

Multiple-species analysis of point count data: a more parsimonious modelling framework

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Summary

1. Although population surveys often provide information on multiple species, these data are rarely analysed within a multiple-species framework despite the potential for more efficient estimation of population parameters.
2. We have developed a multiple-species modelling framework that uses similarities in capture/detection processes among species to model multiple species data more parsimoniously. We present examples of this approach applied to distance, time of detection and multiple observer sampling for avian point count data.
3. Models that included species as a covariate and individual species effects were generally selected as the best models for distance sampling, but group models without species effects performed best for the time of detection and multiple observer methods. Population estimates were more precise for no-species-effect models than for species-effect models, demonstrating the benefits of exploiting species' similarities when modelling multiple species data. Partial species-effect models and additive models were also useful because they modelled similarities among species while allowing for species differences.
4. *Synthesis and applications.* We recommend the adoption of multiple-species modelling because of its potential for improved population estimates. This framework will be particularly beneficial for modelling count data from rare species because information on the detection process can be 'borrowed' from more common species. The multiple-species modelling framework presented here is applicable to a wide range of sampling techniques and taxa.

Key-words: abundance, capture–recapture, multiple-species modelling, point count surveys, population surveys

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Introduction

Most animal sampling methods are not species specific. Methods such as small mammal trapping (Webb 1965; Schwartz & Whitson 1986; Mengak & Guynn 1987), mist netting birds (Nur, Jones & Geupel 1999), electrofishing (Meador, McIntyre & Pollock 2003) and avian point counts (Canterbury *et al.* 2000; Thompson 2002) all provide information on multiple species. Nevertheless, analyses of these types of data aimed at estimating population parameters are frequently performed at the

individual species level. Because the capture/detection process may be very similar among species, better estimates of precision and more parsimonious models are possible through analyses that exploit species' similarities. Parsimonious models prioritize simplicity and represent a balance between squared bias and variance (Burnham & Anderson 2002). We demonstrate the use of multiple-species modelling for single-species parameter estimation with analyses of avian point count surveys as an example of a widely applicable modelling framework.

The methods implemented in this paper can also be used to obtain estimates of community abundance in order to monitor biodiversity. In order to carry out such analyses, the method must be robust to species pooling

to avoid bias as a result of differences in detection probabilities among species (Buckland *et al.* 2004). However, our focus is on improving single-species parameter estimation by 'sharing' information on the detection process across species and not community-level parameters.

The point count survey method is a general sampling approach used to estimate relative abundance and density of bird populations (Ralph, Sauer & Droege 1995; Thompson 2002). Several recent papers have emphasized the necessity of understanding the detection process and the limitations of using counts as indexes of abundance (Nichols *et al.* 2000; Farnsworth *et al.* 2002; Rosenstock *et al.* 2002). This focus on modelling detectability has resulted in a greater application of sampling methods that directly estimate detection probabilities. Currently three distinct methods are available for estimating abundance and modelling the detection process from unrepeated point count surveys. First, distance, or point transect, methods model the probability of detection as a function of distance from the observer, and estimate the density of populations (Ramsey & Scott 1979; Reynolds, Scott & Nussbaum 1980; Buckland *et al.* 2001). Secondly, multiple-observer methods estimate the probability of detection by each observer using a removal (primary–secondary observer) (Nichols *et al.* 2000) or capture–recapture (independent observers) (Allredge, Pollock & Simons 2006) modelling framework. Distance and multiple-observer methods assume all individuals in a sample area are available for detection. Thirdly, the time of detection method estimates the probability of detection over multiple time intervals using a first-detection removal (Farnsworth *et al.* 2002) or a multiple-detection capture–recapture framework (Allredge *et al.* 2007). This method estimates the combined probability that an individual is available for detection and that it is detected given that it is available.

The detection process modelled by all three methods involves a bird making itself available for detection and the ability of observers to detect an available bird. In open habitats such as grasslands, detection may be primarily visual, such that availability depends on a bird being present and not hidden from view. In heavily vegetated habitats, such as forests, detections are primarily auditory (Scott, Ramsey & Kepler 1981) and availability depends on both a bird's presence and the probability that the bird sings or calls during a count (Farnsworth *et al.* 2002). Standard approaches to analysing these data generally estimate the detection function for each species separately, ignoring similarities among species (Ralph, Sauer & Droege 1995). Models of the detection process using standard single-species approaches are overparameterized when similarities in the detection process exist among species. Multiple-species models have fewer model parameters because they exploit similarities among species.

We present a multiple-species modelling framework for estimating single-species population parameters for

three methods of analysing point count data: distance sampling, time of detection and multiple observer methods. Distance sampling uses recorded distances from the observer to detected individuals to estimate a detection function that describes the probability of detecting an individual as a function of distance from the observer. Time of detection sampling uses a capture–recapture approach in which a count is divided into several intervals and observers record whether or not an individual is detected in each interval of the count. The resulting detection history is used to estimate the probability of detecting an individual in a given time interval. The multiple observer method also uses a capture–recapture framework by using the observations of independent observers to develop a detection history for each individual in the count.

We used point count data from primarily forested habitats in the Great Smoky Mountains National Park, USA, to classify 19 bird species into six groups based on truncated maximum detection distance and similarities in singing rates. If multiple-species models are supported, they are likely to offer a significant advantage in population studies if more precise population estimates can be computed. For each of the three methods of analysing point count data described above, we compared the number of parameters, precision and bias of multiple-species and individual-species models.

Our approach to incorporating information from multiple species into models of the detection process involved developing species groups based on assumed similarities in the detection process among species. One of the challenges of multiple-species modelling is developing a reasonable set of candidate models, particularly when the number of species detected or captured is large. Modelling all possible combinations of species is not realistic. Our approach is to define biologically reasonable groups of species and examine differences and similarities in the detection process within groups. Species should be grouped based on similarities in characteristics that affect the capture or detection process. Unfortunately little is known on how various factors affect detection of birds from auditory cues.

When birds are detected by ear, important components of the detection process that can be used to group species are: sound intensity (energy content of a song), sound pitch (frequency of a song), sound modulation (variation in either sound pitch or intensity; Richards 1981), singing rate (Wilson & Bart 1985; McShea & Rappole 1997), and typical perching height (e.g. ground, shrub or canopy). Detection distance may serve as a surrogate for characteristics that directly affect the distance at which a sound can be heard.

Methods

FIELD METHODS

Time-of-detection point transects of breeding songbirds were conducted in the Great Smoky Mountains National

Park during May and June from 1996 to 1999 (Shriner 2001). Survey points were located along low-use hiking trails with a minimum of 250 m between points. Vegetation was closed-canopy deciduous hardwood forest; consequently detections were primarily aural (more than 95%).

All counts were conducted between dawn and 10:15 in the morning on days with good weather (no rain or excessive wind). Observers were trained and tested in identification and distance estimation prior to conducting point counts. Counts were conducted for 10-min intervals divided into three observation intervals, the first 3 min, the next two min and the final five min of the count. The time of initial detection and detections in subsequent intervals were recorded. Detection distance was estimated for all observations and laser range finders were used to calibrate and verify distance estimates at each point.

Data were limited to observations collected by a single observer in 1998 to eliminate temporal and observer effects in the models, resulting in a data set of 323 survey points. We omitted species with fewer than 50 observations from the analyses. While these surveys allowed for both time of detection and distance analyses, the two data sets were not comparable because the time of detection analyses were based on observations from all three time intervals while distance analyses were based only on observations from the first 3-min interval. Further, distance sampling does not account for the portion of the population that is not available.

Multiple independent observer data were also collected in the Great Smoky Mountains National Park. However, these data were collected independently in June 1999 and were not comparable with the other data sets. Four independent observers participated in each multiple observer point count. Observers were highly trained and had been conducting point counts for 6 weeks prior to the survey. Three minute counts were conducted at 70 points and followed a protocol similar to that described previously, mapping the location of each bird detected at a point. Each bird was tracked during the point count to avoid double counting and to simplify matching observations among observers. Following each count observers compared their observations to determine the total number of birds detected and to identify birds detected in common.

SPECIES GROUPS

We used maximum detection distance, following 10% truncation of the observations at the largest distances, as the first criterion for defining species groups. Because many characteristics (sound intensity, pitch, modulation, etc.) can affect maximum detection distance, we defined three general groups: (i) species with maximum detection distance ≤ 100 m; (ii) species with maximum detection distance > 100 m and ≤ 150 m; and (iii) species with maximum detection distance > 150 m. Within these groups, species were further grouped based on singing

rate rankings obtained from seven experts familiar with the species and habitats used for our analyses. Ranks were based on a scale from one to five, with one indicating the smallest value (presumed lowest probability of detection) and five indicating the highest value (presumed highest probability of detection). These ranks were averaged across the seven experts. Experts also ranked sound intensity, sound pitch and sound modulation.

MODEL SELECTION AND ANALYSIS APPROACH

Model selection was based on Akaike's information criterion corrected for small sample size (AIC_c) (Burnham & Anderson 2002). We report ΔAIC_c values, which reflect the difference between the AIC_c value of a particular model and the model with the lowest AIC_c value. The model with a ΔAIC_c of zero is the most parsimonious (best) model and competing models with substantial empirical support are generally considered to be those with $\Delta AIC_c < 2$ (Burnham & Anderson 2002). We also present AIC_c weights, which describe the weight of evidence in favour of a given model relative to the set of candidate models (Burnham & Anderson 2002).

DISTANCE ANALYSIS

We used the program *DISTANCE* (Thomas *et al.* 2002, 2005) to analyse the distance data, with species identification entered as an observation-level variable. This scheme allowed for two multiple-species analytical approaches: post stratification by species (Marques *et al.* 2001; Rosenstock *et al.* 2002) and the use of species as model covariates (Marques & Buckland 2003, 2004). We limited these analyses to observations from the first 3-min interval, truncating the data at 10% of the largest observed distances for all analyses, as recommended by Buckland *et al.* (2001).

We modelled the detection process within species groups using three candidate models: (i) a common detection function for all species within a group (no species effect); (ii) different detection functions for each species within a group (species effect) based on post-stratifying on species; and (iii) a detection function with a common shape parameter for all species, but using species as a covariate to model the scale parameter. We tested the following key functions and adjustments for detection functions for the models with and without species effects for each species group comparison: uniform key function, simple polynomial adjustment; half-normal key function, cosine adjustment; hazard rate key function, cosine adjustment.

For the covariate models, we used both the half-normal and hazard rate key functions with the multiple covariate distance sampling (MCDS) analysis engine of program *DISTANCE* (Thomas *et al.* 2005). The appropriate key function and adjustment models were selected

using AIC_c . AIC_c was subsequently used to choose between the species-effect, no-species-effect and covariate models. We compared the precision of models with and without a species effect using the effective detection radii (EDR) and density estimates (D) from the distance analysis.

TIME OF DETECTION ANALYSIS

Single-species time of detection models are equivalent to closed-population capture–recapture models (Otis *et al.* 1978) that account for variation in detection probabilities associated with the length of the sampling interval, differences in the probability of first and subsequent detections, and differences in the detection probabilities of individual birds (Allredge *et al.* 2007). Zeros in the capture history for this method can represent either a bird that did not sing in a given interval or a bird that sang but was not detected by the observer, which is why the method models both availability and detectability. We used two-point finite mixture models of heterogeneity (Norris & Pollock 1996; Pledger 2000) to account for individual differences in detection probabilities (Allredge *et al.* 2007). Finite mixture models group the surveyed population into a finite number of groups based on differences in detection probabilities. For example, a population may consist of two groups of birds, one group that is easily detected and has high detection probabilities, and another group that is hard to detect and has low detection probabilities. These models require estimation of the proportion of individuals in each group (λ) and the detection probabilities for each group (p_T). We used the constrained form of the model, in which detection probabilities for one of the mixtures is equal to one (Farnsworth *et al.* 2002; Allredge *et al.* 2007). While this is a strong assumption and violation may lead to bias in abundance comparisons across time or space, data sets with only three time intervals are insufficient to estimate all parameters for an unconstrained model. We recommend future studies use four or more time intervals to allow estimation of a full two-point mixture model (Allredge *et al.* 2007). These models can take one of three forms: heterogeneity only, heterogeneity and differences between first and subsequent detections, or heterogeneity and time interval effects.

There are seven single-species candidate models for the time of detection method (see Appendix S1 in the supplementary material), which include models that incorporate time, behaviour and heterogeneity effects. The multiple-species time of detection method includes 20 candidate models based on the seven single-species models (Allredge *et al.* 2007) with or without a species effect (see Appendix S1 in the supplementary material). Models with time and species effects can be parameterized in two ways: an interaction effect between time and species (model M_i^{*sp}), or an additive effect between time and species (model M_i^{+sp}). The interaction effect model is equivalent to a single-species approach with

an equivalent number of parameters. The additive model exploits similarities among species and only requires a single parameter for each additional species.

We also present partial heterogeneity models (models M_h^{part} , M_{bh}^{part} , and M_{th}^{part}). These models assume detection probabilities are the same for all species in a group, but the probability of being in one of the heterogeneity mixtures is not the same for all species within the group. In other words, p_T is the same for all species in the group but λ differs. We assume that the biological mechanism underpinning these models involves a process in which the probability of detection is similar among species at the same breeding stage but varies among breeding stages. Allredge (2004) describes these models and Appendix S1 (see the supplementary material) lists all the models and the associated number of parameters.

We used the program SURVIV (White 1983) to estimate the detection parameters and two-point mixture heterogeneity parameters for the time of detection data. We assumed an instantaneous rates formulation for detection probabilities. This approach was necessary to parameterize models with no time effect because data were based on unequal time interval counts (Allredge *et al.* 2007). All candidate models were run initially, but models with both time effects and differences between probabilities of first and subsequent detections were omitted from further analysis because not all parameters were identifiable.

Population estimates and standard errors were derived from the estimated detection probabilities and heterogeneity parameters (Allredge *et al.* 2007). We report the probability of detecting an individual at least once during a count (\hat{p}_T), the heterogeneity parameter ($\hat{\lambda}$) and the population estimates (\hat{N}) for the selected model. For groups in which a species-effect model was selected, we also report parameters for the alternative no-species-effect model.

MULTIPLE OBSERVER ANALYSIS

Independent observer data were analysed using the full set of multiple observer models presented in Allredge, Pollock & Simons (2006) because data were collected using four observers, allowing for full parameter estimation. Single-species independent observer models are equivalent to closed-population capture–recapture models (Otis *et al.* 1978) and account for observer differences as well as differences in detectability for individual birds (individual heterogeneity). Following this approach, a zero in the capture history represents a bird that was missed by a given observer but was detected by at least one other observer. In the absence of model covariates, the independent observer method includes four single-species candidate models (Allredge, Pollock & Simons 2006). We used two-point finite mixture models (Norris & Pollock 1996; Pledger 2000) to model heterogeneity in detection probabilities among individual birds. The parameters for this finite-mixture closed-population capture–recapture model are the detection

probability for each observer (i) and λ , the proportion of the population in one of the detection probability group. Again, the groups represent birds that have different detection probabilities, such as high and low detection probabilities.

Excluding covariate models, we obtained 12 candidate models for the multiple-species independent observer approach by adding a species effect to the four single-species candidate models. Observer and species effects were modelled as either an interaction effect (model M_{obs}^{*spp}) or an additive effect (model M_{obs}^{+spp}). As above, the interaction effect model was equivalent to the single-species approach. The additive effect model used the similarities among species as a single parameter for each species added to the group. We also present a partial individual heterogeneity effect, similar to that used in the time of detection models, that allowed detection probabilities to remain constant among species but the probability of being in any particular mixture to vary among species. Allredge (2004) describes these models, and Appendix S1 (see the supplementary material) lists the complete set of models and associated number of parameters.

We used program MARK (White & Burnham 1999) with the 'Huggins Closed Captures' and 'Huggins Full Heterogeneity' data types to analyse the four-independent observer count data. We report the individual heterogeneity parameter estimate ($\hat{\lambda}$), the observer-specific detection probabilities and the population estimate (\hat{N}) for the selected model.

Results

SPECIES GROUPS

Nineteen species from the time of detection/distance data sets were selected for analysis. Three groups were defined in the ≤ 100 m category (groups A, B and C), two groups in the 100–150 m category (groups D and E) and one group in the over 150 m category (group F), based on similarities in singing rates (see Appendix S2 in the supplementary material). Group sizes ranged from two to four species.

Because fewer points were sampled using the multiple observer method, sample sizes were sufficient for only eight species. Therefore, no analysis was done for group A, black-throated blue warbler *Dendroica caerulescens* was omitted from group B, and indigo bunting *Passerina cyanea* was omitted from group C. Scarlet tanager *Piranga olivacea* (group D), ovenbird *Seiurus aurocapillus* (group E) and tufted titmouse *Baeolophus bicolor* (group F) were combined into a single group, DEF.

DISTANCE

Species-covariate models were selected as the best model for three of the six groups (B, C and F) and always had some support from the data (AIC_c weights ≥ 0.12) (Table 1), indicating similarities in the underlying detec-

Table 1. ΔAIC_c and AIC_c weights (in parentheses) for distance models using the first 3-min interval of the time of detection data

Species group	No species effect	Species effect	Species covariate
A	6.01 (0.03)	0.00 (0.64)	1.32 (0.33)
B	13.60 (0.00)	3.20 (0.17)	0.00 (0.83)
C	7.38 (0.02)	1.16 (0.35)	0.00 (0.63)
D	0.00 (0.62)	1.76 (0.26)	3.29 (0.12)
E	9.12 (0.01)	0.00 (0.66)	1.37 (0.33)
F	16.64 (0.00)	11.08 (0.00)	0.00 (1.00)

tion process across species within these groups and the utility of multiple-species modelling. A hazard rate detection function was selected for groups B and C and a half-normal detection function with a cosine adjustment term was selected for group F. Species-effect models (equivalent to a single-species approach) were selected as the best model for two of the groups (A and E) and had some support from the data (AIC_c weights ≥ 0.17) for all but group F. Uniform detection functions with simple polynomial adjustment terms were selected for both groups A and E. The no-species-effect model was selected as the best model for group D but had little support from the data (AIC_c weights ≤ 0.03) for all other groups. A uniform detection function with a simple polynomial adjustment term was selected for group D.

Effective detection radii varied within groups, except group D for which the no-species-effect model was selected (Table 2). Differences in effective detection radii among species were > 10 m for all other groups. Estimates of effective detection radii were similar between the species-effect and species-covariate models but were generally larger for the species-covariate models. No assessment of distance measurement error was made but measurement errors could have been substantial because most detections of birds were based on auditory cues with no visual reference.

Density estimates for group D were identical for species-effect and no-species-effect models, but the standard errors were smaller for the no-species-effect model (Table 2). The increase in precision was particularly obvious for the veery *Catharus fuscescens* (0.018 for the species-effect model and 0.009 for the no-species-effect model), which had a smaller observed count. While species with relatively few observations are likely to be associated with larger gains in precision, we emphasize the need for careful a priori grouping because these species are also at greater risk of undetected bias. Density estimates were similar between the species-covariate models and species-effect models but estimates were more precise for the species-covariate models.

TIME OF DETECTION

Models accounting for individual heterogeneity in detection probabilities were selected as the most parsimonious models for all six species groups (Table 3).

Table 2. Distance analysis results for species-effect models and for the selected model based on AIC_c. The observed count is after 10% truncation of the largest detection distances, EDR is the effective detection radius, and density is individuals per hectare. Standard errors are in parentheses

Group	Species	Model	Observed count	Species effect		Selected model	
				EDR	Density	EDR	Density
A	Acadian flycatcher <i>Empidonax vireescens</i>	Species effect	58	53.9 (6.86)	0.20 (0.041)		
	Black-and-white warbler <i>Mniotilta varia</i>		90	43.5 (1.63)	0.47 (0.072)		
	Golden-crowned kinglet <i>Regulus satrapa</i>		64	47.1 (2.34)	0.29 (0.061)		
	Worm-eating warbler <i>Helmitheros vermivorus</i>		56	46.9 (3.14)	0.25 (0.056)		
B	Black-throated blue warbler <i>Dendroica caerulescens</i>	Species covariate	145	59.9 (2.16)	0.40 (0.060)	56.6 (1.96)	0.45 (0.066)
	Dark-eyed junco <i>Junco hyemalis</i>		109	49.2 (2.75)	0.44 (0.080)	58.4 (2.30)	0.31 (0.051)
	Hooded warbler <i>Wilsonia citrina</i>		192	64.5 (4.41)	0.46 (0.078)	68.4 (1.82)	0.40 (0.046)
	Blue-headed vireo <i>Vireo solitarius</i>		98	52.8 (4.88)	0.35 (0.079)	58.7 (2.44)	0.28 (0.044)
C	Black-throated green warbler <i>Dendroica virens</i>	Species covariate	273	77.6 (2.98)	0.45 (0.049)	78.0 (1.49)	0.44 (0.038)
	Indigo bunting <i>Passerina cyanea</i>		40	54.5 (2.03)	0.13 (0.027)	58.5 (3.85)	0.12 (0.027)
	Red-eyed vireo <i>Vireo olivaceus</i>		270	78.8 (6.11)	0.43 (0.075)	78.8 (1.49)	0.43 (0.038)
D	Scarlet tanager <i>Piranga olivacea</i>	No species effect	114	70.6 (1.85)	0.23 (0.029)	70.1 (1.51)	0.23 (0.025)
	Veery <i>Catharus fuscescens</i>		39	69.0 (2.54)	0.08 (0.018)		0.08 (0.009)
E	Ovenbird <i>Seiurus aurocapillus</i>	Species effect	328	72.3 (1.69)	0.62 (0.061)		
	Eastern towhee <i>Pipilo erythrophthalmus</i>		54	54.5 (1.75)	0.18 (0.037)		
F	Red-breasted nuthatch <i>Sitta canadensis</i>	Species covariate	30	104.9 (15.86)	0.03 (0.011)	129.2 (9.32)	0.02 (0.005)
	Tufted titmouse <i>Baeolophus bicolor</i>		79	100.7 (9.11)	0.08 (0.018)	120.8 (5.51)	0.05 (0.009)
	Winter wren <i>Troglodytes troglodytes</i>		80	105.7 (7.58)	0.07 (0.014)	120.6 (5.46)	0.05 (0.009)
	Wood thrush <i>Hylocichla mustelina</i>		135	73.6 (10.84)	0.25 (0.077)	104.9 (3.88)	0.12 (0.017)

Time effects were included in models selected for groups B, C, E and F. Models with differences in detection probabilities between first and subsequent detections were never selected. All models including time effects

Table 3. ΔAIC_c and ΔAIC_c weights (in parentheses) for time of detection multiple-species models for unlimited radius plots with 10% truncation of the largest detection distances. Smaller values of ΔAIC_c indicate more parsimonious models. Larger weights indicate more support for a given model. Models with weights ≥ 0.20 are in bold for each species group, indicating competing models. Models with unrealistic parameter estimates were omitted (blanks)

Model	Groups					
	A	B	C	D	E	F
M_0^0	55.5 (0.00)	145 (0.00)	124 (0.00)	41.1 (0.00)	72.1 (0.00)	180 (0.00)
M_0^{spp}	58.3 (0.00)	123 (0.00)	127 (0.00)	36.9 (0.00)	73.4 (0.00)	84.0 (0.00)
M_1^0	43.6 (0.00)	131 (0.00)	106 (0.00)	36.3 (0.00)	59.8 (0.00)	143 (0.00)
M_1^{+spp}	36.2 (0.00)	79.3 (0.00)	48.4 (0.00)	36.4 (0.00)	52.3 (0.00)	44.4 (0.00)
M_1^{*spp}	51.4 (0.00)	108 (0.00)	107 (0.00)	34.4 (0.00)	61.2 (0.00)	48.5 (0.00)
M_h^0	55.9 (0.00)	147 (0.00)	123 (0.00)	43.1 (0.00)	74.1 (0.00)	182 (0.00)
M_h^{spp}	62.6 (0.00)	115 (0.00)	125 (0.00)	40.7 (0.00)	75.6 (0.00)	92.2 (0.00)
M_{th}^0						
M_{th}^{+spp}						
M_{th}^{*spp}						
M_h^0	0.0 (0.51)	20.3 (0.00)	3.6 (0.04)	3.2 (0.08)	5.8 (0.03)	75.2 (0.00)
M_h^{part}	4.5 (0.05)	4.3 (0.09)	5.0 (0.02)	0.0 (0.40)	6.6 (0.02)	5.9 (0.05)
M_h^{spp}	9.6 (0.00)	8.4 (0.01)	7.2 (0.01)	1.9 (0.16)	7.7 (0.01)	8.9 (0.01)
M_{hh}^0	2.0 (0.18)	22.3 (0.00)	5.6 (0.02)	5.2 (0.03)	7.9 (0.01)	77.3 (0.00)
M_{hh}^{part}	6.6 (0.02)	6.3 (0.03)	7.0 (0.01)	2.1 (0.14)	8.6 (0.01)	8.0 (0.02)
M_{hh}^{spp}	18.1 (0.00)	15.7 (0.00)	11.1 (0.00)	6.1 (0.02)	11.8 (0.00)	17.3 (0.00)
M_{th}^0	1.7 (0.21)	21.0 (0.00)	0.0 (0.27)	15.1 (0.00)	22.3 (0.00)	69.4 (0.00)
M_{th}^{part}	6.4 (0.02)	5.3 (0.06)	1.3 (0.14)	2.0 (0.15)	0.8 (0.36)	0.0 (0.92)
M_{th}^{+spp}	23.7 (0.00)	19.2 (0.00)	0.23 (0.24)	16.8 (0.00)	12.9 (0.00)	10.8 (0.00)
M_{th}^{*spp}	17.3 (0.00)	0.0 (0.80)	0.14 (0.25)	6.5 (0.02)	0.0 (0.55)	10.5 (0.00)

and differences between first and subsequent detections did not give realistic estimates of detection probabilities (probabilities > 1). The global model fit the observed data and no extra-binomial variation was detected, so a variance inflation factor (Burnham *et al.* 1987) of one was used for all models.

Models with no species effect were selected as the most parsimonious models for groups A and C. Partial species-effect models were selected for groups D and F. Therefore, more parsimonious models were obtained for the multiple-species approach for groups A, C, D and F, indicating gains in estimate precision when information on the detection process was shared across species. The most general model accounting for individual differences in detection probabilities with a time and species interaction effect was selected for both groups B and E, indicating that species effects were important for these groups or that our grouping criteria were not appropriate for these species (models equivalent to a single-species approach).

Estimates of the probability that an individual of a given species or species group (depending on the model selected) was detected at least once during the 10-min, three-interval count ranged from 0.81 (group F) to 0.92 (group E) (Table 4). The estimated heterogeneity parameter (probability of being in the first heterogeneity group) ranged from 0.15 to 0.79, with both estimates occurring for species in group F. Models that used common parameters among species in a group showed increased precision for all parameter estimates. This was most clearly seen in the increased precision for the abundance estimates, particularly for species with smaller observed counts (e.g. the indigo bunting in group C). Note that abundance estimates apply only to the area sampled.

Table 4. Parameter estimates for the time of detection method for each species. The probability that an individual is detected at least once during the count, \hat{p}_T , the probability of being in the first heterogeneity group, $\hat{\lambda}$, and the estimated abundance, \hat{N} , are given for the best model and for the best single-species model. The instantaneous rates formulation was used to estimate detection probabilities. Standard errors are given in parentheses

Group	Species	Observed count	Selected model			Alternative single-species model		
			\hat{p}_T	$\hat{\lambda}$	\hat{N}	\hat{p}_T	$\hat{\lambda}$	\hat{N}
A	Acadian flycatcher	87	0.89 (0.049)	0.58 (0.047)	98 (6.4)	0.91 (0.172)	0.51 (0.115)	95 (18.2)
	Black-and-white warbler	137	0.89 (0.049)	0.58 (0.047)	154 (9.5)	0.86 (0.113)	0.58 (0.078)	160 (21.7)
	Golden-crowned kinglet	82	0.89 (0.049)	0.58 (0.047)	92 (6.1)	0.92 (0.089)	0.67 (0.155)	89 (9.0)
	Worm-eating warbler	96	0.89 (0.049)	0.58 (0.047)	108 (6.9)	0.92 (0.249)	0.54 (0.098)	104 (28.5)
B	Black-throated blue warbler	197	0.90 (0.094)	0.48 (0.081)	220 (23.6)	Same model		
	Dark-eyed junco	189	0.83 (0.092)	0.72 (0.058)	227 (26.0)			
	Hooded warbler	274	0.84 (0.062)	0.65 (0.057)	326 (25.4)			
	Solitary vireo	148	0.91 (0.440)	0.42 (0.060)	163 (79.1)			
C	Black-throated green warbler	377	0.89 (0.053)	0.53 (0.035)	424 (26.2)	0.9 (0.066)	0.55 (0.057)	419 (31.5)
	Indigo bunting	64	0.89 (0.053)	0.53 (0.035)	72 (5.2)	0.93 (0.505)	0.55 (0.092)	69 (37.6)
	Red-eyed vireo	397	0.89 (0.053)	0.53 (0.035)	446 (27.5)	0.87 (0.086)	0.51 (0.048)	454 (45.6)
D	Scarlet tanager	161	0.85 (0.067)	0.52 (0.062)	189 (16.0)	0.86 (0.085)	0.53 (0.068)	186 (19.0)
	Veery	67	0.85 (0.067)	0.75 (0.088)	79 (7.2)	0.82 (0.111)	0.74 (0.093)	82 (11.9)
E	Ovenbird	444	0.92 (0.053)	0.51 (0.062)	483 (28.6)	Same model		
	Eastern towhee	79	0.89 (0.277)	0.50 (0.078)	89 (28.1)			
F	Red-breasted nuthatch	54	0.81 (0.062)	0.79 (0.087)	67 (6.4)	0.79 (0.139)	0.80 (0.099)	68 (12.7)
	Tufted titmouse	104	0.81 (0.062)	0.78 (0.068)	128 (11.2)	0.77 (0.093)	0.78 (0.068)	135 (17.4)
	Winter wren	106	0.81 (0.062)	0.50 (0.069)	131 (11.4)	0.87 (0.102)	0.56 (0.107)	121 (14.8)
	Wood thrush	153	0.81 (0.062)	0.15 (0.047)	188 (15.9)	0.85 (0.331)	0.13 (0.047)	180 (70.4)

Table 5. ΔAIC_c for the four independent observer multiple-species models for unlimited radius plots with 10% truncation of the largest detection distances. ΔAIC_c weights are in parentheses. Models with weights ≥ 0.20 are in bold for each species group indicating competing models

Models	Groups		
	B	C	DEF
M_0^0	56.33 (0.00)	103.52 (0.00)	114.68 (0.00)
M_0^{spp}	55.94 (0.00)	103.22 (0.00)	107.66 (0.00)
M_{obs}^0	61.04 (0.00)	105.35 (0.00)	116.26 (0.00)
M_{obs}^{+spp}	60.69 (0.00)	105.07 (0.00)	109.22 (0.00)
M_{obs}^{*spp}	70.55 (0.00)	109.37 (0.00)	111.91 (0.00)
M_h^0	0.00 (0.72)	0.76 (0.22)	1.18 (0.26)
M_h^{part}	2.10 (0.25)	0.40 (0.26)	0.00 (0.47)
M_h^{spp}	7.73 (0.02)	4.47 (0.03)	4.61 (0.05)
$M_{obs,h}^0$	9.20 (0.01)	0.00 (0.32)	5.91 (0.02)
$M_{obs,h}^{part}$	11.34 (0.00)	1.30 (0.17)	4.29 (0.06)
$M_{obs,h}^{+spp}$	17.42 (0.00)	*	6.39 (0.02)
$M_{obs,h}^{*spp}$	25.54 (0.00)	*	2.70 (0.12)

*Models did not give realistic estimates. Standard errors for detection probabilities were much larger than one.

MULTIPLE OBSERVER

Heterogeneity models explained the information in the independent observer data in a more parsimonious manner for all three species groups than models not incorporating heterogeneity (Table 5), indicating that individuals within a species could be placed in either a high- or low-detection probability group. The heterogeneity model with no observer or species effects was

selected for group B and was a reasonable alternative model for the other two groups (ΔAIC_c weights ≥ 0.22). The heterogeneity model with no observer or species effects on probabilities of detection and a partial species effect on the heterogeneity parameter was selected for group DEF and was also a reasonable alternative model for groups B and C (ΔAIC_c weight ≥ 0.25). An individual heterogeneity model with an observer effect on the probability of detection and no species effect was selected for group C. Again, the multiple-species approach provided gains in estimate precision by sharing information across species. As with the time of detection models, a variance inflation factor (Burnham *et al.* 1987) of one was used for all models because the global model fit the observed data with no indications of extrabinomial variation.

The heterogeneity parameter ranged from 0.34 to 0.58 for the independent observer model estimates. The detection probability was generally > 0.90 for one of the mixtures in the heterogeneity models for all species groups. The detection probabilities for the other mixtures were ≤ 0.36 for all species groups (Table 6). Comparisons of the abundance estimates for the selected model to the abundance estimates for the ‘best’ species-effect model showed very similar estimates but considerably smaller standard errors for the selected models, with no or partial species effects.

Discussion

Application of multiple-species models to population survey data offers a promising approach when more than one species occurs in the sample. We have demonstrated that grouping species with similar detec-

Table 6. Independent observer results based on the selected model for group B, C and DEF. The probability of being in the low or high detectability groups is given by $\hat{\lambda}$ and the probability of detection by one of the four observers is given by $\hat{p}_1, \hat{p}_2, \hat{p}_3$ and \hat{p}_4 . The abundance estimate \hat{N} is given for the selected model and for the selected species-effect model

Group	Species	Count	Group probability and observer detection probabilities					$\hat{N}_{selected}$	$\hat{N}_{species}$
			$\hat{\lambda}$	\hat{p}_1	\hat{p}_2	\hat{p}_3	\hat{p}_4		
B	Dark-eyed junco	36				0.24 (0.083)		41 (2.9)	44 (5.7)
	Hooded warbler	38	0.34 (0.065)			0.90 (0.027)		43 (3.0)	40 (2.0)
	Solitary vireo	51						57 (3.7)	59 (5.9)
C	Black-throated								
	Green warbler	47	0.40 (0.057)	0.20 (0.091)	0.13 (0.070)	0.19 (0.072)	0.11 (0.051)	59 (5.4)	60 (7.2)
	Red-eyed vireo	72		0.99 (0.016)	0.95 (0.030)	0.85 (0.054)	0.91 (0.050)	90 (7.6)	88 (7.9)
DEF	Ovenbird	90	0.36 (0.066)			0.36 (0.062)		96 (3.3)	96 (3.7)
	Scarlet Tanager	61	0.58 (0.094)					68 (3.6)	70 (5.6)
	Tufted Titmouse	44	0.44 (0.097)			0.96 (0.021)		48 (2.4)	48 (3.3)

tion processes results in more parsimonious models and more precise estimates. Evidence from the analyses presented here clearly indicates that, in many cases, single-species models are overparameterized and a more efficient use of data is achieved using multiple-species models. Estimates from models that ‘shared’ information across similar species showed very little bias relative to single-species models but were generally much more precise.

Multiple-species analyses allow for direct comparisons between models with and without species effects to determine whether group-based parameter estimates are warranted. Another approach to multiple-species analyses simply assumes similarities among species and analyses similar species as a group. This approach has been used for less common species when observed counts are not sufficient for a single-species approach (Nichols *et al.* 2000). Our approach actually evaluates similarities in detection probability among species and can provide a justification for this type of analysis.

We used both quantitative and qualitative information to define species groups. In general, the approach used to define species groups should consider species’ characteristics that influence the detection process. In our study, the use of maximum detection distance worked well to categorize species into broad groups but it did not allow complete classification of species groups. Singing rate information provided a useful framework for defining species groups within distance categories. Although not used in these analyses, classifications based on behaviour may also be helpful in assigning a priori species groupings. For example, in forested habitats it may be appropriate to group bird species based on typical singing heights by separating canopy species from those that sing closer to the ground. Movement behaviour is another potential grouping factor. While each of the methods presented here assumes birds do not move during the recording period, grouping species with considerably different movement characteristics may cause bias, particularly for surveys with longer recording times.

For surveys based on visual observations, factors such as visibility, activity patterns, size and social behaviour might be appropriate classification characteristics. Direct measures of characteristics such as singing rates and song frequencies used to define species groups are desirable whenever possible.

Current knowledge of the detection process and the effects of various factors is very limited. The species groups used in this paper were used to demonstrate possible approaches to grouping species and our knowledge of factors that may influence detection probabilities. Future implementation of the multiple-species approach should include research to determine which factors are most important in the detection process and possibly quantitative measures of these factors. The limited information available on which characteristics affect the detection process led us to using maximum detection distance and rankings from experts on other characteristics. Inappropriate grouping could produce bias in model estimates and reduce the benefits of the multiple-species modelling approach. In situations where detailed information is not available, grouping based on expert knowledge is a viable approach and worked well for our example analyses.

A sequential approach to multiple-species modelling could also be used, where the within-group structure is examined first and then the between-group structure is analysed to determine whether groups could be combined to improve estimate precision without introducing substantial bias. The gains in precision are relative to the number of individuals in the survey for each species. In our examples the number of species in a group was relatively small because there were several common species with large sample sizes. If a survey consisted of several species with small sample sizes then species groups would need to consist of more species to obtain similar gains in precision.

Models based on distance sampling data generally did not show as much improvement from sharing information for multiple species data as observed for the

other methods. Increased precision was demonstrated when no-species-effect or species-covariate models were selected. Distance models have few parameters to begin with, so little reduction in the number of parameters is achieved with the multiple-species approach. Multiple-species covariate models (Marques & Buckland 2004) showed slight improvements over no-species-effect models. Covariate distance models require that the shape of the detection function is similar among species. Models with no species effects require similarity in both the shape and the scale of the detection function among species.

While our results did not provide as much support for multiple-species modelling for distance sampling, this lack of support may be related to the a priori species groupings used for these analyses. It is possible that different characteristics of the detection process are important in distance sampling and could prove useful when using a multiple-species approach. The distance data used here were primarily from auditory detections of birds, which probably has a large distance estimation error (M. Alldredge *et al.*, unpublished data). The substantial error associated with these data may obscure the benefits of the approach. In situations where distances can be estimated accurately, the multiple-species approach is likely to provide better gains in precision over a single-species approach.

The multiple-species approach provided more precise estimates of abundance for both time of detection and multiple observer methods. These methods exploit similarities among species in song structure and singing behaviour and are not as sensitive to differences in detection distance. As these models are closed-population capture–recapture models, similar benefits are likely to be realized for capture–recapture experiments of other taxa.

Many sources of variation can cause individual differences in animal surveys (Burnham 1981; Johnson, Burnham & Nichols 1986). Temporal variation in singing rates (Wasserman 1977; Lein 1981) is one potential source of these differences. Habitat, local abundance and proximity to observers have all been shown to affect singing rates of breeding songbirds (McShea & Rappole 1997). Models incorporating individual differences among birds were always selected as the most parsimonious models for our data. Further investigation is needed to determine the effect of singing rate on detection probability and to identify and account for other sources of variation in detection probabilities.

The analyses presented were based on surveys where detections of birds were auditory, and thus our groupings were based on auditory characteristics likely to affect the detection process. Survey data where animals are detected visually (open habitat point counts, aerial surveys, etc.) or are physically captured (mist-netting, small mammal trapping, electrofishing, etc.) could also be analysed within this multiple-species framework. Grouping of species for these situations would depend on characteristics directly related to the sampling

methods. Groups for visual surveys would be based on factors affecting visibility, such as size, colour and activity. Factors affecting the probability of physical capture are related to the selectivity of the capture methods being used.

CONCLUSIONS

Multiple-species modelling approaches provide more efficient analyses of multiple species data. Because two of the methods presented here are based on closed-population capture–recapture models, application to similar approaches, such as Cormack–Jolly Seber (Seber 1982; Williams, Nichols & Conroy 2002) and tag return models (Brownie *et al.* 1985; Williams, Nichols & Conroy 2002), should be similarly beneficial. Although the additive models were not selected in the analyses presented here, in some cases they were reasonable alternative models. Application of additive and partial effect models for multiple-species analysis should be investigated further as they do not require similarity in the detection process among species. The use of covariates, such as detection distance, as additive effects in multiple-species models may also prove useful in explaining species' differences. This will be particularly true for rare species, when sample sizes are limiting. A multiple-species approach allows more precise models of rare species because information for parameter estimation can be 'borrowed' from similar but more common species.

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Supplementary material

The following supplementary material is available as part of the online article (full text) from <http://www.blackwell-synergy.com>.

Appendix S1. Models for the time of detection and multiple observer methods.

Appendix S2. Number of parameters in candidate model for the multiple observer method.