2C). Proportion of detections captured by plots of 25 and 50 m radius ranged from 27 to 59% and from 74 to 98%, respectively (Appendix). Estimated annual P_a ranged over 4-fold, varying significantly from each other and the group mean (Table 1, Fig. 3C). Statewide trends were down for relative abundance in 25 m radius plots but were up for density, 50 m radius plots, and unlimited distance plots; relative abundance trends again increased with increasing plot radius (Fig. 4C, Table 2).

Yellow Warbler (YWAR).—Total detections (n = 2476) ranged annually from 170 to 414 ($\bar{x}$ = 353.7 ± 79.17) (Fig. 2D). Proportion of annual detections captured by plots of 25 and 50 m radius ranged from 32 to 64% and 85 to 99%, respectively, the narrowest ranges of all species analyzed (Appendix). Estimated P_a ranged almost 3-fold between years, differing significantly between years and group mean (Fig. 3D, Table 1). Statewide trends in density and the three relative abundance measures all indicted YWAR are increasing statewide (Fig. 4D, Table 2). Yellow Warbler was the only species that did not show an increasing positive bias in relative abundance trend with increasing plot radius.

Discussion

Relative-abundance indices derived from point-count methods have been widely preferred to all other methods of assessing bird abundance. That preference is apparently based on the conviction that the assumption of constant proportionality is easier to meet and less stringent than the assumptions inherent in competing methods such as distance sampling. Because we had no standard of "true" density with which to compare (e.g. territory mapping used by DeSante 1981, 1986; Tarvin et al. 1998, but see Verner and Milne 1990, Buckland et al. 2001), we explored the effects of relatively common assumption violations upon each method and compared the conclusions (trends) from each method.

We made as fair a comparison between methods as possible by using a common study design and standardized frequently used survey methods that met underlying assumptions (i.e. that

Table 1. Annual relative-abundance and distance-sampling analyses results (with percent CV) for four selected species in Utah (note both the probability of detection and the effectively surveyed area vary widely by species and by year). Relative-abundance values for each plot radius (RA_{25} = 25 m radius, RA_{50} = 50 m radius, RA_{∞} = unlimited radius plots) are the mean number of birds detected statewide per point per visit per site per year and have no units *per se* (see text); estimated annual densities ($\hat{D}$) are given in number of birds per hectare; P_a = estimated unconditional probability of detection; EDR = effective detection radius (m)—the estimated plot radius within which the number of birds missed equals the number of birds observed farther away (Gates 1979).

Species[a]	Year	RA_{25} (CV)	RA_{50} (CV)	RA_{∞} (CV)	$\hat{D}$ (CV)	P_a	EDR
	1992	0.029 (37.4)	0.050 (31.2)	0.058 (26.6)	0.26 (17.65)	0.256	34.1
	1993	0.031 (31.4)	0.096 (31.6)	0.126 (37.5)	0.41 (27.48)	0.358	40.4
	1994	0.051 (38.1)	0.070 (36.0)	0.079 (34.7)	0.31 (22.23)	0.131	24.4
BHCO	1995	0.039 (29.7)	0.137 (33.5)	0.170 (33.6)	0.45 (20.53)	0.377	41.4
	1996	0.015 (71.5)	0.054 (49.5)	0.100 (38.2)	0.26 (31.65)	0.608	52.6
	1997	0.029 (54.6)	0.104 (35.2)	0.153 (29.1)	0.37 (26.92)	0.433	44.4
	1998	0.034 (53.0)	0.112 (35.9)	0.158 (28.4)	0.43 (31.92)	0.311	37.7
	1992	0.026 (41.1)	0.044 (38.4)	0.046 (38.6)	0.39 (25.02)	0.116	28.5
	1993	0.035 (35.3)	0.072 (32.5)	0.100 (28.9)	0.41 (22.24)	0.247	41.5
	1994	0.034 (40.0)	0.077 (40.2)	0.082 (39.7)	0.45 (40.34)	0.130	30.2
BUOR	1995	0.048 (34.6)	0.125 (31.1)	0.150 (30.8)	0.72 (24.26)	0.186	36.0
	1996	0.021 (43.4)	0.053 (46.2)	0.072 (36.4)	0.42 (30.00)	0.284	44.5
	1997	0.004 (70.0)	0.051 (38.1)	0.077 (32.0)	0.38 (26.02)	0.539	61.3
	1998	0.033 (47.6)	0.088 (38.3)	0.110 (35.9)	0.54 (26.06)	0.285	44.6
	1992	0.155 (17.8)	0.237 (16.5)	0.266 (17.2)	0.86 (14.43)	0.078	20.2
	1993	0.179 (17.2)	0.511 (13.9)	0.578 (13.0)	1.61 (12.12)	0.342	42.4
	1994	0.232 (15.5)	0.399 (15.1)	0.407 (14.7)	1.32 (13.07)	0.133	26.4
WAVI	1995	0.114 (18.7)	0.296 (15.8)	0.350 (15.0)	1.10 (13.76)	0.317	40.8
	1996	0.123 (16.6)	0.266 (15.5)	0.304 (14.6)	0.80 (14.67)	0.301	39.8
	1997	0.152 (19.3)	0.413 (16.9)	0.549 (15.7)	1.47 (12.70)	0.297	39.5
	1998	0.164 (18.3)	0.481 (14.6)	0.600 (14.9)	1.52 (12.18)	0.209	33.2
	1992	0.179 (37.0)	0.252 (32.6)	0.284 (31.4)	1.10 (29.79)	0.116	23.0
	1993	0.190 (27.5)	0.479 (20.9)	0.560 (20.2)	2.06 (20.61)	0.336	39.1
	1994	0.385 (22.5)	0.721 (20.3)	0.725 (20.2)	2.36 (19.72)	0.144	25.6
YWAR	1995	0.346 (25.6)	0.612 (23.4)	0.675 (23.3)	2.54 (23.92)	0.205	30.6
	1996	0.357 (25.6)	0.660 (21.0)	0.685 (20.6)	2.47 (20.55)	0.191	29.5
	1997	0.261 (22.7)	0.626 (19.6)	0.739 (20.0)	2.29 (21.51)	0.230	32.4
	1998	0.339 (26.1)	0.639 (20.0)	0.691 (19.0)	2.37 (19.43)	0.183	28.8

[a]Abbreviations: BHCO = Brown-headed Cowbird, BUOR = Bullock's Oriole, WAVI = Warbling Vireo, and YWAR = Yellow Warbler.

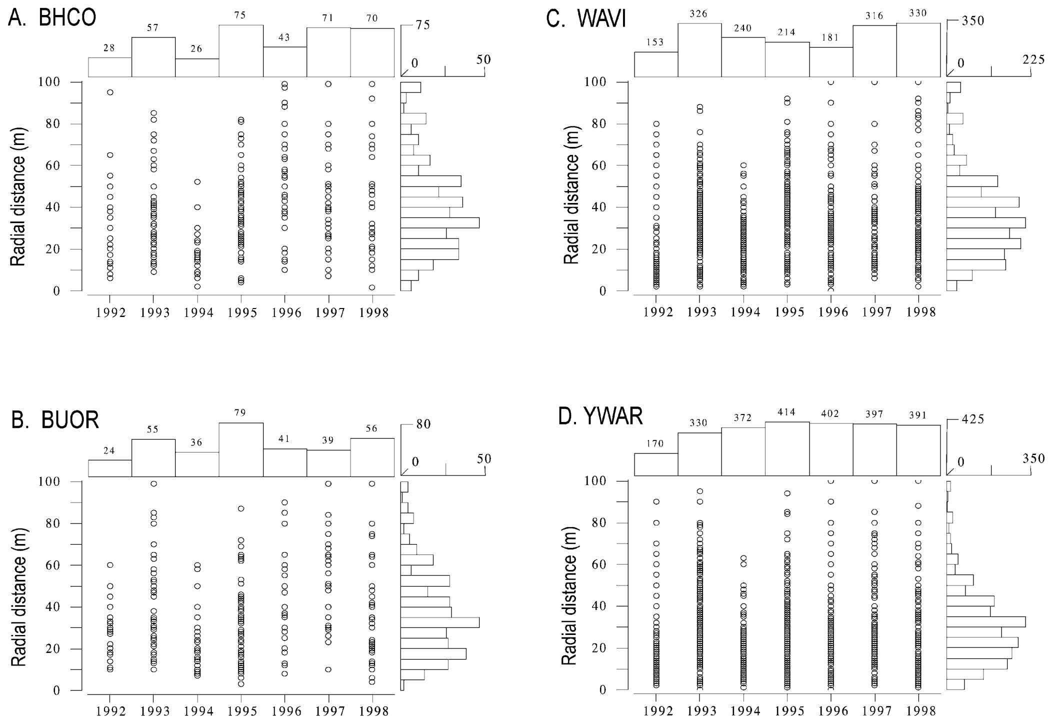

FIG. 2. Distributions of estimated radial distances by species by year: (A) Brown-headed Cowbird [BHCO], (B) Bullock's Oriole [BUOR], (C) Warbling Vireo [WAVI], (D), Yellow Warbler [YWAR]. The *x* axis summary histograms show the patterns of yearly variation for total numbers of detections for each species. In general, first year totals were low with generally increasing numbers in later study years. The *y* axis summary histograms show overall detection distance distributions by species (note the increasing tendency for rounding errors with increasing distance). The body of the figures illustrate the relative shape of the annual distribution of detection distances (note that the distance distributions are similar for all four species within each year).

the study has been well designed, the methods rigorously adhered to, and the birds identified correctly). Our "meso-habitat" (sensu Bowers 1997) based study design, however, both violated and met the scale-dependent assumption that points were randomly located with respect to the distribution of birds across the study area: study sites and starting points were both randomly selected, but subsequent point-to-point spacing was occasionally increased to avoid large areas without riparian vegetation; similarly, point-to-stream spacing was allowed to vary with the width of the riparian corridor. Although that approach is recommended for relative-abundance methods in limited habitat contexts (Ralph et al. 1993), such as Utah's naturally narrow and disjunct riparian habitats, it has the potential to affect distance-sampling methods by welding together two habitat specific detection functions. That is, if a given species occurs in both riparian and upland contexts with different habitat-specific detectabilities, then distance data collected at the ecotone will be confounded. That may have somewhat compromised the direct comparability of our density estimates themselves to other studies but does not hamper our methodological comparison because it is based upon the same set of survey points.

There were several aspects of our analysis that did not readily lend themselves to an ideal comparison. Because relative-abundance methods do not incorporate detectability variance components, standard errors of annual values are biased low making for an apparently precise result. Annual statewide density estimates, however, incorporate the variation in detectability into the calculation of annual standard errors resulting in an unbiased variance estimate that appears imprecise by contrast. Also hampering

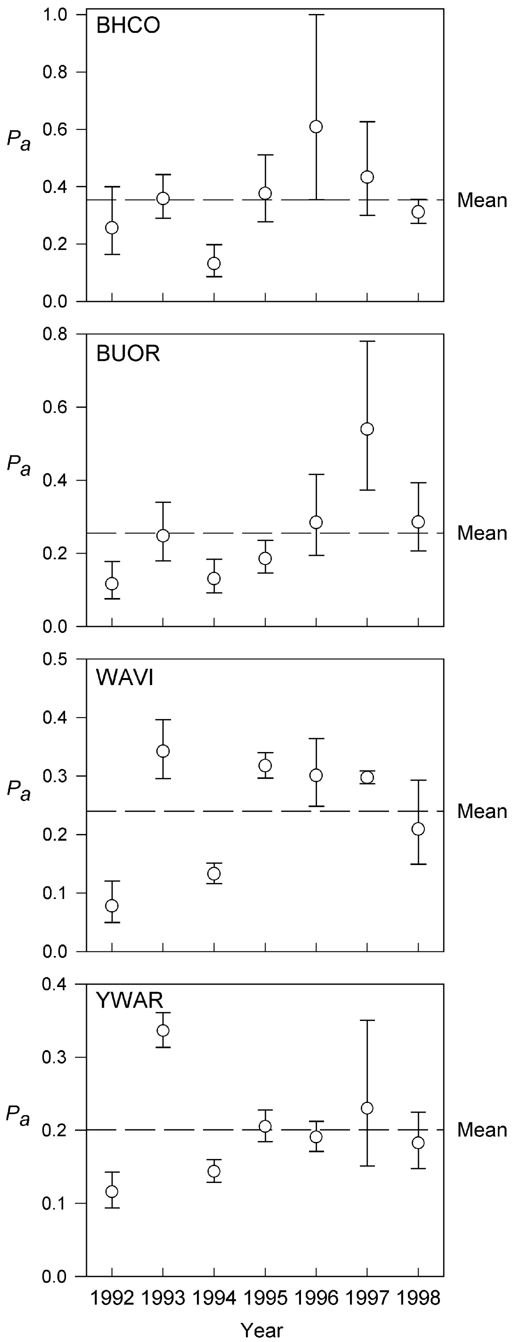

FIG. 3. Annual estimated detection probabilities for Brown-headed Cowbird (BHCO), Bullock's Oriole (BUOR), Warbling Vireo (WAVI), and Yellow Warbler (YWAR) in riparian habitat, 1992–1998, with 95% confidence intervals and group means shown. Estimated detectability varied significantly between years and from the group mean for every species examined.

TABLE 2. The trend (average annual change) in mean statewide density and relative abundance from 1992 to 1998, expressed as a percentage of the mean of each parameter for each species during the same period. Parameters are estimated density per hectare ($\hat{D}$), relative abundance for 25 m radius fixed plots (RA_{25}), relative abundance for 50 m radius fixed plots (RA_{50}), and relative abundance for unlimited radius plots (RA_{∞}). Note the increasingly positive trends with increasing plot radius for relative abundance indices for all species, except Yellow Warbler (YWAR).

Species	$\hat{D}$	RA_{25}	RA_{50}	RA_{∞}
BHCO	3.81	–2.74	7.46	11.11
BUOR	2.72	–6.72	3.24	5.34
WAVI	3.40	–3.04	3.87	6.89
YWAR	7.21	7.22	8.74	8.83

Abbreviations: BHCO = Brown-headed Cowbird, BUOR = Bullock's Oriole, WAVI = Warbling Vireo.

an ideal comparison, a single set of distance-sampling analysis grouping cutpoints was used for each species to maximize comparability between years, although at the expense of some precision. Thus, standard errors presented for relative abundance values are biased low, and those for the density values could be improved; both should be interpreted with caution.

Calculating standard errors for trends based upon those values in a common scale is a more difficult issue. Using the route-regression approach for the relative-abundance trends incorporates site-to-site variability into the relative abundance standard error value and avoids the potential for pseudoreplication; however, we opted for using identical, albeit simplified calculation methods for both parameters because differing methods can themselves give disparate results (Thomas 1996, Thomas and Martin 1996). Other, more advanced trend-analysis methods exist, such as several variants of route-regression, log-linear or Poisson regression, and smooths (e.g. Fewster et al. 2000) that will likely give better individual results, though at the expense of a clear comparison. Even within the current simplified method, distance-sampling trends could be improved by precision-weighting the regression analysis.

Assumptions specific to relative-abundance methods.—The foundation of all relative-abundance methods (indices) is the requirement of constant proportionality (Pendleton 1995, Thompson et al. 1998). Although relative-

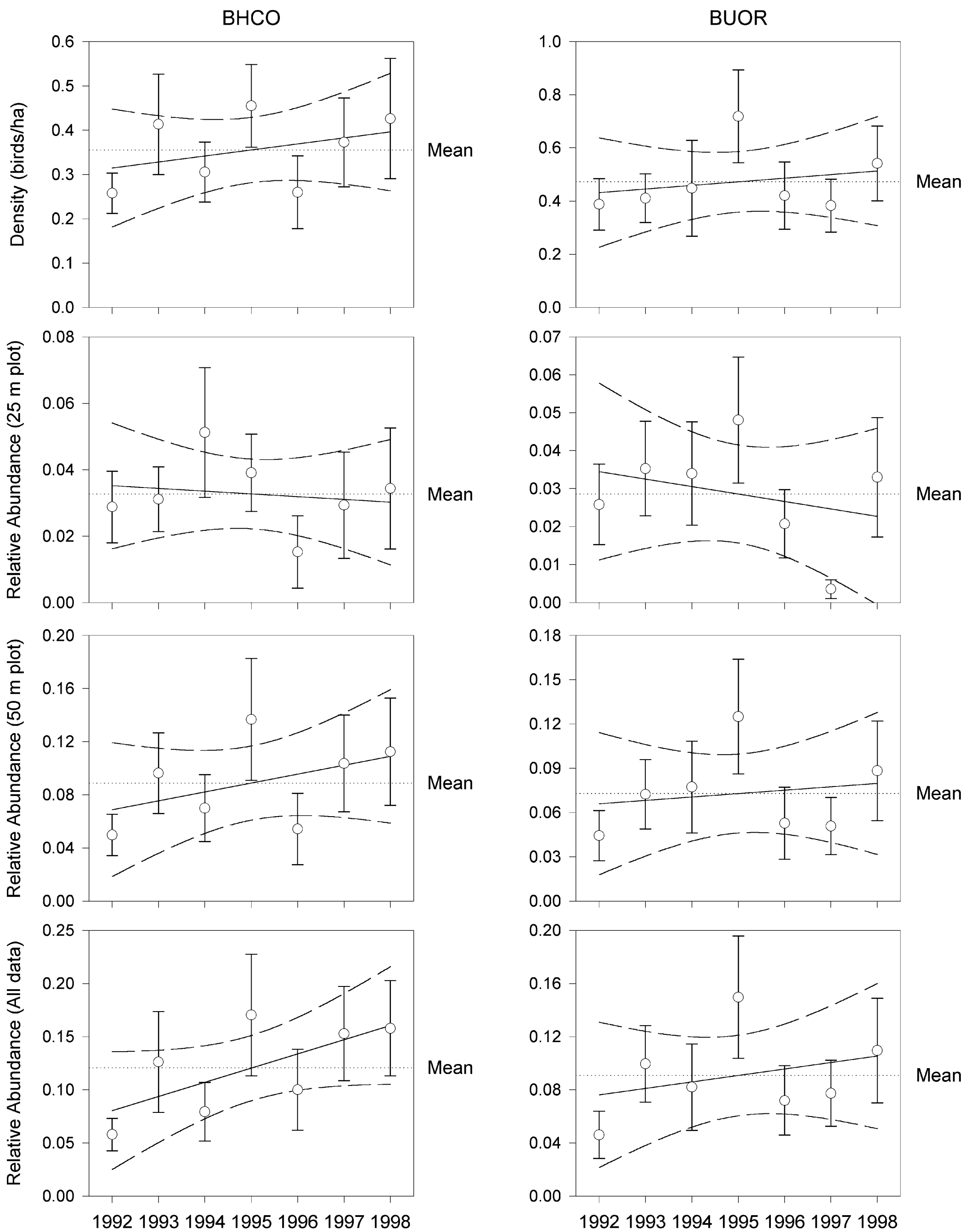

FIG. 4. Trends in estimated density and relative abundance (at three plot radii) for (A) Brown-headed Cowbird (BHCO) and (B) Bullock's Oriole (BUOR) from 1992 to 1998. Estimated annual density values are given (with the mean and 95% CIs) in the top figure for each species; relative abundance values (mean number of birds observed per point per visit per site per year, with the mean and Poisson 95% CIs) for 25 m, 50 m bounded, and unbounded survey plots are given in the lower three plots, respectively. (*Figure 4 is continued on the next page.*)

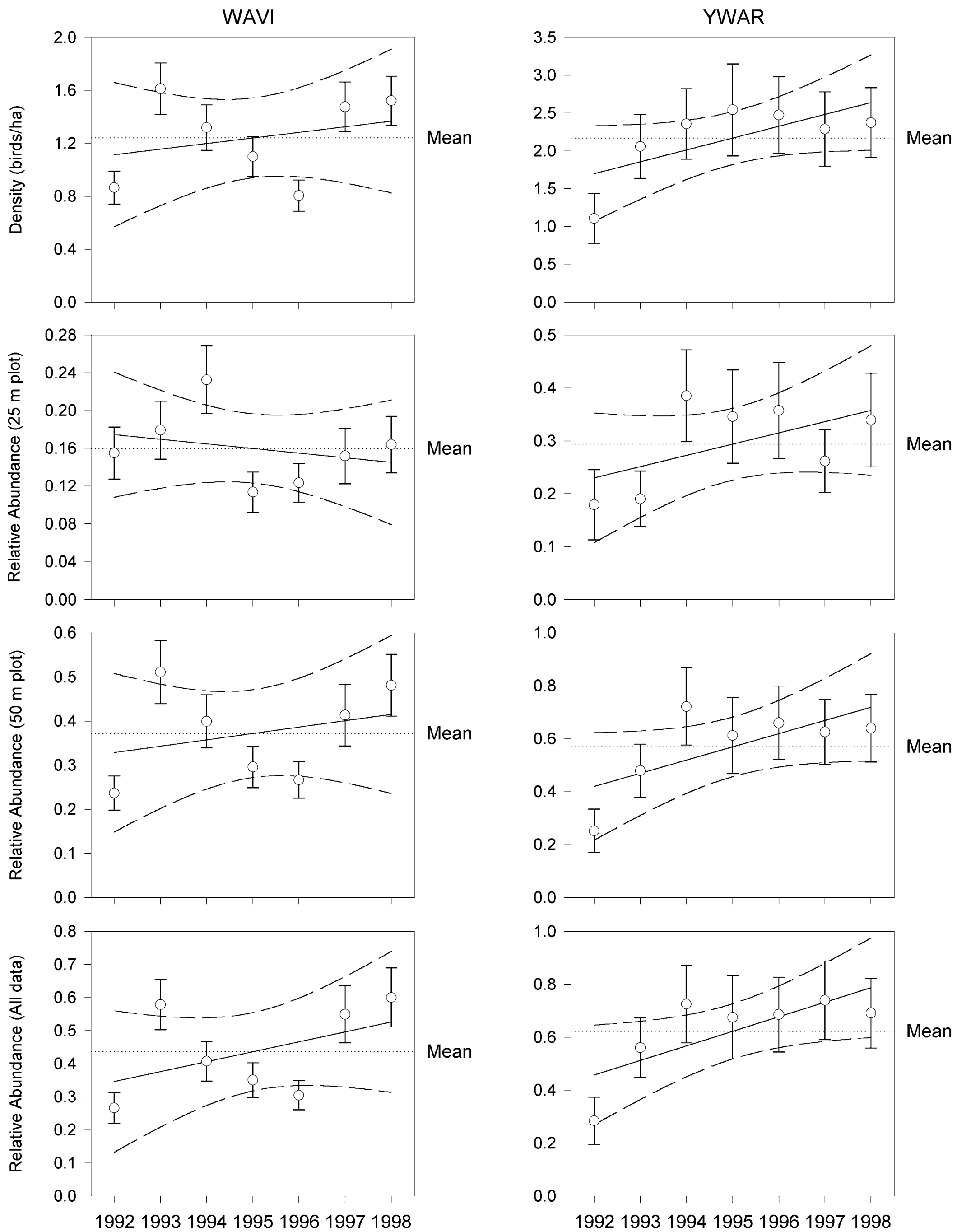

FIG. 4. (*Continued.*) Trends in estimated density and relative abundance (at three plot radii) for (C) Warbling Vireo (WAVI) and (D) Yellow Warbler (YWAR) from 1992 to 1998. Simple linear regression trends are shown, with 95% confidence bands, for comparison between density and relative abundance figures for each species (see Table 2 for trend values and significance). If the three relative-abundance plots were capturing consistent proportions of the available observations, there would at least be concordance between the lower three rows of plots; instead note that the magnitude and direction of the trend varies with both analysis method and survey plot radius for all species but Yellow Warbler.

abundance counts can be biased and still retain utility, they must be consistently biased—over 95% consistent according to a simulation study by White and Bennetts (1996)—across all survey instances. Constant proportionality is widely assumed to have been met because standardized data collection methods are used (e.g. Ralph et al. 1993, 1995; Huff et al. 2000; but see Bart and Schoultz 1984), but our data show that even for a well-designed study using widely recommended methods, the assumption of constant proportionality is consistently violated to a degree that precludes valid inference and confounds trend analyses. The strongest evidence for that is found in the large annual variation of P_a where the assumption of equal probability of detection was clearly violated for every species we examined. The proportion captured by fixed plot methods, one of the most commonly applied correctives to unequal detectability, dramatically varied between years because of changes in the shape of each year's data distribution.

Further, although the runs tests of P_a have low power because of small number of years, it was significant for one species presented here, a result typical of >20% of all species analyzed to date (R. Norvell unpubl. data). That strongly suggests that despite professional observers, intensive training, and standardized methods, systematic changes in observer efficiency occur over the course of a long-term study. Those changes can bias relative-abundance-based trends. Use of fixed plots was ineffective at eliminating observer bias in our study because the apparent increase in detectability occurred disproportionately at longer distances. Relative-abundance trend analyses have a strong sensitivity to survey plot radius that cannot be separated from underlying changes in true abundances.

Assumptions specific to distance-sampling methods.—There was little evidence for the violation of the assumption that birds at the point were detected with certainty; the minor deviations from the expected values seen in the detection functions are typical of small samples (Appendix). Similarly, there was no strong evidence of violation of the assumption of no undetected responsive movement by birds prior to their initial observation.

Although the assumption of accurately measured distances was clearly violated to some degree every year given that most distances collected were estimates to aural detections, it is the least critical of the distance-sampling assumptions (Buckland et al. 2001). Further, because our distance data were collected as exact distances but were grouped for analysis in intervals, we had wide latitude to compensate for rounding errors (the most common problem seen in our distance data), thereby improving the accuracy of the data. To improve the quality of distance data estimation in the field, we strongly recommend training observers in the analysis methods and using laser rangefinders.

The final assumption for distance sampling, that of a "shoulder" of near-perfect detectability extending for some distance from the point (the shape criterion, Buckland et al. 2001) was also largely met, although the degree to which it existed varied both by species and by year, a condition reflected in the standard error of each year's estimate.

Conclusion.—Our data show that the assumption of constant proportionality was consistently violated to a degree that makes comparisons of relative abundance between years within a single species and within a single habitat tenuous. In addition, changes in observer efficiency occurred over the course of our study, a phenomenon that can introduce serious but hidden bias into relative-abundance trend analyses. Finally, we demonstrate that distance sampling is a field-worthy alternative, even in low-visibility multispecies settings.

Statistically, an index such as relative abundance should track the parameter of interest with constant proportionality; logistically, it should be sufficiently simple and inexpensive such that inherent losses in precision may be offset by gains in sample size. An estimator (such as detection probability corrected density) should be robust to assumption violations, exhibit minimum variance, and be unbiased. In our study, P_a varied widely, systematically, and to a degree that undermined confidence in relative abundance results. Fixed plot indices of relative abundance captured inconsistent proportions of the annual detections, providing no relief from inconsistency. Distance sampling largely met assumptions and gave acceptably precise unbiased results despite a study design based on a relative-abundance approach.

One complaint leveled against distance sampling is that distance estimation in the field is a difficult and inaccurate affair and that it is more plausible for observers to have only a few distance categories from which to choose (Verner 1985 among others). It is true that the field technician's lot would be simplified by using just 5–7 distance categories, while still retaining the ability to model the data well in a distance sampling context (Buckland et al. 2001). To illustrate the point, we reanalyzed the data for those four species using just three distance categories (0–25, 25–50, 50–75 m) and found both the annual results and trend results closely followed the full data. But we feel recording of exact distances in the field is still preferable because it allows inspection for assumption violations (such as rounding distances or responsive movement) and for more flexibility at the analysis stage. Our results show that even in a multispecies (>200 possible) survey setting with limited visibility, excellent quality data can still be obtained despite the complicating collection of exact distances.

The four species presented here enable a fair comparison between methods because they are ideal candidates for each approach: easily identified, abundant, and territorial species with typically clear songs and calls. Distance-sampling methods will work well for species with similar characteristics but may perform poorly for rare or clumped species where small sample sizes are likely to produce large standard errors (e.g. Hayward et al. 1991). In the relative-abundance analysis setting, however, unequal detection probabilities problems plague even ideal species analyses. That problem is likely to be worse for "less than ideal" species.

The pattern of increasing detection distances in the later years of our study is likely an artifact of increasing observer efficiency (as might be expected from a >65% repeat rate for our observers in later years). Such effects are common in large-scale multiobserver studies (Sauer et al. 1994, Kendall et al. 1996) and should be directly addressed in both study design and subsequent analyses. The wide range of relative-abundance trend slopes based on different radius plots (and diverse management conclusions that could be drawn from those) resulted in part from that apparent increase in observer efficiency. That assertion is generally supported by the nonparametric runs tests results. In a traditional relative-abundance analysis, that trend in detectability would badly bias results, but the analyst would have no means of discovering it.

The comparability and popularity of relative-abundance indices rest upon the assumed insignificance of differential detectability, despite extensive evidence to the contrary. Our data suggest that comparisons between or even within studies using relative abundance (as either an assumed census or as an index to density) are based on a tenuous premise. When constant detectability is not achieved in such studies, we fail as researchers to accumulate information in a form that is comparable between times, habitats, or species. We feel the robust estimates derived from distance sampling warrant the increased effort needed to model detection probabilities given the sensitivity of traditional relative-abundance indices to commonly violated assumptions that compromises their use.

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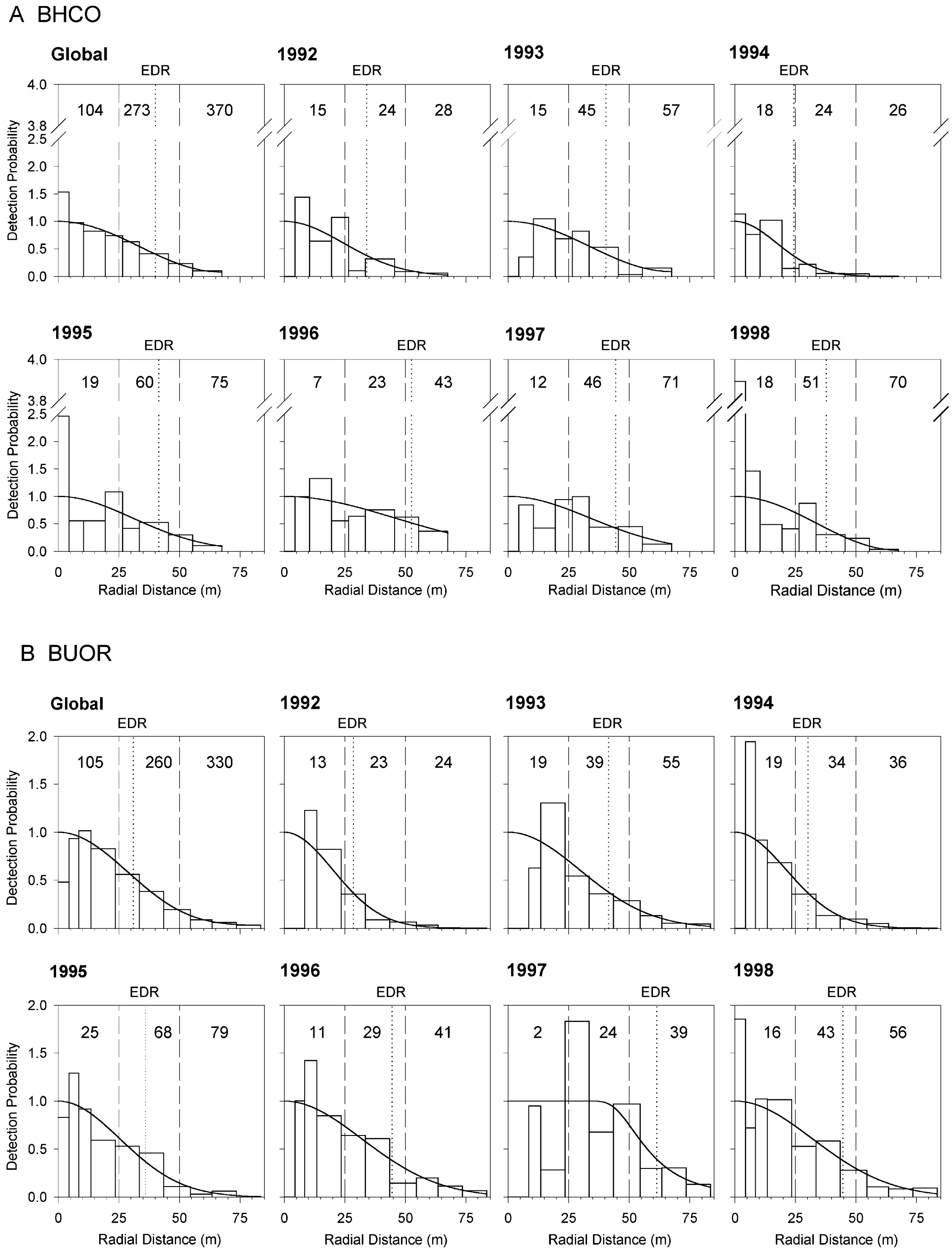
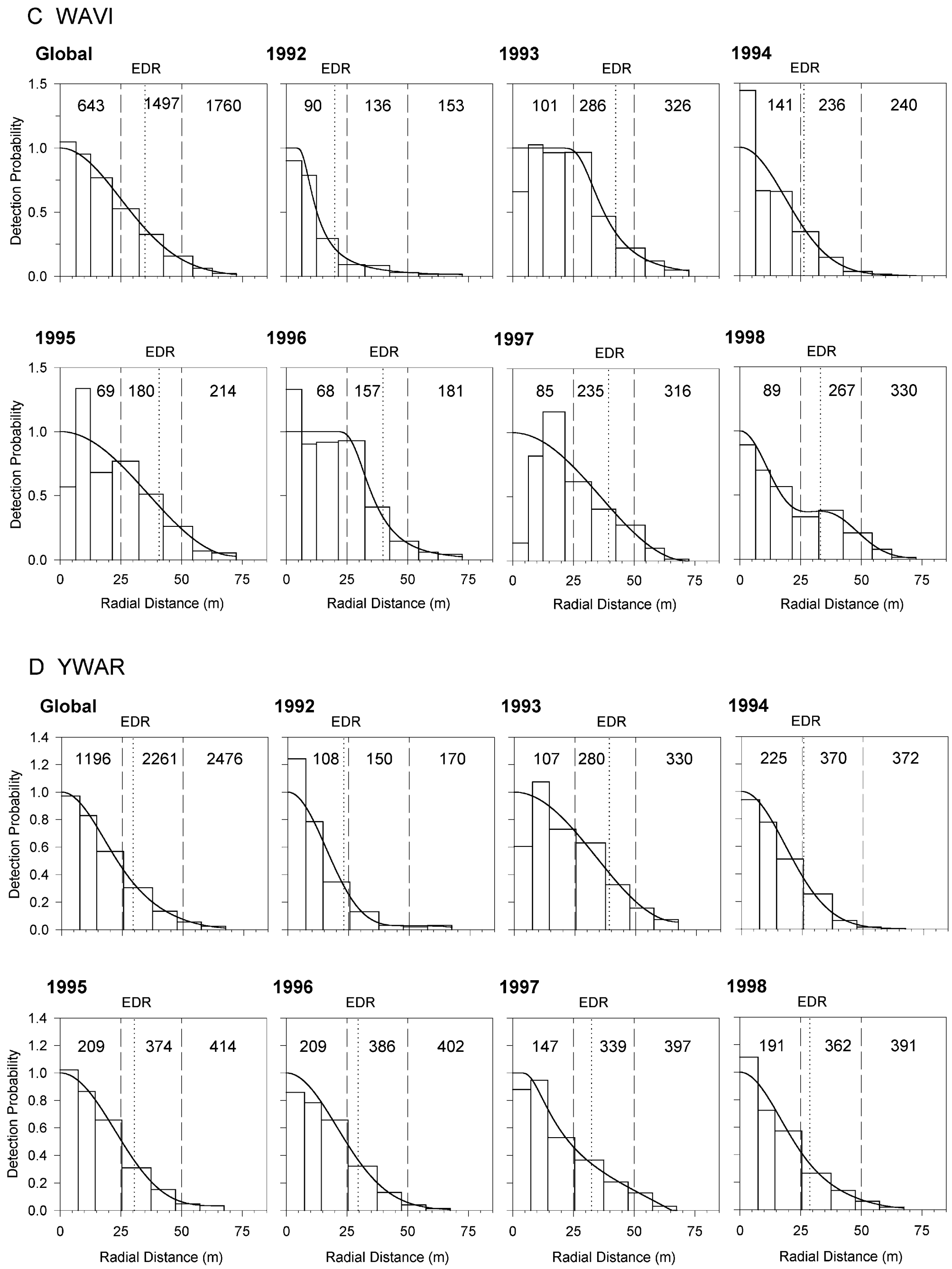


Appendix. Global and annual detection functions (1992–1998) for (A) Brown-headed Cowbird (BHCO), (B) Bullock's Oriole (BUOR), (C) Warbling Vireo (WAVI), and (D) Yellow Warbler (YWAR) (note that the area under the histograms of observed data has been scaled to equal the area under the fitted function to allow better visual assessment of model fit). In the body of each plot, the vertical dashed lines denote 25 and 50 m survey plot radii, and the sum of all detections for each plot radii are shown above (e.g. n = 15 for BHCO in 1992 for 25 m survey plots). The EDR (see Table 1 for exact values) is denoted by the vertical dotted line. (*Continued on next page.*)



APPENDIX. (*Continued.*) Note the varying proportion of the sample distributions captured by fixed plot radii between years and the changing value of the EDR between years. Both those variations indicate a violation of the assumption of constant proportionality (Thompson et al. 1998). Histogram widths and right-ward data truncation distances (BHCO = 67.5 m, BUOR = 83.5 m, WAVI = 72.5 m, and YWAR = 67.5 m) were iteratively selected in the global detection function analysis for each species (Buckland et al. 2001) and carried into the annual detection function analyses so as to provide a consistent, albeit less efficient, context for comparison of annual distance data distributions and model fit.