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RELIABILITY OF OCCUPANCY AND BINOMIAL MIXTURE MODELS FOR ESTIMATING ABUNDANCE OF GOLDEN-CHEEKED WARBLERS (*SETOPHAGA CHRYSOPARIA*)

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Abstract.—Reliable estimates of population parameters derived from survey methods are essential for decision making in management of endangered species. We evaluated whether point-count surveys used in conjunction with occupancy and binomial mixture models (BMMs) constituted a reliable approach for monitoring the federally endangered Golden-cheeked Warbler (*Setophaga chrysoparia*) on a preserve in central Texas. Occupancy and abundance were estimated using point-count surveys conducted on each of five 113-ha detection grids in 2008 and seven grids in 2009. Single-season occupancy models and BMMs were used to estimate occupancy and abundance, respectively. Occupancy estimates per grid ranged from 0.48 to 1.0 in 2008 and from 0.52 to 1.0 in 2009. Estimates of abundance were compared with territory densities independently estimated using spot mapping, the standard by which all other avian survey methods are often compared. Abundance estimates produced by BMMs were significantly higher than territory density estimates at all but one site in 2008 and two sites in 2009. While estimation techniques incorporating detection probabilities should be considered in monitoring programs, our results suggest that BMMs deserve careful scrutiny before being used to estimate abundance or to monitor population trends. *Received 26 April 2011, accepted 5 December 2011.*

Key words: binomial mixture model, detection probability, Golden-cheeked Warbler, point-count survey, population estimate, *Setophaga chrysoparia*, spot mapping.

Fiabilidad de los Modelos de Ocupación y Mezcla Binomial para Estimar la Abundancia de *Setophaga chrysoparia*

Resumen.—Los estimadores confiables de parámetros poblacionales derivados de métodos de censo son esenciales para la toma de decisiones sobre el manejo de especies en peligro. Evaluamos si los estudios de conteo por puntos usados en conjunto con modelos de ocupación y mezcla binomial (BMMs, por sus siglas en inglés) constituyen una aproximación confiable para el monitoreo de la especie federalmente amenazada *Setophaga chrysoparia* en una reserva en el centro de Texas. La ocupación y la abundancia fueron estimadas usando censos hechos en puntos de conteo en cada uno de cinco cuadrantes de detección de 113 ha en 2008 y siete cuadrantes en 2009. Los modelos de ocupación de una sola estación y los BMMs fueron usados para estimar la ocupación y la abundancia, respectivamente. Las estimaciones de ocupación por cuadrante variaron de 0.48 a 1.0 en 2008 y de 0.52 a 1.0 en 2009. Los estimados de abundancia fueron comparados con densidades territoriales estimadas independientemente usando mapeo por puntos, el método estándar con el que todos los demás estudios de aves son frecuentemente comparados. Los estimados de abundancia producidos por los BMMs fueron significativamente mayores que las densidades territoriales estimadas en todos menos un sitio en 2008 y menos dos sitios en 2009. Aunque las técnicas de estimación que incorporan probabilidades de detección deberían ser tomadas en cuenta en los programas de monitoreo, nuestros resultados demuestran que los BMMs deben ser cuidadosamente revisados antes de ser usados para estimar la abundancia o para monitorear tendencias poblacionales.

Obtaining reliable population estimates is an essential component of informed decision making in management of endangered species (Gerrodette 1987, Forcada 2000, MacKenzie and Nichols 2004, Blakesley et al. 2010). Thus, a fundamental challenge is developing and implementing feasible survey techniques in conjunction with robust, unbiased, and precise estimation of population parameters. Evaluating methodologies using field tests that compare estimates against known population size is a critical, but often overlooked, step to assessing the reliability of population estimators (Ringvall et al. 2000, MacKenzie and Royle 2005, Toms et al. 2006, Gale et al. 2009, Lubow and Ransom 2009).

Abundance, or population size, is a core parameter in ecological studies (Dice 1941, He and Gaston 2000). If the estimation of abundance is not logistically feasible, counts obtained from

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population surveys are often used as indices of relative abundance (Johnson 2008). Indices can be used to make inferences about abundance across temporal (Thogmartin et al. 2007) and spatial scales (Amar et al. 2010) if counts represent the same proportion of the population(s) surveyed for each sampling occasion (Nichols et al. 2009). However, the condition of constant proportionality is rarely met in field studies (Thompson et al. 1998; but see Weckerly 2007). As a consequence, variation in counts can indicate variation in actual population size and/or variation in the detectability of the species among sampling locations or times. This relationship is described by the equation

$$E(C) = N^*p \tag{1}$$

where C is the recorded count of a species during a survey, N is the true number of individuals in the survey area, and p is the probability of detecting an individual of the species (Johnson 2008). Rarely is a species detected 100% of the time during a survey. Consequently, spatial and temporal variation in the extent of imperfect detection leads to variation in p, which confounds the ability of indices to make inferences regarding relative abundance across time and space (Johnson 2008). Failure to account for imperfect detection may result in misleading inferences regarding spatial and temporal population dynamics (MacKenzie et al. 2002, Tyre et al. 2003, Rota et al. 2009). Estimating detection probabilities is thus a necessary step in dealing with imperfect detection in survey design. A conceptual framework of how survey methods account for imperfect detection is illustrated by using Equation 1 to lead to the estimator:

$$E(\hat{N}) = C/p \tag{2}$$

Although this equation is the basic premise of detectability-adjusted estimators, different approaches to estimating p are in use. Capture–recapture techniques, for example, use information from the resight or recapture of marked individuals to estimate p (Seber 1982, Williams et al. 2002). However, capture–recapture approaches involve frequent efforts to capture or observe marked animals, and the logistics of applying this technique on a large spatial scale is not feasible for some species (Royle 2004). Other survey methods, such as multiple-observer (Alldredge et al. 2007) and time-of-detection (Farnsworth et al. 2002), utilize capture–recapture techniques in a way that does not require resighting or physical recapture of animals. However, even these methods often have limited application because of strict assumptions and requirements necessary to estimate p properly (Johnson 2008).

The inherent challenges of obtaining detectability-adjusted estimates of abundance have prompted the development of methods for estimating occupancy as a surrogate (MacKenzie et al. 2002). Occupancy (a rate equal to the proportion of areal units occupied by a species) is estimated using presence–absence data gathered from a series of sampling units. Methods for estimating occupancy have been refined over the past few decades (Geissler and Fuller 1987, Azuma et al. 1990, MacKenzie et al. 2002, Tyre et al. 2003). MacKenzie et al. (2002) developed a comprehensive likelihood-based model to estimate both occupancy and detection probabilities for closed populations. A valuable feature of occupancy models is the ability to incorporate covariates such as habitat type, weather conditions, and time of season that may influence occupancy and detection probabilities (MacKenzie 2005). Occupancy models have an expanding range of applications, including research on species distribution (Ceballos and Ehrlich 2002, Goehring et al. 2007, Karanth et al. 2009), habitat and resource use (MacKenzie 2006, Krishna et al. 2008, Zylstra and Steidl 2009), and metapopulation biology (Moilanen 2002, Hodgson et al. 2009).

Advances in survey design for estimating occupancy have also spurred the development of similar approaches for estimating abundance (Royle 2004, Kéry et al. 2005). Furthermore, the difficulties of implementing capture–recapture techniques on large spatial scales have led to interest in developing feasible alternatives to estimating population size (Kéry et al. 2005). For example, binomial mixture models (BMMs) developed by Royle (2004) use temporally and spatially replicated count data to estimate abundance and detection probabilities of closed populations. This class of models assumes that the abundance at each sampling unit is governed by a statistical distribution, such as the Poisson (Royle 2004), negative binomial (Wenger and Freeman 2008), or a zero-inflated variety of the Poisson or negative binomial distributions (Joseph et al. 2009). The Poisson distribution is often considered a likely candidate for modeling abundance when the abundance at each sampling unit is assumed to be random across the surveyed area (Royle 2004, Kéry et al. 2005, Joseph et al. 2009). The mean of the distribution, representing the average abundance across all sampling units in the surveyed area, can then be estimated by integrating the binomial likelihood of the count data over possible values of abundance for each site (Royle 2004).

Previous studies have demonstrated that BMMs can generate unbiased estimates of abundance under simulated conditions (Royle 2004) and provide ecologically realistic abundance estimates in the field (Dodd and Dorazio 2004, Kéry et al. 2005, Wenger and Freeman 2008). Importantly, this method does not require individual identification of animals during successive surveys and has demonstrated the ability to estimate abundance for some data sets (Royle 2004). The advantages afforded by BMMs suggest the potential of this approach as a useful tool for monitoring populations at large spatial extents, and such use has been strongly advocated (Royle 2004, Kéry 2008). Yet BMMs have, for some species, provided biologically unrealistic estimates of abundance accompanied by inflated estimates of error (Dodd and Dorazio 2004, Kéry et al. 2005, Joseph et al. 2009); thus, continued assessment of the technique's reliability is warranted.

Spot mapping is an established method used to estimate the territory density of breeding birds by mapping territories within designated plots (Bibby et al. 1992). This technique has long been considered the standard by which all other avian survey methods are compared (Verner and Ritter 1988, Verner and Milne 1990, Bibby et al. 1992, Buckland 2006). However, accurate delineation of territories is a function of sampling effort (Rhodes et al. 2006), and delineating territories of individual birds that cannot be uniquely identified can be challenging (Verner and Milne 1990). Moreover, spot mapping does not provide estimates of error. Nevertheless, under conditions in which results of spot mapping are considered robust and reliable, comparisons of abundance estimates derived from spot mapping with estimates of occupancy and abundance adjusted for imperfect detection provide a test of the reliability of occupancy and abundance estimators.

We investigated whether point-count surveys in conjunction with occupancy models and BMMs constitute reliable methods for monitoring the federally endangered Golden-cheeked

Warbler (*Setophaga chrysoparia*) by comparing estimates derived from these models with territory densities estimated using the more labor-intensive spot-mapping method. The Golden-cheeked Warbler (hereafter "warbler") is a Neotropical migrant songbird with a breeding range restricted to central Texas (Pulich 1976, Morrison et al. 2010). Effective management of the warbler depends on reliable tracking of spatial and temporal variation in population dynamics.

The present study was replicated over two breeding seasons and across multiple study sites each year, with four objectives: (1) to evaluate covariates that might influence detection of warblers; (2) to estimate the occupancy rate on each study site surveyed; (3) to estimate the abundance of warblers at each study site by means of BMMs; and (4) to compare our estimates of warbler abundance derived from BMMs with estimates of territory density independently derived from spot mapping at each site.

METHODS

We tested the reliability of occupancy models and BMMs using spot mapping and point-count data gathered at the Balcones Canyonlands Preserve in Travis County, Texas. The Balcones Canyonlands Preserve is a discontinuous collection of properties consisting of 5,365 ha managed for the warbler and other endangered species (Becker and Koehler 2004). One goal of the Balcones Canyonlands Preserve is to maintain and increase the warbler population on the preserve (Becker and Koehler 2004). Since 1998, the city of Austin has annually monitored warblers on the preserve by conducting spot-mapping surveys within 40.5-ha plots established at each of seven study sites. At five study sites (Ivanhoe, Forest Ridge, St. Edwards, Emma Long, and Barton Creek), survey plots were positioned in areas of prime warbler habitat, which consists of mature Ash Juniper (*Juniperus ashei*) and oak (*Quercus* spp.) forest with at least 75% of the area containing >70% canopy cover (Abbruzzese and Koehler 2002). The remaining two plots located at study sites Bohls and Double J&T were positioned in transitional warbler habitat, which was defined as areas with <75% prime habitat (Abbruzzese and Koehler 2002). Territory densities have been estimated annually by the city of Austin on the prime habitat plots and biannually on the transitional plots. Spot mapping consists of ten 6-h surveys, with one survey each week during the breeding season, for a total survey effort of 60 h plot^{-1} (Becker and Koehler 2004).

On each of the seven study sites monitored by the city of Austin, we established a grid of 36 sample units to provide the framework for conducting point-count surveys. Each sample unit consisted of a circular area with a 100-m radius from which point counts were conducted from the center of each unit (hereafter "detection stations"). Detection grids encompassed an area of 113 ha and overlaid the 40.5-ha spot-mapping plot on each study site. Detection stations within each grid were positioned 200 m apart. This inter-detection-station distance, also used by Watson et al. (2008), was selected to promote independence of detections. Point-count surveys consisted of an observer recording all warblers detected by sight or sound during a 5-min interval at each detection station. For the present study, only male warblers detected by song were considered in the analysis. For each male detected, observers estimated the compass direction and binned the estimated distance of the bird from the survey point into one of three categories: close proximity (0–20 m), medium to distant (20–100 m), and far away (>100 m). On the basis of subsequent inspection of the composite distance and direction data recorded, we chose to analyze only those detections of males estimated to be within 100 m of each detection station, in a conservative attempt to further promote independence between detection stations. Surveys began shortly after sunrise under weather conditions approved by the U.S. Fish and Wildlife Service (1992) for detecting warblers. The order in which detection stations 1–36 were surveyed in each grid was reversed for each successive site visit to reduce time-of-day bias for detection stations at the beginning and end of each grid. The ruggedness of the terrain and the time required for traversing it prevented randomization of visitation order for the detection stations. Thus, detection stations in the interior of grids were surveyed during the approximate middle of each visit. Each study site was surveyed weekly four times from late March to early April in 2008 and 2009. Five study sites were surveyed in both 2008 and 2009, and an additional two study sites were added in 2009.

Survey data were analyzed by means of both single-season occupancy models and BMMs using PRESENCE, version 3.1 (MacKenzie et al. 2002, Hines 2006). Each year was analyzed separately in both types of models. Single-season occupancy models included parameters for occupancy (ψ) and probability (p) of detecting the species (MacKenzie et al. 2002), whereas BMMs included parameters for abundance (λ) and probability (p) of detecting individuals (Royle 2004). The abundance parameter λ represents the estimated average number of animals per detection station and is used here to make inferences regarding the number of male warblers on each of the seven 113-ha detection grids.

The essential first step in estimating occupancy and abundance was to determine the covariates that influenced detection of warblers at both the species and the individual level, respectively. Covariates of detection considered in this first step of model selection included study site, season (survey week), and time of day (both linear and quadratic). Additionally, a covariate for observer was included in the BMMs to control for previously described significant differences in the probability of detecting individual warblers among the surveyors involved in the present study (Hunt 2010). Differences among surveyors in the probability of detecting the species were not evident; thus, an observer covariate was not included in the occupancy models (Hunt 2010). The covariates study site, season, and observer were categorical variables, whereas time of day (referring to the minutes after sunrise that a detection was recorded) was a continuous variable. We considered both linear and quadratic time-of-day covariates in model selection because previous research revealed that both were equally important in modeling probabilities of detecting warblers at both the species and the individual level (Hunt 2010). Because this first stage of model selection examined only covariates that influenced detection, both occupancy and abundance were modeled as constant to reduce the number of models analyzed. Model selection was conducted using an information-theoretic approach (Akaike 1973), with Akaike's information criterion corrected for small sample size (AIC_c; Sugiura 1978).

The next step of model selection for both single-season occupancy models and BMMs focused on selecting models to estimate occupancy and abundance for the 113-ha grid at each study site for each year. Models considered in this analysis included categorical study-site covariates for occupancy or abundance as well as the covariates for detection selected in the first step of model selection. In cases in which multiple models had equally competitive AIC_c values (≤4 AIC_c units), model averaging was used to obtain parameter estimates from competitive models that estimated the particular parameter (Burnham and Anderson 2004).

Finally, estimates of abundance of territorial male warblers produced by point-count surveys in conjunction with BMMs were compared with territory densities independently estimated by the city of Austin's biologists using spot mapping at each respective study site at the same time during the 2008 and 2009 breeding seasons. Because territory density was estimated on 40.5-ha plots, comparisons between methodologies used territory densities extrapolated to 113 ha.

RESULTS

Across the five detection grids in 2008 and the seven in 2009, we detected, respectively, a total of 623 and 722 male warblers during the four surveys conducted each year. Nearly all detections (99%) of warblers were aurally based. Among detection stations where warblers were detected, the majority of stations had a maximum of two or more individuals detected during an individual survey across the 4-week sampling season (Fig. 1A). Inspection of the distribution of detections as a function of distance revealed that most detections (88% in 2008 and 87% in 2009) were estimated as being 20–100 m from the detection station (Fig. 1B). The distribution of observer-estimated distances provides additional confirmation that the 200-m distance between detection station centers was sufficient for insuring that detections were independent between stations within a given survey occasion.

Model selection examining potential covariates that influenced detection of occupancy indicated two equally competitive single-season occupancy models in each year that were superior to all other candidate models considered (Table 1). Both models contained site and season covariates for detection and differed only in containing either the covariate time (linear) or the covariates time and $time^2$ (quadratic). These results indicated that the probability of detecting warblers was influenced by time of day and time of season and differed among sites. We found differences in detection probabilities among the study sites each year, ranging from 0.29 to 0.81 in 2008 (five sites) and 0.19 to 0.70 in 2009 (seven sites) (Fig. 2). Furthermore, detection probabilities for each study site were consistent across the 2 years and the rank order among sites (from lowest to highest probabilities) was identical in each year, indicating that the estimation of detection probabilities accounted for important covariates influencing detection of warblers. Seasonal variation in detection showed a consistent pattern among all sites; the first survey week for each year had the highest probability of detection, and detection probabilities consistently declined thereafter. Detection probabilities for each week in 2008 were comparatively higher than estimates in 2009. Both time-of-day coefficients (linear and quadratic) revealed that the probability of detecting warblers declined throughout a day.

Two single-season occupancy models containing the covariates of detection as well as site covariates for the occupancy parameter ψ were equally competitive in both 2008 and 2009 (Table 2). Naive occupancies (proportion of detection stations where observers detected warblers) ranged among study sites from 0.43

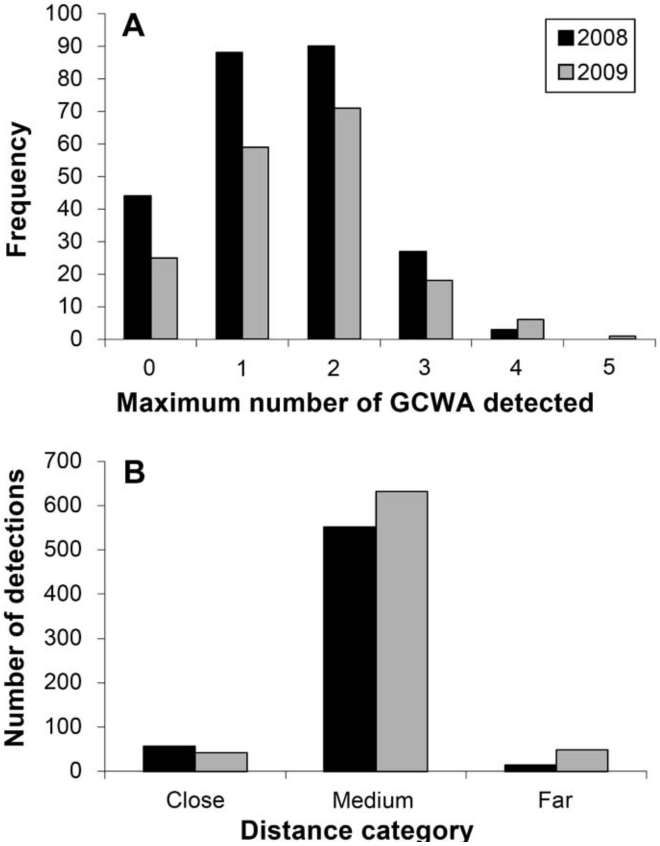

FIG. 1. (A) Maximum number of Golden-cheeked Warblers (GCWA) detected per detection station across the 4-week sampling period and across all study sites, 2008 and 2009. (B) Distribution of detections of male Golden-cheeked Warblers as a function of the estimated distance from the center of the detection stations (2008, *n* = 623; 2009, *n* = 722). Distance was binned into three categories: 0–20 m (close), 20–100 m (medium), and >100 m (far). Detections >100 m were not used in subsequent analysis.

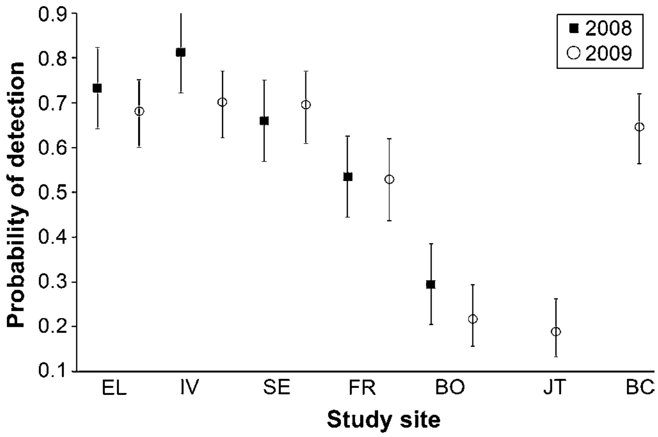

FIG. 2. Average probabilities of detection (species) of Golden-cheeked Warblers during the 4-week sampling period for each of five study sites in 2008 and seven study sites in 2009. Error bars represent 95% confidence intervals. Site abbreviations: EL = Emma Long, IV = Ivanhoe, SE = St. Edwards, FR = Forest Ridge, BO = Bohls, JT = Double J&T, and BC = Barton Creek.

TABLE 1. Summary of model selection for the single-season occupancy models in 2008 and 2009, showing covariates that influenced the probability of detecting Golden-cheeked Warblers at Balcones Canyonlands Preserve, Texas. Parameters estimated were occupancy (ψ) and probability of detection (*p*). Covariates investigated were site, season, time of day with a linear effect (time), time of day with a quadratic effect (time^2), and no influence of a covariate (.). Model selection statistics: delta values of Akaike's information criterion corrected for small sample size (ΔAIC_c), Akaike weight (*w*), number of parameters, and twice the log likelihood (–2LL). Sample sizes (number of detection stations surveyed across all study sites per week) were 180 and 252 for 2008 and 2009, respectively. Selected models are in bold.

	2008				2009			
Model	ΔAIC_c	*w*	Number of parameters	–2LL	ΔAIC_c	*w*	Number of parameters	–2LL
ψ (.) *p* (site, season, time)	**0.00**	**0.709**	**8**	**822.91**	**0.00**	**0.739**	**10**	**1,190.23**
ψ (.) *p* (site, season, time^2)	**0.56**	**0.291**	**9**	**822.47**	**1.99**	**0.249**	**11**	**1,190.22**
ψ (.) *p* (site, season)	18.42	<0.001	7	844.33	10.92	0.003	9	1,203.15
ψ (.) *p* (site, time)	22.55	<0.001	7	848.46	9.50	0.007	9	1,201.73
ψ (.) *p* (site, time^2)	23.91	<0.001	8	847.82	11.50	0.002	10	1,201.73
ψ (.) *p* (site)	40.69	<0.001	6	868.60	20.45	<0.001	8	1,214.68
ψ (.) *p* (.)	73.03	<0.001	2	908.94	109.03	<0.001	2	1,315.26

TABLE 2. Summary of model selection for the single-season occupancy models in 2008 and 2009, showing selected covariates for probability of detection (*p*) and categorical site covariates for occupancy (ψ) by Golden-cheeked Warblers at Balcones Canyonlands Preserve, Texas. Model selection statistics: delta values of Akaike's information criterion corrected for small sample size (ΔAIC_c), Akaike weight (*w*), number of parameters, and twice the log likelihood (–2LL).

	2008				2009			
Model	ΔAIC_c	*w*	Number of parameters	–2LL	ΔAIC_c	*w*	Number of parameters	–2LL
ψ (site) p (site, season, time)	0.00	0.675	12	783.51	0.00	0.727	16	1,164.17
ψ (site) p (site, season, time^2)	1.04	0.325	13	782.65	1.66	0.273	17	1,163.83

(Bohls) to 1.0 (Ivanhoe and St. Edwards) in 2008, and from 0.45 (Bohls) to 1.0 (Emma Long, Barton Creek, and Ivanhoe) in 2009. Across both years, there were four study sites with a naive occupancy of 1.0 (i.e., 100% of the stations occupied by warblers). Single-season model-averaged estimates of occupancy adjusted for imperfect detection, with the obvious exception of sites with $\psi = 1$, were higher than naive occupancy at each site (Fig. 3).

Model selection for the BMMs, containing potential covariates influencing detection of individual warblers, revealed four models in each year that were equally competitive (Table 3). All four models included covariates for site, season, and time of day (linear and quadratic), and two models included an observer covariate. Because all models were equally competitive, we concluded that each combination of covariates represented in these models influenced detection of warblers on the individual level. The subsequent inclusion of site covariates for the abundance parameter λ in BMMs that contained these four combinations of covariates influencing detection of individuals resulted in each model being equally competitive in 2008 (Table 4). In 2009, the inclusion of site covariates for λ resulted in the two models containing the covariate observer being equally competitive. Model-averaged estimates of λ per study site, which for this study represented the average number of male warblers per detection station, ranged from

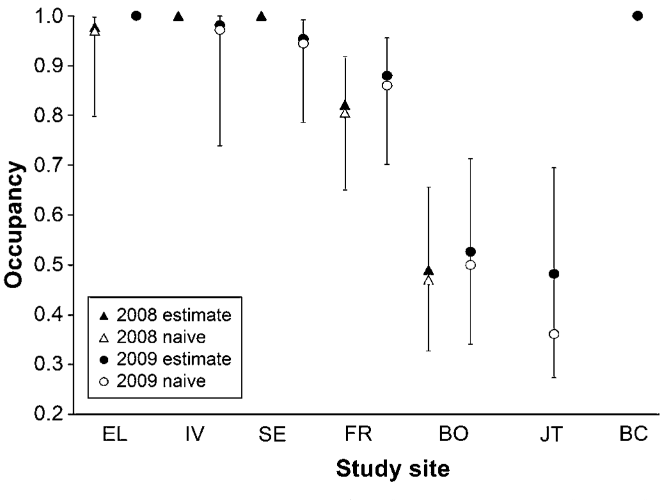

FIG. 3. Naive occupancy (proportion of 36 detection stations with ≥1 male Golden-cheeked Warblers detected, open symbol) and estimates (est.) of occupancy adjusted for imperfect detection (closed symbol) for each of five study sites surveyed in 2008 and seven study sites in 2009. Naive occupancy is shown for sites with occupancy <1. Error bars represent 95% confidence intervals, indicated for sites with occupancy <1.

Table 3. Summary of model selection for the binomial mixture models in 2008 and 2009, showing covariates that influenced the probability of detecting Golden-cheeked Warblers at Balcones Canyonlands Preserve, Texas. Parameters estimated were abundance (λ) and probability of detection for individuals (*p*). Model selection statistics: delta values of Akaike's information criterion corrected for small sample size (ΔAIC_c), Akaike weight (*w*), number of parameters, and twice the log likelihood (–2LL). Sample sizes were 180 and 252 for 2008 and 2009, respectively. Selected models are in bold.

	2008				2009			
Model	ΔAIC_c	*w*	Number of parameters	–2LL	ΔAIC_c	*w*	Number of parameters	–2LL
λ (.) *p* (site, season, time)	**0.00**	**0.561**	**8**	**1,538.29**	**0.00**	**0.513**	**10**	**1,963.38**
λ (.) *p* (site, season, time^2)	**1.94**	**0.191**	**9**	**1,538.23**	**1.48**	**0.223**	**11**	**1,962.86**
λ (.) *p* (site, season, time, observer)	**2.00**	**0.185**	**9**	**1,538.29**	**2.00**	**0.172**	**11**	**1,963.38**
λ (.) *p* (site, season, time^2, observer)	**3.94**	**0.062**	**10**	**1,538.23**	**3.48**	**0.074**	**12**	**1,962.86**
λ (.) *p* (site, time)	24.79	<0.001	7	1,565.08	9.80	0.004	9	1,975.18
λ (.) *p* (site, season)	24.80	<0.001	7	1,565.09	7.67	0.012	9	1,973.05
λ (.) *p* (site, time^2)	26.55	<0.001	8	1,564.84	11.21	0.001	10	1,974.59
λ (.) *p* (site)	48.00	<0.001	6	1,590.29	17.58	<0.001	8	1,984.96
λ (.) *p* (site, observer)	50.00	<0.001	7	1,590.29	19.58	<0.001	9	1,984.96
λ (.) *p* (observer)	115.60	<0.001	2	1,665.89	187.23	<0.001	2	2,166.61
λ (.) *p* (.)	162.15	<0.001	2	1,712.44	119.67	<0.001	2	2,099.05

0.7 (Bohls) to 1.7 (Ivanhoe) in 2008, and from 0.6 (Double J&T) to 2.6 (Forest Ridge) in 2009. Estimates of λ extrapolated across all 36 detection stations (λ × 36) revealed estimates of the total number of male warblers for each 113-ha site (rounded to the nearest whole number) that ranged from 26 (Bohls) to 61 (Ivanhoe) in 2008 (Fig. 4A) and from 20 (Double J&T) to 95 (Forest Ridge) in 2009 (Fig. 4B). The 95% confidence intervals for many estimates were wide, particularly at Forest Ridge in 2009.

A comparison of BMM-derived estimates of abundance based on point-count data with territory densities estimated from spot mapping revealed systematic discrepancies between the methodologies in the estimated abundance of male warblers at detection grids in both years (Fig. 4A, B). Across study sites and seasons, only 3 of 12 estimates of the number of territories per 113-ha detection grid based on spot mapping fell within the respective confidence intervals associated with BMM estimates of abundance (2008, Ivanhoe; 2009, Ivanhoe and St. Edwards). For all other site–year combinations, the BMM estimate of warbler abundance per grid was substantially higher than the extrapolated spot-mapping estimate of the number of territories.

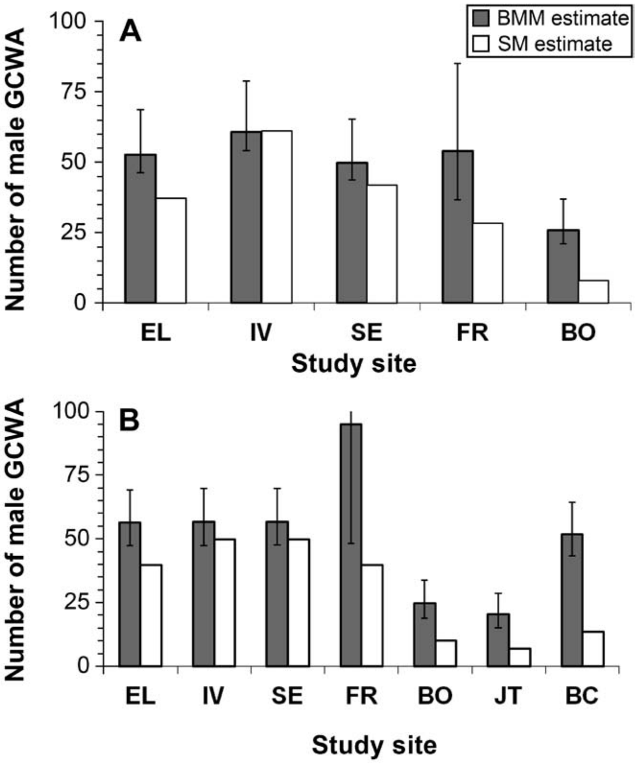

Fig. 4. Estimated number of male Golden-cheeked Warblers (GCWA) per 113 ha for each of (A) five study sites in 2008 and (B) seven study sites in 2009 inferred from binomial mixture models (BMM) compared with territory abundance assessed by spot mapping (SM). Error bars represent 95% confidence interval (= 194 for FR in 2009).

Discussion

Reliable estimates of population parameters are essential for making informed decisions about the treatment of threatened, endangered, or otherwise managed species. Recent developments in survey methods that provide detectability-adjusted estimates provide useful tools for monitoring occupancy and abundance of threatened and endangered populations (Nichols et al. 2009). Our findings on estimated occupancy rates suggest that detection-based estimates of occupancy were consistent between years for sites where occupancy was estimated in both years. The evidence is growing that detection-based occupancy estimators provide credible estimates of warblers and other endangered species (Jackson et al. 2006, Watson et al. 2008, Collier et al. 2010, Delaney and Leung 2010). Moreover, detection-based estimates of occupancy were particularly helpful when detection probabilities of warblers were low (Bohls and Double J&T). When detection probabilities are low, few birds are detected during surveys, which can add to the impression that occupancy is low. Yet at Bohls and Double J&T, where detection probabilities were similarly low,

Table 4. Summary of model selection for binomial mixture models in 2008 and 2009, showing selected covariates for probability of detection of individuals (p) and categorical site covariates for abundance (λ) of Golden-cheeked Warblers at Balcones Canyonlands Preserve, Texas. Model selection statistics: delta values of Akaike's information criterion corrected for small sample size (ΔAIC_c), Akaike weight (w), number of parameters, and twice the log likelihood (–2LL).

	2008				2009			
Model	ΔAIC_c	w	Number of parameters	–2LL	ΔAIC_c	w	Number of parameters	–2LL
λ (.) p (site, season, time)	0.00	0.554	12	1,512.33	0.00	0.715	14	1,948.12
λ (.) p (site, season, time^2)	1.97	0.205	13	1,513.98	1.96	0.375	15	1,947.82
λ (.) p (site, season, time, observer)	2.24	0.181	11	1,518.87	8.53	0.014	13	1,958.89
λ (.) p (site, season, time^2, observer)	4.13	0.060	12	1,518.46	9.46	0.009	14	1,957.78

the deviations between naive and estimated occupancy varied between 1% and 11%. It is worth repeating that detection does not necessarily inform us about occupancy (MacKenzie et al. 2006, O'Connell et al. 2006, Weller 2008).

Evaluating survey methods by comparing estimates against known population size is critical for assessing the reliability of survey methods (Tarvin et al. 1998, Ringvall et al. 2000, Toms et al. 2006, Alldredge et al. 2007, Gale et al. 2009, Lubow and Ransom 2009). We conducted 12 such field tests of BMMs for the federally endangered warbler by comparing BMM abundance estimates with the numbers of territories recorded using spot mapping at five and seven sites in 2008 and 2009, respectively. We treated territory abundance enumerated by spot mapping as equivalent to "known population size" for the purposes of comparing the two methods. We justified this decision on the basis of the fact that the number of territories per 40.5-ha plot enumerated by spot mapping at each of the seven study sites across 12 years has remained nearly stable or increased only weakly at some study sites. Most importantly, over this period, differences among sites in the number of estimated territories have consistently exceeded the change in numbers within study sites across time (F. W. Weckerly and J. R. Ott unpubl. data). Thus, territory abundance obtained by spot mapping has produced consistent estimates of numbers of territories across time for each study site. Across the seven sites, territory abundance enumerated by spot mapping of warblers has varied by almost an order of magnitude. The discrepancy between BMM estimates of warbler abundance and spot-mapping estimates of territory number that we found in the present study represent biologically meaningful differences in abundance. For example, BMM estimates of the number of male warblers per 113-ha grid at five study sites rivaled ($n > 54$), and at one site exceeded ($n = 94$), the maximum territory density per 100 ha ($n = 63$) currently known for the species (Wahl et al. 1990). These discrepancies indicate that BMMs deserve closer scrutiny before they are widely applied in monitoring programs.

The limited application of BMMs in published studies to date has revealed that this technique can generate reliable estimates under simulated conditions (Royle 2004) and, for some species, has provided reasonable estimates of abundance (Dodd and Dorazio 2004, Royle 2004, Kéry et al. 2005, Wenger and Freeman 2008, Etterson et al. 2009). However, the ability of BMMs to provide unbiased estimates of abundance under field conditions is difficult to assess when there is no available information on the true population size (Royle 2004, Kéry et al. 2005). To our knowledge, only two published studies have compared BMM estimates of abundance with independently derived estimates of territory density obtained from spot mapping (Kéry et al. 2005, Chandler et al. 2011). Kéry et al. (2005) compared BMM estimates of abundance with territory densities for eight avian species and found that the BMM estimates were systematically higher than estimates based on territory mapping. For most species considered, BMM abundance estimates were about twice as high as territory density estimates, whereas one species had an abundance estimate that was 8.9× greater than the territory density estimate. Chandler et al. (2011) found that the BMM estimate of Chestnut-sided Warbler (*S. pensylvanica*) abundance was more than 3× greater than the estimate of territory density obtained from spot mapping. We found that BMM estimates of abundance for the Golden-cheeked Warbler were, on average, twice the size of spot-mapping estimates (range: 0.98–3.92). Determining why BMM estimates reported by Kéry et al. (2005), by Chandler et al. (2011), and in the present study were so much greater than estimates obtained from spot mapping requires a close examination of the assumptions of the BMMs.

In our study, territory densities obtained from spot mapping were used as a baseline comparison to evaluate the reliability of detectability-adjusted estimates of abundance obtained from point-count data. Our estimates of warbler abundance from BMMs consistently exceeded territory densities estimated on these same plots by independent researchers using spot mapping. Moreover, the degree of difference between BMM estimates and territory density varied among sites, with the greatest discrepancies noted at the lowest-density sites. There are a number of possibilities for explaining the large discrepancy between the BMM estimates and territory density estimates based on spot mapping. A fundamental assumption of BMMs is that populations within surveyed areas are closed during the total sampling season (Royle 2004). We chose a compact survey season of 4 weeks, lasting from late March to early April, to coincide with the beginning and first part of the warbler breeding season. Population closure for a period of 4 weeks during this time of year is likely to be met for territory-holding males of this species (Watson et al. 2008). However, BMMs can estimate "superpopulation" size (Williams et al. 2002), which in our study includes all male warblers that could potentially use a study site, which are territorial males and nonterritorial floater males. We could not distinguish between territorial and nonterritorial males detected during our surveys; thus, our BMM estimates could be inflated partly for this reason (Chandler et al. 2011).

The assumption that the distribution of the population across the surveyed area fits some statistical distribution is difficult to assess in the present study. Estimates from BMMs and their associated estimates of error appear to be sensitive to the type of statistical distribution used to model the population's spatial distribution (Kéry et al. 2005, Joseph et al. 2009). The Poisson distribution assumes that the true abundance at each point is random and independent of the number of individuals at any other point (Kéry et al. 2005). Independence between survey points is likely to be met for warblers when points are ≥200 m apart (Ladd and Gass 1999, Watson et al. 2008). Survey data from our study suggest that the majority of birds were detected within 100 m of each detection station. Thus, it seems unlikely that the biased estimates we obtained from the BMMs were solely due to violation of the assumption of independence. Assuming a Poisson distribution for warbler abundance may be inappropriate because territoriality could interfere with random movement of birds across the landscape (Wahl et al. 1990, Ladd and Gass 1999). It should be stated, however, that there are two possible reasons for the failure of the BMMs: (1) the variance of abundance differed from mean abundance and (2) we did not consider ecological covariates (e.g., percent canopy cover of trees) that might influence local abundance within the population (Royle 2004, Joseph et al. 2009). Models that omit such covariates would be unlikely to account for heterogeneity in count data resulting from variation in ecological interactions and habitat characteristics (Royle 2004). Although we did not directly include habitat and terrain covariates for abundance in our analysis, the categorical site covariates included in the models that we considered reflected a broad range of habitat and terrain features. Moreover, Watson et al. (2008) reported that occupancy by warblers was not influenced by canopy height, canopy cover, slope, or aspect covariates that were measured within a 20-m radius of detection stations.

The negative binomial distribution has also been considered for modeling abundance and is appropriate when there is significant variation in abundance (Wenger and Freeman 2008). However, several studies have demonstrated that the negative binomial distribution not only often results in a poorer fit to survey data (i.e., larger AIC) compared with models using Poisson distributions but also yields estimates of abundance that are unreasonable and have inflated errors (Wenger and Freeman 2008, Joseph et al. 2009). Unlike the models that we used in the program PRESENCE, the zero-inflated variants of both the Poisson and negative binomial BMM show great potential in that these models simultaneously estimate probability of detection, abundance, and occupancy (Etterson et al. 2009, Joseph et al. 2009). Although these models appear to be appropriate for data sets that are truly "zero-inflated," the zero-inflated Poisson distribution would most likely be unsuitable for our warbler survey data; virtually all detection stations were occupied at sites with abundant populations; consequently, there was no opportunity for numerous unoccupied detection stations.

The use of detectability-adjusted estimators has been strongly advocated as an alternative to the use of raw counts as indices of abundance (Forcada 2000, Williams et al. 2002, MacKenzie et al. 2006, Alldredge et al. 2007). However, the inherent assumptions and restrictions involved in obtaining reliable estimates of detection and population parameters can sometimes preclude their usefulness as tools in wildlife management. We demonstrated that BMMs provided estimates of abundance for a federally endangered songbird that are likely (or possibly) biased high. Management decisions regarding the conservation of threatened and endangered species must be based on unbiased and precise population estimates. Although the repeated-count approach employed by BMMs offers numerous logistical advantages over other detectability-adjusted estimators, our results suggest that this technique deserves closer scrutiny before being widely applied in monitoring programs.

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