



DETECTION HETEROGENEITY AND ABUNDANCE ESTIMATION IN POPULATIONS OF GOLDEN-CHEEKED WARBLERS (*SETOPHAGA CHRYSOPARIA*)

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ABSTRACT.—Abundance estimators that account for imperfect detection, such as *N*-mixture models, assume that detection of individuals is independent of abundance. Using spot-mapping and *N*-mixture models applied to point-count data, we estimated abundance of Golden-cheeked Warblers (*Setophaga chrysoparia*) in two years at six study sites at the Balcones Canyonlands Preserve, Austin, Texas. *N*-mixture model estimates deviated from spot-mapping estimates at the site level by overestimating at low abundances, and at the survey-station level by underestimating at high abundance, which suggests that model assumptions may have been violated. We tested whether detection of individuals is influenced by abundance by assessing per capita song rate in relation to abundance. Per capita song rate increased with abundance, illustrating how the behavior of a territorial passerine may violate the independent-detectability assumption. We next explored violation of this assumption at the survey-station level by applying *N*-mixture models to simulated data exhibiting heterogeneity in detection. This exercise revealed a slight but increasingly negative bias (underestimation of abundance) in the estimator as the actual abundance increased, given positive density-dependent detection. The simulations also revealed a potential effect of sampling variation on misestimation by *N*-mixture model estimators. Assessing the strength, basis, and prevalence of density-dependent detection; further analyzing the effects of nonrandom heterogeneity in producing estimator bias; and accounting for nonrandom detection heterogeneity in abundance estimators are fruitful areas for further study. Received 31 January 2013, accepted 13 September 2013.

Key words: abundance estimators, detection probability, Golden-cheeked Warbler, *N*-mixture model, *Setophaga chrysoparia*, song rate.

Hétérogénéité de détection et estimation de l'abondance dans les populations de *Setophaga chrysoparia*

RÉSUMÉ.—Les estimateurs d'abondance qui représentent une détection imparfaite, comme les modèles de *N*-mélange, supposent que la détection des individus est indépendante de l'abondance. À l'aide de la méthode des plans quadrillés et de modèles de *N*-mélange appliqués aux données de points d'écoute, nous avons estimé l'abondance de *Setophaga chrysoparia* pendant deux ans à six sites d'étude de la *Balcones Canyonlands Preserve*, à Austin, au Texas. Les estimations des modèles de *N*-mélange différaient des estimations des plans quadrillés au niveau du site en surestimant lorsqu'il y a de faibles abondances, et au niveau de la station d'échantillonnage en sous-estimant lors de fortes abondances, ce qui suggère que les hypothèses des modèles n'ont pu être respectées. Nous avons testé si la détection des individus est influencée par l'abondance en évaluant le taux de chant par individu par rapport à l'abondance. Le taux de chant par individu a augmenté avec l'abondance, illustrant la façon dont le comportement d'un passereau territorial peut transgresser l'hypothèse de la détectabilité indépendante. Nous avons exploré le non-respect de cette hypothèse au niveau de la station d'échantillonnage en appliquant des modèles de *N*-mélange aux données simulées présentant une hétérogénéité dans la détection. Cet exercice a révélé un biais négatif léger mais croissant (sous-estimation de l'abondance) dans l'estimateur à mesure qu'augmentait l'abondance réelle, en considérant une détection dépendante de la densité positive. Les simulations ont aussi révélé un effet potentiel de la variation de l'échantillonnage sur la mauvaise estimation des estimateurs des modèles de *N*-mélange. L'évaluation de la force, de la base et de la prévalence de la détection dépendante de la densité, une analyse plus poussée des effets de l'hétérogénéité non aléatoire dans la production d'un biais de l'estimateur, ainsi que la prise en compte de l'hétérogénéité de détection non aléatoire dans les estimateurs d'abondance sont des domaines intéressants pour d'autres études.

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RELIABLE POPULATION ESTIMATES are important for developing effective monitoring, management, and conservation programs. Although raw counts reliably estimate population size in some instances, unbiased and accurate population estimators often require accounting for imperfect detection (Johnson 1995). This may be a particular concern for estimating abundance of relatively small, highly active, and cryptic organisms such as many passerine birds. Occupancy (MacKenzie et al. 2002) and N -mixture models (Royle 2004) use presence–absence or count data, respectively, to estimate occupancy and abundance, respectively, while accounting for detection–nondetection. A major advantage of these models is the ability to incorporate covariates to account for heterogeneity in detection among sample units. For example, habitat attributes (Warren et al. 2013), temporal factors (Hunt et al. 2012), distance from observer (Allredge et al. 2007a), vegetation (Pacifi et al. 2008), and variation among observers (Diefenbach et al. 2003) can be included as covariates upon which probability of detection can be conditioned within the model framework (MacKenzie et al. 2002, MacKenzie 2006). Increasingly, these models are employed to assess within- and among-population variation in occupancy, distribution, and/or abundance across a range of geographic scales (MacKenzie et al. 2002, 2009; MacKenzie 2006; Chandler et al. 2009).

A potential factor that may translate into bias associated with population estimation techniques, including occupancy and N -mixture model estimators, is nonrandom heterogeneity in the probability of detection of the individual among sample units (Royle and Nichols 2003, Royle 2006). When present, variation in detectability among sample units that is related to variation in the abundance (density) of the organisms whose population size is to be estimated presents an intriguing challenge within the occupancy and N -mixture model framework. This is because these models are predicated on there being no relationship between the probability of detecting an *individual* and local abundance. Royle and Nichols (2003) expressed the probability of detecting occupancy (p_i) conditional on the number of individuals at a sample unit (N_i) as

$$p_i = 1 - (1 - r)^{N_i}$$

where r is the binomial probability that a given individual is detected. Therefore, as the number of individuals increases, the probability of detecting at least one individual (and species occupancy) also increases. Two key assumptions of this equation are that (1) all individuals at a sample unit are equally detectable (r is a constant) and (2) the detection of one individual is independent of the detection of other individuals; hence, nondetection probabilities ($1 - r$) can be multiplied (Royle and Nichols 2003). If either of these assumptions is violated, the above equation does not hold; the estimated p_i may be inaccurate. Thus, any relationship between the probability of detecting an individual (r) and local abundance could lead to bias in the occupancy or abundance estimator.

N -mixture models actually take advantage of the above equation by reasoning that variation (or heterogeneity) in p_i is a direct indicator of variation in abundance (N_i) among sample units (Royle and Nichols 2003). However, this logic still requires that the probability of detecting an individual (r) is not itself related to N_i . Moreover, N -mixture models likely perform

best (with the least error and no bias) when there is minimal heterogeneity in r . N -mixture models have been employed to provide estimates of population abundance for a number of passerine species (Kéry et al. 2005, Joseph et al. 2009, Schlossberg et al. 2010, Chandler et al. 2011, Hunt et al. 2012). However, for some species and applications, N -mixture models have led to erroneous estimates of abundance when applied to populations for which abundance was known or had been estimated independently by other means (Joseph et al. 2009, Chandler et al. 2011, Hunt et al. 2012). Both Kéry et al. (2005) and Joseph et al. (2009) hypothesized that estimation errors resulted from inappropriate use of the negative binomial distribution, whereas Chandler et al. (2011) showed that overestimation of abundance by the N -mixture model was corrected by incorporating temporary emigration into the model.

One approach to understanding the basis of any estimation error associated with abundance (density) in N -mixture models is to examine the relationship between “known” population abundance and N -mixture model estimates across multiple populations (or individual populations followed across time) and then explore the ecological and/or behavioral mechanisms behind nonrandom heterogeneity in detection. A complementary approach is to use simulations that explicitly incorporate nonrandom heterogeneity in the probability of detection in the form of density-dependent detection to determine whether such heterogeneity leads to bias in the N -mixture model estimator.

The Golden-cheeked Warbler (*Setophaga chrysoparia*; hereafter “warbler”) provides an appropriate study system for investigating probability of detection as a function of variation in density. Given that the species is a territorial songbird, males might increase their frequency of singing when surrounded by several other males. Surveying for the species is typically conducted by observers listening for and recording the songs of individual males at stationary points during a given time interval. Therefore, such acoustic detections (or counts of males) could be affected by differences among males in singing rate (i.e., the count data at and among sample points might include an effect of heterogeneity in individual detection probability). In a larger context, conservation concern for this endangered species, endemic to south-central Texas (Pulich 1976), has led to strong interest in reliable and accurate estimates of abundance at multiple spatial scales (Wahl et al. 1990; Anders and Dearborn 2004; Peak 2007, 2011; Watson et al. 2008; Collier et al. 2010; City of Austin [COA] 2011; Hunt et al. 2012; Mathewson et al. 2012).

In the present study, we applied N -mixture models to estimate warbler abundance at six different study sites near Austin, Texas. We also obtained abundance estimates at each of 36 survey stations within each site. We compared model estimates with estimates derived from spot mapping of territories at both the study-site and survey-station levels. We then examined the ecological and behavioral basis of heterogeneity in detection (r) in these same populations by estimating per capita song rate and examining the relationship between per capita singing rate and warbler abundance at the site and station levels. Finally, we used a series of data simulations to compare the effects of random and nonrandom heterogeneity in individual detection probability on estimates of abundance produced by N -mixture models.

METHODS

Study system.—We assessed the relationship between local abundance, N -mixture model estimates of abundance, and probability of detection—dependent on singing behavior—in natural populations of the warbler. Variation in warbler abundance among our study sites, previously examined by Hunt et al. (2012), and across the species range (Wahl et al. 1990, Mathewson et al. 2012), in conjunction with observed relationships between song rate and local abundance in other passerines (Penteriani et al. 2002, Sillett et al. 2004, Laiolo 2008, Laiolo and Tella 2008), suggests the possibility that the warbler's per capita song rate and, hence, probability of detection of the individual (r) may be influenced by local abundance.

We studied warblers at five sites previously studied by Hunt et al. (2012) in 2008 and at six of the seven sites studied by Hunt et al. in 2009. We excluded one site in 2009 from all analyses because we did not record warbler vocalizations at this site. Study sites were distributed throughout the Balcones Canyonlands Preserve (BCP) located in Travis County, Texas. The BCP consists of 5,365 ha of discontinuous land interspersed with residential and mixed-use properties and is managed by multiple agencies for the conservation of the warbler and other endangered species (COA and Travis County 1996). Descriptions of the study sites are provided in COA (1999) and Hunt et al. (2012).

Estimates of abundance.—We estimated the abundance of warblers per unit area during the 2008 and 2009 breeding seasons for each study site by means of two techniques. Estimates of abundance (density) were derived independently from spot mapping (used here as the known abundance) and N -mixture models (Royle 2004). In this instance, using estimates of abundance derived by spot mapping as a surrogate for known abundance is justified by results of long-term spot mapping of warblers at these study sites. Inspection of spot-mapped abundance estimates reveals that the estimates are repeatable across years and differ consistently among study sites (COA 2011). From 1998 through 2012, the COA has estimated the number of territorial male warblers within 40.5-ha plots at each of the study sites by means of the spot-mapping technique (Bibby et al. 1992). In 2008, territory abundance ranged from 3 to 21.5 per spot-mapping plot, and in 2009, the season in which we also examined the relationship between singing rate and abundance, the number of territories ranged from 2.5 to 18 per study site (COA 2011). In 2008, a 1-km² point-count grid, positioned to overlay the COA 40.5-ha spot-mapping plot, was established at each study site. Each point-count grid consisted of 36 survey stations equally spaced at 200-m intervals in a 6 × 6 array (Fig. 1). Point-count surveys ($n = 4$), conducted at weekly intervals and based on a 5-min survey per survey station, provided the data used in conjunction with N -mixture models to estimate the abundance of male warblers at the five study sites in 2008 and the six study sites in 2009. Following Hunt et al. (2012), only those detections of warblers deemed to be ≤100 m from the center of each survey station were used to estimate abundance; thus, each point-count grid surveyed an effective area of 113 ha.

Spot mapping involves determining territory size, shape, and location from repeated detections (observations) of known individuals. Although the method is laborious and perhaps not practical across large spatial scales—hence the desire to develop

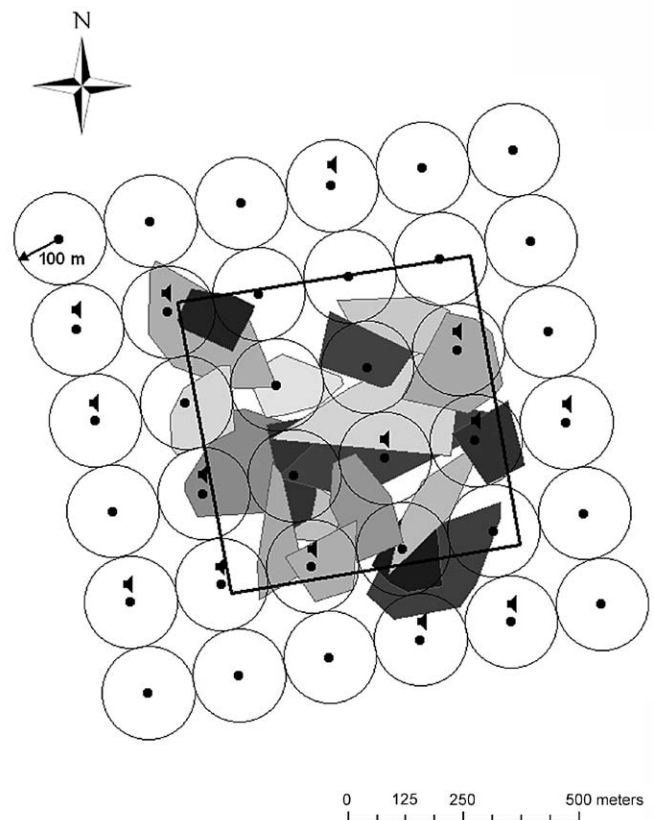


FIG. 1. Field design for data collection, illustrated for one of the six study sites. Point-count grids sampled 113 ha and were composed of 36 survey stations (black circles; spaced at 200-m intervals) laid out in a 6 × 6 array. Each survey station sampled Golden-cheeked Warblers within a 100-m detection radius. Survey stations at which ARUs recorded warblers are indicated by the “audio” symbol. Spot-mapped warbler territories (shaded polygons) were delineated within the City of Austin 40.5-ha study plot (square). Territories outside this plot were not delineated. The number of territories that overlapped the detection radius at each survey station was used to estimate spot-mapped abundance per survey station.

alternative methods—spot mapping is often considered the standard (i.e., the approximate known population size) for comparing methods of estimating avian abundance (Verner and Ritter 1988, Verner and Milne 1990, Bibby et al. 1992, Buckland 2006, Chandler et al. 2011, Peak 2011, Hunt et al. 2012). We compared the estimates of abundance derived from N -mixture models (λ) to estimates derived from spot mapping to determine whether the magnitude of error (λ /spot-mapped estimate) was a function of spot-mapped abundance per study site in both 2008 and 2009. Because N -mixture model estimates of abundance were based on a 113-ha grid, we scaled the 40.5-ha spot-mapping estimates of abundance to 113 ha. All estimates of abundance are, thus, numbers of male warblers per 113 ha.

We next compared λ and spot-mapping estimates of abundance at the station level. We examined the correspondence between known (spot mapped) and predicted numbers (N -mixture model estimates) of warblers per survey station and the structure of any deviation between the two methods for each year. To estimate the number of male warblers per

survey station based on spot mapping, we projected a 100-m buffer around each survey station and then, using the COA spot-mapping data for each year, tabulated the number of territories that overlapped the 100-m detection radius for each survey station in ARCMAP, version 10 (ESRI, Redlands, California) (Fig. 1). Specific information on the spatial relationships of warbler territories was available for the subset of the 36 survey stations at each study site that fell within the 40.5-ha COA spot-mapping plot (range: 9–12 survey stations per study site; 2008: $n = 57$; 2009: $n = 67$). Because COA biologists mapped only those territories that fell primarily within the 40.5-ha study plot, we excluded those survey stations with $\geq 50\%$ of the buffer area outside the study plot. Spot-mapped abundance represented the number of territorial male warblers potentially available at each survey station to be detected by surveyors in 2008 and by both surveyors and autonomous recording units in 2009.

To obtain an estimate of warbler abundance per survey station (λ) in both 2008 and 2009, we extended the N -mixture model previously used by Hunt et al. (2012) (λ [study site], p [site, season, time²]) by adding a habitat covariate (slope of the terrain at each survey station). Slope has been shown to affect warbler occupancy positively, presumably through an effect on vegetation structure (Warren et al. 2013). Use of the habitat covariate to produce unique station-specific estimates of warbler abundance was further justified by comparison of the two models, which showed that the habitat covariate model (λ [study site, slope], p [site, season, time²]) was superior to Hunt et al.'s (2012) model (habitat model $AIC_c = 1,760.61$, $-2*LL = 1,739.74$, $K = 10$, $w = 0.999$; Hunt et al.'s model $AIC_c = 1,780.28$, $-2*LL = 1,763.58$, $K = 8$, $w < 0.001$). We used PRESENCE, version 3.1 (MacKenzie et al. 2002, Hines 2006), to build the model. Linear regression was then used to test whether station-specific deviation in model-estimated abundance was a function of spot-mapped abundance per survey station in each of the two years. Finally, station-specific estimates of abundance produced by spot mapping were used to examine the relationship between abundance and per capita singing rate during the 2009 breeding season.

Estimates of song rate.—To test the assumption that the detection of an individual at a sample unit (point count survey station for our study) is independent of the detection of other individuals present, we recorded the singing behavior of male warblers in 2009 and examined the relationship between per capita singing rate and warbler abundance at the survey station and site levels. In March 2009, we deployed SM1 Song Meter Autonomous Recording Units (ARUs) (Wildlife Acoustics, Concord, Massachusetts) at each of 14 randomly selected survey stations within each of the six point-count grids established by Hunt et al. (2012). Recordings were collected from 15 March through 3 May, corresponding to the warbler breeding season.

Importantly, we deployed ARUs prior to the delineation of territories; thus, ARU positioning mimicked the random selection of survey-station locations that would be followed by human observers in the design of a typical point-count survey. At each survey station, ARUs were attached at breast height to a small tree to allow $\approx 360^\circ$ recording and were programmed to record for 5-min intervals with a 1-min pause between recordings from approximate sunrise to approximate sunset ($\approx 13 \text{ h day}^{-1}$) for two consecutive days. The ARUs were then moved to the next survey

station, until 14 stations had been sampled per study site. The 5-min recording corresponds to the 5-min survey interval typically used in passerine point-count surveys (Lynch 1995, Ralph et al. 1995, Watson et al. 2008) and concurrently used at these same study sites and survey stations in 2008 and 2009 (Hunt et al. 2012). SONG SCOPE software (Wildlife Acoustics) provided a sonogram of vocalizations that was inspected to identify and manually count all warbler songs. This procedure provided an accurate record of warbler vocalizations within the detection radius of each ARU at each sampled survey station throughout the 7-week study season. We considered a song to be a discrete vocalization, typically no longer than 2 s in duration. Each ARU recorded the vocalizations contributed by all singing male warblers within its detection radius. Thus, song rate per survey station was computed as the average number of songs recorded per 5-min interval across all ~ 280 intervals per station and represents the number of songs available at a point-count station during a survey interval for a surveyor to detect the species (p) or an individual (r). Like other members of the family Parulidae, warblers use a multi-category song system (Pulich 1976, Bolsinger 2000, Leonard et al. 2010). In estimating song rate, we pooled “A” and “B” category songs, because preliminary analyses found no difference in an ARU's ability to detect the two major song types of the warbler as a function of distance. Across all sites, 8% of recordings were excluded because weather exceeded U.S. Fish and Wildlife Service (2010) survey parameters, non-warbler zoogenic or anthropogenic noise, or equipment failure. After excluding these recordings, we analyzed an average of 3,188 five-minute samples recorded from a minimum of 13 survey stations per study site. In total, we analyzed 19,127 five-minute samples that included 80,107 songs from 80 survey stations across the six study sites.

Detection radii of ARUs.—Estimates of warbler abundance per study site (Hunt et al. 2012) and per survey station (present study) included only those warbler detections estimated by observers to have been within 100 m from each survey point (Hunt et al. 2012; Fig. 2). Because testing our hypotheses about singing rate and warbler abundance involved data gathered by both observers (used in estimating λ) and ARUs (used to calculate song rates), we assessed whether the area sampled per survey station was comparable between humans and ARUs in a preliminary study. To determine the maximum detection distance and verify consistency of ARUs, we suspended ARUs ($n = 6$) side by side, 1.5 m above the ground, in an open field in calm weather conditions. We then played a 1-min recording of A and B songs calibrated to 55 dB at 6 m for both song types (the average volume of 10 male warblers singing in the wild on BCP properties at an average of 6 m) at distances of 5, 10, 30, 50, 75, 100, and 150 m. Inspection of sonograms showed that A and B songs were routinely detected at 75 m but, with the exception of a single A song, no songs were detected at 100 m. Thus, under ideal circumstances, the detection radius of ARUs was ≤ 100 m, and ARU data were comparable with data collected by human observers. The ARUs did not vary in their ability to detect warbler songs.

Site-level warbler abundance and song rate.—Mean song rate per study site was calculated by using both data from all survey stations sampled by ARUs and data from only those stations where ARUs detected one or more warbler songs. Preliminary analysis

showed that the relationship between mean song rate and the number of territories per study site did not differ between the two methods; thus, we present results based on data from all stations ($n = 80$) sampled by ARUs. We used analysis of variance to determine whether significant variation in mean song rate was present among study sites. Linear regression was used to test the hypothesis that per capita song rate per study site (i.e., mean number of songs per survey station per 5 min, divided by estimated study site abundance) was influenced by territory abundance.

Station-level warbler abundance and song rate.—To test the hypothesis that song rate was related to abundance, we regressed per capita song rate recorded at each survey station on the number of territories estimated to overlap each station in 2009. Station-level data were pooled across study sites for these regressions. All analyses were conducted in R, version 2.9.2 (R Development Core Team 2009). Means and regression coefficients are presented \pm SE throughout.

Simulation study.—We simulated hypothetical abundance and count data to explore the effect of heterogeneity in individual detection probability (r) on abundance estimates obtained from N -mixture models. We conducted four sets of simulations, each set consisting of 1,000 iterations. In each set, abundance data (N_i) at each of 36 survey stations were simulated as a Poisson distribution with a mean (N_x) set as a random variable between 0 and 5 (this resulted in stations having between 0 and 12 individuals). Iterations with N_x near 0 tended to produce abundance values of 0, 1, 2, or 3 at the stations, whereas iterations with N_x near 5 tended to produce abundance values mostly between 3 and 8, with some values as high as 12. Set 1: r at each station was a constant at 0.5; this simulated a scenario without any heterogeneity in r . Set 2: at each station, r was taken as a random variable from a uniform distribution bounded between 0.1 and 0.9. This simulated a scenario with random heterogeneity in r . Set 3: at each station, r was obtained from a logit-logistic function of abundance and a latent (not density-dependent) detection probability, r_{lat} . That is, $r_i = e^{L + b(N_i - N_x)} / (e^{L + b(N_i - N_x)} + 1)$, where $L = \text{logit}(r_{\text{lat}}) = \log[r_{\text{lat}} / (1 - r_{\text{lat}})]$ with station abundances (N_i) centered on the mean (N_x). In this simulation, we used $r_{\text{lat}} = 0.5$ and $b = 0.5$; the latter constant produces positive density dependence in r as a sigmoidal function. Set 4: at each station, r was obtained from a linear function, $r_i = 0.05 + (N_i \times 0.05)$. This simulated a scenario in which each additional individual increases detection probability by an increment of 0.05, beginning with $r_i = 0.1$ when only one individual was present.

Using the r_i values at each station, simulated count data were obtained from a binomial distribution with probability of success = r_i and number of trials = N_i . Therefore, these simulations effectively mimicked a binary surveying process in which observers either do or do not detect each individual at the station. For each of the 36 stations, count data were simulated for four hypothetical repeat surveys in order to resemble the study design of the actual warbler surveys. We also conducted versions of these simulations with 200 stations to assess the effect of sampling variation on abundance estimates under each detection scenario. For each iteration of a simulation, count data were then used in an N -mixture model (the “pcount” function in R package “unmarked”; Fiske and Chandler 2011) to get abundance estimates (i.e., estimated λ). The data simulation and N -mixture models were conducted in R, version 2.15.2. The computer code is given in the Appendix.

RESULTS

Abundance at the site level.—The magnitude of the difference between N -mixture model and spot-mapped estimates of warbler abundance at the level of the study site was negatively related to spot-mapped abundance in both 2008 ($\beta = -0.057 \pm 0.01$, $t = -5.07$, $P = 0.015$, $R^2 = 0.90$) and 2009 ($\beta = -0.034 \pm 0.01$, $t = -3.54$, $P = 0.024$, $R^2 = 0.76$; Fig. 2). Differences in the two estimates of abundance were greatest at the study sites known to have the lowest spot-mapped abundance of warblers, where the ratio of λ /spot-mapped abundance approached 3 \times . With increasing abundance of warblers at a site, the ratio approached 1, indicating good agreement between the two estimators.

Song rate at the site level.—The ARUs detected male warblers at all sampled survey stations at three study sites and at 76%, 85%, and 92% of survey stations at the remaining three sites. Thus, warblers were available to be detected at most survey stations. Comparison of the distribution of the number of songs recorded by ARUs per 5-min survey interval across the six study sites (Fig. 3) provides a general depiction of the differences in singing frequency among study sites and also highlights the relationship between the frequency of nondetection (0 songs per 5-min survey interval) and spot-mapped abundance per study site. Warblers were least frequently detected by ARUs at survey stations within the two study sites that exhibited the lowest territory density. Mean song rate varied over an order of magnitude among study sites ($F = 5.98$, $df = 5$ and 67, $P < 0.001$), with an average of 0.49 ± 0.17 and 7.51 ± 1.8 songs recorded per 5 min at the study sites with the lowest and highest spot-mapped estimates of abundance, respectively. The observed variation in song rate within and among study sites provided the variation necessary to test hypotheses relating song rate and warbler abundance. Song rate was converted into a per capita measure (mean song rate/abundance estimate per study site) to examine the relationship with spot-mapped warbler abundances across study sites. Per capita song rate increased significantly with

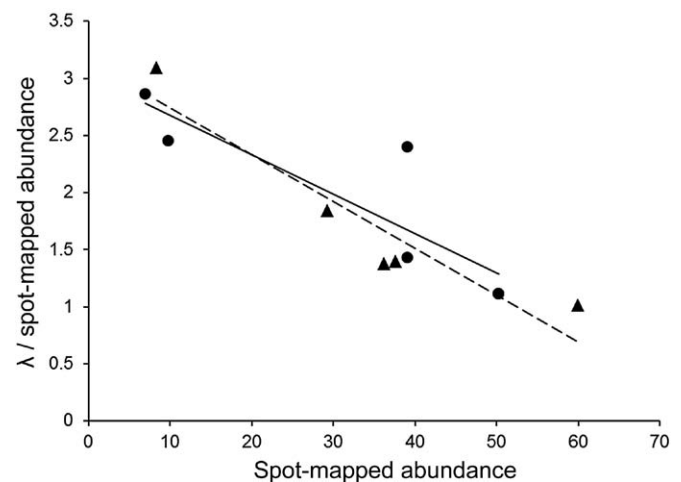


FIG. 2. Ratio of the abundance of male Golden-cheeked Warblers estimated by N -mixture models (λ) and abundance estimated by spot mapping of territories, for 2008 and 2009, in relation to known abundance: 2008 = triangles and dashed line, $n = 5$; 2009 = circles and solid line, $n = 6$.

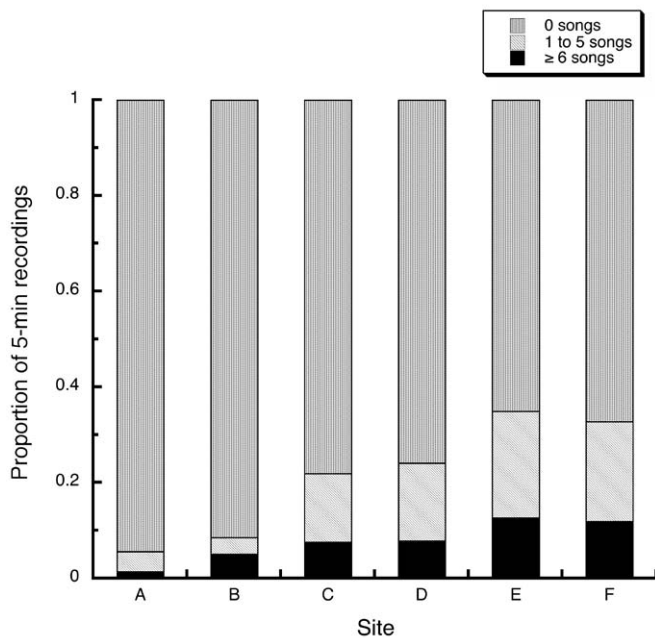


FIG. 3. Distribution of the number of Golden-cheeked Warbler songs recorded by ARUs per 5-min survey interval summed across all survey stations at each of the six study sites. Histograms are ordered according to spot-mapped abundance per study site: lowest (left) to highest (right). The number of 5-min survey intervals recorded at each study site ranged from 2,874 to 3,356.

spot-mapped abundance per study site ($\beta = 0.0013 \pm 0.0003$, $t = 4.74$, $P = 0.009$, $R^2 = 0.85$; Fig. 4A).

Abundance and song rate at the station level.—A comparison of spot-mapped abundance and estimated λ per survey station revealed that the two estimators of warbler abundance were moderately correlated within each year (2008: $r = 0.61$, $P = 0.001$, $n = 57$; 2009: $r = 0.71$, $P = 0.001$, $n = 67$). However, in both years, estimated λ deviated from spot-mapped abundance per survey station with the magnitude of the deviation being a negative function of spot-mapped abundance (2008: $\beta = -0.645 \pm 0.06$, $t = -10.36$, $P < 0.001$, $R^2 = 0.67$; Fig. 5A; 2009: $\beta = -0.702 \pm 0.04$, $t = -19.45$, $P < 0.001$, $R^2 = 0.85$; Fig. 5B). At survey stations for which spot-mapped abundance was ≤ 2 territories, the distribution of differences between λ and spot-mapped abundance was symmetrical about 1, indicating no bias in the N -mixture model estimator. However, at stations with higher territory abundances, λ increasingly underestimated spot-mapped abundance, indicating a negative bias in the estimator. Per capita song rate increased with spot-mapped abundance of warblers per survey station, although the relationship was highly variable ($\beta = 0.153 \pm 0.06$, $t = 2.68$, $P = 0.013$, $R^2 = 0.22$, $n = 28$; Fig. 4B).

Simulation study: Nonrandom detection heterogeneity and N -mixture model bias.—Data simulated from a constant detection probability ($r = 0.5$) showed no bias (i.e., a symmetrical distribution of estimates about unity) in the N -mixture model estimator across the range of simulated mean abundances. However, there was substantial sampling variation, as indicated by the scatter of abundance estimates based on $N = 36$ point count stations (Fig. 6A). The simulation of data with random heterogeneity in detection

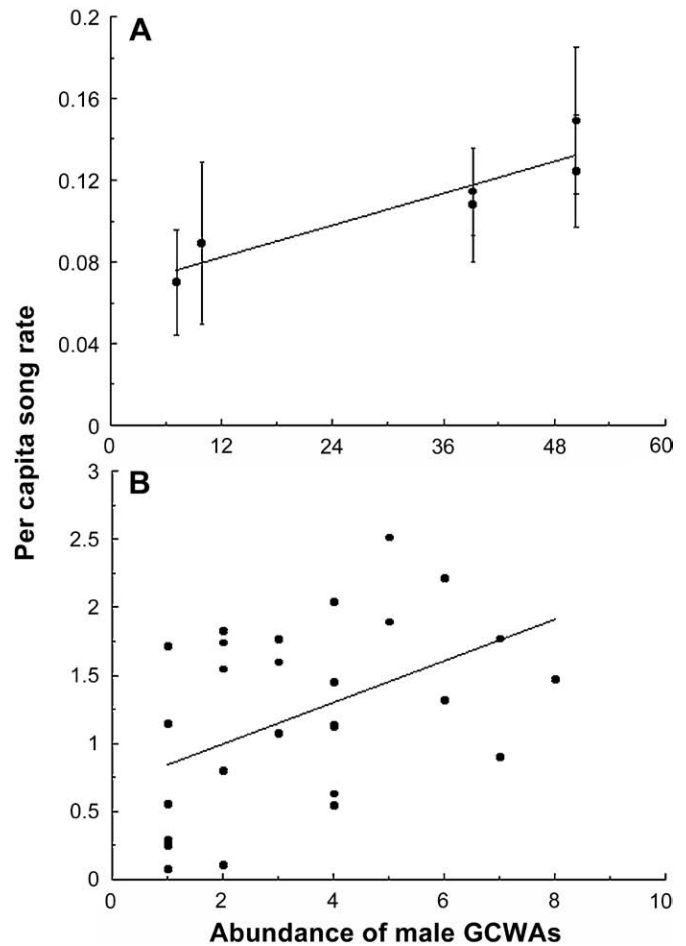


FIG. 4. (A) Relationship between spot-mapped abundance of male Golden-cheeked Warblers (GCWAs) per study site in 2009 and per capita song rate (\pm SE). (B) Relationship between spot-mapped abundance of male GCWAs per survey station and per capita song rate. Axis scale varies between plots.

probability (r drawn from uniform distribution 0.1 to 0.9) revealed greater amounts of variation in the N -mixture model estimates, although again with no evidence of estimator bias across the simulated range of mean abundances per station (Fig. 6B). By contrast, a negative bias in the N -mixture model estimator (underestimation of actual abundance, on average) was revealed in the simulations where count data were produced under a condition in which r was density dependent (Fig. 6C, D). More specifically, this condition tended to lead to more underestimation rather than overestimation as density increased. All simulations that involved 36 stations had some sampling variation (error) that arose from a limited sample size compared with the simulations of 200 stations, which had substantially less scatter in the plots (not shown).

DISCUSSION

A primary goal of our study was to examine whether nonrandom heterogeneity in individual detection probability might introduce bias in N -mixture models used to estimate abundances of warblers

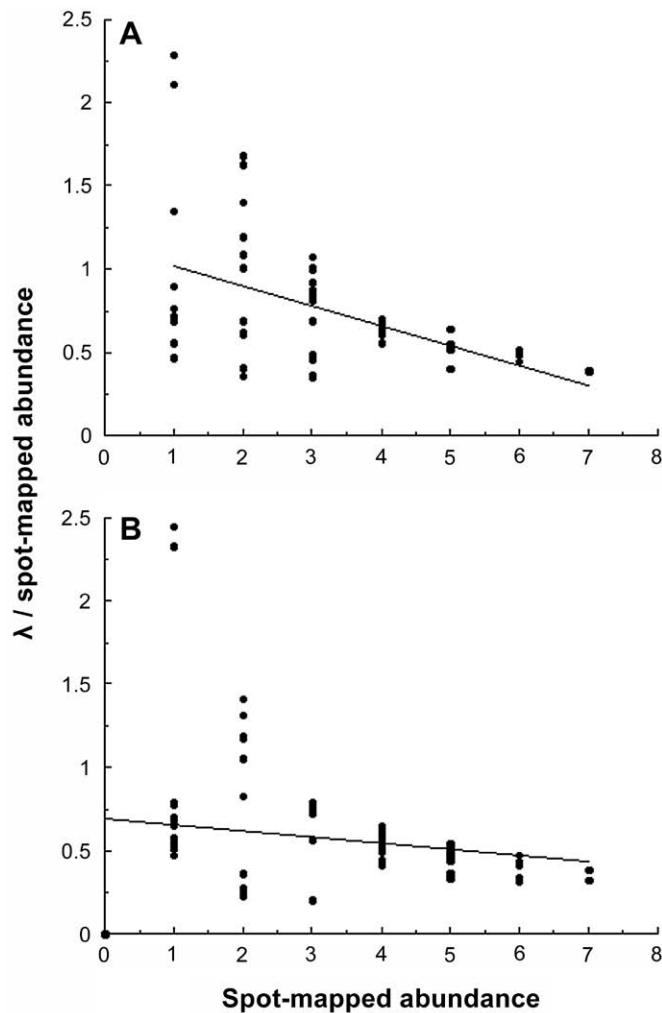


FIG. 5. Ratio of difference between estimated abundance (λ) of male Golden-cheeked Warblers, based on N -mixture models, and known abundance, based on spot-mapped territories, within a 100-m detection radius of each survey station for (A) 2008 and (B) 2009. Each dot represents a survey station (2008: $n = 57$; 2009: $n = 67$).

at our study sites. We assumed that spot-mapped abundances of warbler territories were the most valid estimates of actual abundance at the study-site and station levels; thus, we compared these versions of the truth to estimates of abundance derived from N -mixture models. Our analyses revealed possible systematic error in N -mixture model estimates of abundance. At the site level, the N -mixture model overestimated abundance with the degree of overestimation inversely related to known population abundance. At the station level, the N -mixture model estimator generally underestimated abundance, particularly when spot-mapped abundance was >3 . The latter result accords with the presumed way in which heterogeneity in detection probability should bias abundance estimators such as the N -mixture model and related mark–recapture estimators. Specifically, the bias should be expressed as negative (underestimation of actual abundance), on average, and this pattern was revealed in the station-level estimates (Fig. 5) and data simulations (Fig. 6C, D). Possible explanations for these observed patterns include

violation of model assumptions, poor fit of the N -mixture model (missing covariate or misspecification of the underlying abundance distribution), violations of assumptions involved in comparing spot-mapped and N -mixture model estimates, and aspects of the behavior and biology of the warbler.

We explored the relationship between abundance estimated by spot mapping and the potential detectability of warblers (i.e., singing rate) within and among study sites. In so doing, we indirectly tested a key assumption of Royle’s (2004) model—that detection of an individual is independent of the detection of other individuals at sample units. Our results showed that per capita singing rate at survey stations increased with estimated local abundance. The increased rate of singing could be explained by either the primary individual males being sampled by ARUs singing more in response to increased local abundance or the multiple males being sampled by ARUs individually singing less but collectively producing more songs per recording interval. Although our study did not directly test whether singing by one male warbler causes another to begin singing, density-dependent per capita singing rate is consistent with that behavioral mechanism. Given the established role of song in territorial interactions in warblers (Bolsinger 2000), the hypothesis that males sing more in response to increased local abundance may be more parsimonious than the “more males but fewer songs” hypothesis. Direct evidence of increased singing rate would be the strongest indication of biologically and statistically nonindependent detection—individuals directly and immediately affect each other’s availability to be detected.

In most passerines, detection at a survey station is primarily dependent on observers hearing singing males. Thus, per capita singing rate is intimately related to the probability of detection. Given that per capita song rate (a core component of individual detectability) was positively related to warbler abundance at both the survey-station and study-site levels, detection of individuals of this species was likely influenced by abundance. Under conditions where abundance (density) influences per capita singing rate, a core assumption of N -mixture models—that the detection of individuals is independent of the detection of other individuals at sample units—may be violated. To date, density-dependent detectability has received little attention. Our results suggest that such a relationship may contribute to N -mixture models producing erroneous abundance estimates.

The density dependence of song rate essentially leads to unmodeled among-individual heterogeneity in detection probability. That is, an individual’s probability of being detected depends directly on the density of conspecifics in its immediate environment. In the classic mark–recapture design, this would be a scenario in which individuals with inherently high detection or capture probability are more likely to be captured, marked, and then recaptured than are unmarked individuals (Royle and Dorazio 2008). This is a clear violation of the “equal catchability” or “resighting” assumption of mark–recapture design because it overestimates recapture or detection probability and, hence, underestimates true population size. Although we did not have a mark–recapture design, any density-based bias in detection probability (e.g., among stations or singing rate of a songbird) could lead to underestimation of abundance. That is, stations with a high density of birds would have high detection probabilities (because

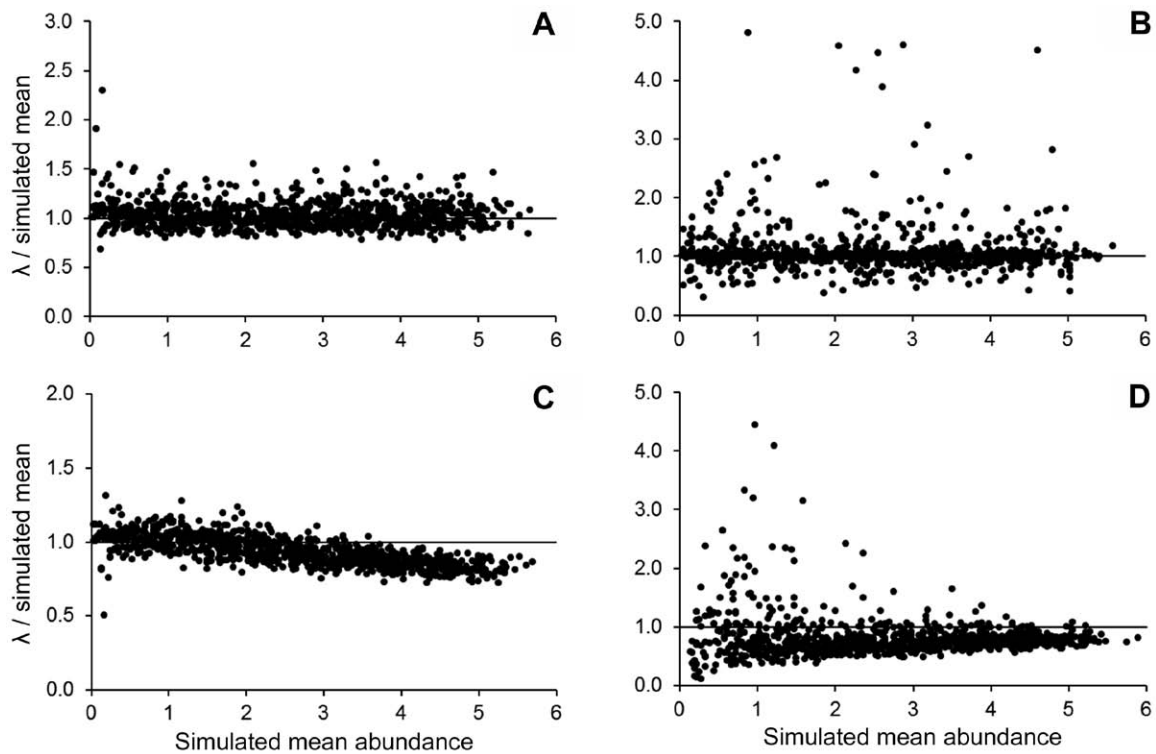


FIG. 6. Results of simulation studies. All plots show simulated mean abundance over 36 survey stations and the ratio of the model-estimated λ to the simulated mean abundance of Golden-cheeked Warblers. Each point represents one of the 1,000 iterations of the given simulation. (A) Count data are simulated on the basis of an individual detection probability (r) that is a constant set at 0.5. This simulation represents count data without any heterogeneity in r . (B) Count data are simulated on the basis of a random r taken from a uniform distribution bounded between 0.1 and 0.9. This simulation depicts count data with random heterogeneity in r ; that is, r is not a function of the simulated abundance at a station. (C) Count data are simulated on the basis of r as a logistic (binary sampling) function of abundance at a station. This simulation represents count data derived under a condition where r is an increasing sigmoidal function of abundance at a station. (D) Count data are simulated where r is a linear function of abundance at a station, $r = 0.05 + (0.05 \times N)$. This simulation represents a scenario where each additional bird at a station increases individual detection probability by an increment of 0.05, with a minimum value of 0.1 when there is only one bird at a station. Note that there is also sampling variation in all the simulations that is derived from having a limited sample size (36 stations).

birds sing more often at high density) with the consequence that N -mixture models underestimate actual abundance. Stations with a low density of birds might have lower detection probabilities if the birds sing very little or not at all. However, this should still generally lead to underestimation of actual abundance because the N -mixture model estimator is negatively biased when there is nonrandom heterogeneity in detection probability. In practice, given the restrictions in the number of point-count stations that can be sampled, abundance estimates from N -mixture models can be either overestimates or underestimates (Fig. 6). Much of this misestimation is due simply to sampling error that arises from a limited sample size (e.g., 36 stations instead of 200). Nonetheless, density-based heterogeneity in detection probability can affect the performance of N -mixture models even for large sample sizes, as illustrated by our simulations involving 200 survey stations (similar patterns to those in Fig. 6C and D were obtained). The negative bias in the estimator is not due to sampling error.

Understanding the relationship between density and detectability (p or r) is facilitated by examining the components of detection. Marsh and Sinclair (1989) and Johnson (2008) divided detection into “perceptibility” (likelihood of detection

given presence at a survey station) versus “availability” (likelihood of presence during a survey interval). Passerine birds are primarily enumerated by sound-based surveys (Mayfield 1981, Ralph et al. 1995); hence, the presence of an individual at a sample unit may not be sufficient for the species or individual to be detected. Availability for detection is primarily dependent on song rate (i.e., the number of songs produced per time per sample unit or per individual bird), which translates into the number of opportunities for detection during a survey. Behaviors linked to local abundance are therefore likely to affect the availability component of detection (Diehl 1981, Bart and Schoultz 1984, Verner 1985). Factors that affect availability have been investigated for select taxa (Johnson 2008), but our understanding of the mechanisms underlying variation in availability in relation to local abundance remains underdeveloped for many taxa. Moreover, because of differences among taxa and survey protocols (Stanislav et al. 2010, Reidy et al. 2011), the direction of, and mechanisms underlying, detection bias may differ between studies and study systems.

Many passerine species increase singing rate with increased local abundance (Penteriani et al. 2002, Sillett et al. 2004, Ríos

Chelén et al. 2005, Sexton et al. 2007, Laiolo and Tella 2008), and song rate has been shown to influence detection probabilities (p) positively in some species (Mayfield 1981, Wilson and Bart 1985, McShea and Rappole 1997, Alldredge et al. 2007b). We observed a positive effect of abundance on per capita song rate of warblers. However, factors other than local abundance have been found to influence passerine song rate—for example, temporal factors (Amrhein et al. 2004, Liu and Kroodsma 2007, Avey et al. 2008), habitat attributes (Hoi-Leitner et al. 1995, McShea and Rappole 1997), and pairing status (McKillip and Islam 2009). These factors (not measured in the present study) may contribute to the variation in song rate of warblers evident in Figure 4.

Intra-territorial movements of male warblers may also contribute to variation in the relationship between abundance and per capita song rates, because the probability that an individual warbler is detected at a randomly placed survey station may be a function of the proportion of its territory that overlaps the detection radius of the survey station. Thus, the assumption that all individuals are equally detectable from a survey station may be violated when heterogeneity exists in the extent that individual territories overlap the detection radius of survey stations (Fig. 1). In territorial wood warblers like the Golden-cheeked Warbler, resource availability or defensibility may limit the size of breeding territories or home ranges (Smith and Shugart 1987, Anich et al. 2010). In this way, local abundance may influence the size of breeding territories (Morse 1976). In a separate analysis, we found that the size of territories maintained by male warblers in 2009 decreased as a function of known abundance per study site ($\beta = -0.93 \pm 0.023$ ha, $t = -4.12$, $P < 0.001$). Hence, male warblers in our lower-density study sites, for example, may spend less time at any given point within their territory that is within the detection radius of a survey station. Thus, temporary emigration could translate to decreased song rate per survey station and lower detection availability at lower densities, even without an effect of local abundance on individual song rate. Therefore, we suggest two non-mutually exclusive explanations for the observed relationship between spot-mapped abundance and per capita song rate: (1) an increase in the number of neighboring territories increases the stimulus for singing; and (2) an increase in territory density results in smaller territories or territories that overlap to a greater extent, increasing the potential for an observer to be within the detection radius of multiple individual males. We are currently examining the latter possibility using a multi-year data set from the same study sites.

Our primary conclusions of density-dependent bias in N -mixture models and density-dependent detection availability of male warblers depend on accurately delineating territories and estimating territory abundance within and among study sites. High-resolution territory mapping of color-banded warblers beginning in 2009 (27 ± 1 relocations used to delineate territories) has confirmed previous estimates of abundance based on spot mapping and verified the long-standing among-study-site differences in warbler abundance (COA 2011). Thus, spot mapping provides reliable estimates of “known” abundances. To make spot-mapped estimates (based on 40.5-ha areas) comparable to the site-level N -mixture model estimates (based on 113 ha), we scaled COA territory estimates to 113 ha. Extrapolation assumes that warbler territory densities throughout the 113-ha survey grids were equivalent to territory densities within the 40.5-ha plots. Because the COA spot-mapping plots were placed

in areas known to be warbler habitat, it is unlikely that habitat quality outside spot-mapping plots exceeded habitat quality within the plots. If habitat was less suitable outside the 40.5-ha area than within it, the relationship shown in Figure 2 may be conservative and provide only a lower bound for the discrepancy between N -mixture model and spot-mapped estimates of abundance.

In summarizing our work, we note that it was the magnitude and negative density-dependent pattern of overestimation by the N -mixture model in relation to the spot-mapped estimator at the site level (Fig. 2) that motivated (1) inspection of the difference between these estimators at the survey-station level, (2) field study of per capita song rate and the relationship between abundance and per capita song rate at both the study-site and survey-station level, and (3) simulations of the possible effects of nonrandom heterogeneity in detection probability in producing bias in the N -mixture model estimator. A major goal of our work has been to examine how any relationships revealed by the above investigations explain, combine to explain, fail to explain, and/or point to the need for further study of mechanisms that underlie the original observations at the study-site level.

In practice, N -mixture model estimates of abundance at the survey-station level sum to site-level estimates of λ . At the survey-station level, *ceteris paribus*, we expected λ to overestimate abundance when spot-mapped abundance was low and to be equivalent to spot-mapped abundance estimates at higher spot-mapped abundances. Instead, we saw in our field studies that the N -mixture model estimator was unbiased at low spot-mapped abundances but became progressively negatively biased at higher spot-mapped abundances. Although particular estimates of λ can still overestimate (or underestimate) abundance at low spot-mapped abundances, it appears unlikely that the pattern of misestimation at the survey station can explain the study-site-level pattern of misestimation. Temporary emigration, modeled successfully by Chandler et al. (2011) to bring N -mixture model estimates into accord with “known abundances,” perhaps combined with variation in availability that is related to abundance, represents one possible explanation.

The positive density-dependent relationship we observed between per capita song rate and local abundance justified exploring, via simulations, the possible role of nonrandom heterogeneity in detection probabilities in leading to N -mixture model bias. Importantly, simulation results show that although heterogeneity in r alone can produce underestimation of abundance at the survey-station level, it is positive density-dependent heterogeneity in r that produces the systematic negative bias in the N -mixture model estimator, with the error in individual estimates of abundance compounded by sampling variation when only a limited number of stations are sampled. These simulation results suggest that the relationship between density-dependent detection and estimator bias merits closer inspection via more thorough modeling.

Model-based abundance estimators that correct for imperfect detection are powerful tools that can improve both the efficiency and accuracy of studies aimed at estimating population abundance. Our research draws attention to the role that density-dependent detection can play in biasing the N -mixture model estimator and the behavioral basis for density-dependent detection in a territorial songbird. We urge that careful attention be paid to the model assumptions, particularly in relation to the biology and behavior of territorial organisms. Assessing the strength and prevalence of density-dependent detection, and the conditions that favor it; analyzing more comprehensively

the effects of nonrandom heterogeneity in producing estimator bias; and accounting for nonrandom heterogeneity of detection in abundance estimators are fruitful areas of further study. Recent studies that recommend adjusted methodologies as a means of lessening bias due to violation of other model assumptions, such as population closure in this (Peak 2011) and other passerine species (Chandler et al. 2011), may serve as templates for future improvements in response to density-associated bias.

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APPENDIX. R computer code for generating simulated data and applying the N -mixture model (Royle 2004); the code requires the “unmarked” R package (Fiske and Chandler 2011). The code simulates abundance and count data at $S = 36$ survey points for each site and for $T = 4$ repeat survey periods. Other values could be used for these parameters. The N -mixture model uses no covariates.

Code below simulates the data.

```
sim.fn=function(S=36,T=4,lambda=lambda, mean.r=0.5,
betaN=0.5){
require(unmarked)
y=array(dim=c(S,T))
lambda <- runif(1,0,5.0)
N=rpois(n=S,lambda=lambda)
r=plogis(log(mean.r/(1-mean.r))+betaN*(N-mean(N))) #see note
at end of document
for(j in 1:T){y[,j]=rbinom(n=S,size=N,prob=r)}
av.r=round(mean(r),3)
```

Code below applies the N -mixture model.

```
unmf=unmarkedFramePCount(y = y)
fm=pcount(~1 ~1,unmf,K = 100+max(y))
lambda_hat=round(exp(fm@estimates@estimates$state@
estimates),3)
p_hat=round(plogis(fm@estimates@estimates$det@
estimates),3)
```

Code below summarizes the results and prints them to the R console window.

```
cat(i, lambda, lambda_hat, p_hat, paste(N), "\n") return(i)
invisible(list(S=S,T=T,lambda=lambda,mean.r=mean.r,av.
r=av.r,betaN=betaN,
N=N,y=y,lambda_hat=lambda_hat,p_hat=p_hat))})
```

Code below runs the simulation for 1,000 iterations.

```
simreps=1000
estimates.beta.pos.7=array(NA,dim=c(simreps,2))
colnames(estimates.beta.pos.7)=c("lambda_hat","p_hat")
avge.p.beta.pos.7=array(NA,dim=simreps)
for(i in 1:simreps){#cat("\n\n***Sim Number",i,)
tmp1=sim.fn(mean.r=0.4,betaN=1)
estimates.beta.pos.7[i,]=c(tmp1$lambda_hat,tmp1$p_hat)
avge.p.beta.pos.7[i]=tmp1$av.r}
```

NOTE: Line of code given in the above program is for simulating individual detection probability as a logit-logistic function of abundance. For simulating other detection probabilities, the code should be replaced with one of the following:

```
p=0.5 #simulates detection probability as a constant
p <- runif(n=1, min=0.1, max=0.9) #simulates detection prob-
ability as a random number drawn from a uniform distribution
bounded between 0.1 and 0.9
p=(0.05 * N)+ 0.05 #simulates an incremental increase in detec-
tion probability with increasing abundance at a station
```