

SINGING BEHAVIOR LEADS TO DETECTION

BIAS IN A TERRITORIAL SONGBIRD

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ABSTRACT

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The development of models to account for variation in the probability of detection, such as N -mixture models, have advanced methods of estimating wildlife abundance and resource use. A core assumption of these models is that the detection of individuals is not influenced by conspecific density. A recent study of the Golden-cheeked Warbler, *Setophaga chrysoparia*, compared N -mixture model estimates of abundance to estimates of territory density based on spot mapping in each of six populations and demonstrated a negative density-dependent bias in N -mixture model estimates of abundance. Here we provide an indirect test of the assumption that detection of individuals is not influence

by conspecific density by investigating the singing behavior of male GCWA as a function of territory density within the same populations previously studied. Using automated recording units placed at randomly selected survey stations throughout the six study sites we found evidence of a significant positive effect of territory density on the average song rate per unit bird, measured as the number of songs recorded per 5 min, recorded per survey station. This pattern indicates that the number of opportunities to detect an individual (i.e. number of songs) within a survey interval is influenced by local territory density and documents a violation in this species of the implicit assumption of N -mixture models that the probability of detecting an individual is independent of the conspecific density. Failure to account for a density-detectability bias within the N -mixture model framework may result in biased estimates of occupancy or abundance.

INTRODUCTION

Reliable population estimates are fundamentally important in developing effective monitoring, management, and conservation programs. Although raw counts reliably estimate population size in some instances, unbiased and accurate population estimates often require accounting for imperfect detection (Johnson 1995). Both occupancy (MacKenzie et al. 2002) and N -mixture models (Royle and Nichols 2003) (henceforth OBMs) use presence-absence or count data, respectively, to estimate population size while accounting for imperfect detection. Increasingly these models are employed to assess within- and among-population variation in distribution and abundance across a range of geographic scales (MacKenzie et al. 2002, MacKenzie 2006, MacKenzie et al. 2009).

A significant source of potential bias associated with population estimation techniques, including OBMs, is spatial heterogeneity in the probability of detection of the individual or species among sample units (Royle and Nichols 2003, Royle 2006). A major advantage of OBMs is the ability to incorporate covariates to account for heterogeneity in detection among sample units. For example, factors such as distance from observer (Alldredge et al. 2007a), vegetation (Pacifi et al. 2008), and variation among observers (Diefenbach et al. 2003) can be included as parameters upon which probability of detection can be conditioned within the OBM framework (MacKenzie et al. 2002, MacKenzie 2006). However variation in detectability among sample units that is related to variation in the density of the organisms whose population size is to be

estimated presents an intriguing challenge within the OBM framework. This is because an *a priori* density covariate for probability of detection is not possible given that an estimate of occupancy or abundance per sample unit and (or) total abundance per study site is the desired output of the model. In their N -mixture model Royle and Nichols (2003) included a mixture distribution as a measure of possible population states into the estimate of probability of detection (of the individual) as a means of modeling variation in density (Royle 2006). OBMs are predicated on there being no relationship between the probability of detecting an individual and conspecific density. Royle and Nichols (2003) express 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. Two key assumptions of this model are (1) all individuals at a sample unit are equally detectable and (2) the detection of one animal is independent of the detection of other animals at a sample unit (Royle and Nichols 2003). Thus any positive or negative relationship between the probability of detecting an individual (r) and conspecific density could lead to biased estimates of occupancy or abundance. To understand density-associated detection bias the ecological and (or) behavioral mechanisms behind such biases must be explored. N -mixture models have been applied to a wide variety of taxa (e.g. reptiles: Dore et al. 2011, birds: Schlossberg et al. 2010, mammals: Rytwinski and Fahrig 2011). As a result of inherent differences between taxa and differences in survey protocols both the possible direction and mechanisms underlying density-detectability bias may vary between studies and study systems.

N -mixture models have been employed to provide population estimates for a number of passerine species (Kéry 2008, Chandler et al. 2009, Joseph et al. 2009, Schlossberg et al. 2010, Chandler et al. 2011, Hunt et al. In press). However, in some instances N -mixture models have led to biased estimates of abundance (Kéry et al. 2005, Joseph et al. 2009, Chandler et al. 2011, Hunt et al. In press). Both Kéry et al. (2005) and Joseph et al. (2009) hypothesized that biased estimates resulted from inappropriate use of the negative binomial distribution in the application of N -mixture models. However, ecological and (or) behavioral mechanisms, related to conspecific density that may have contributed to the biased estimates were not considered. More recently, Hunt et al. (In press) used N -mixture models to estimate abundance of six populations of the Golden-cheeked Warbler, *Setophaga chrysoparia* (GCWA) and concluded that the abundance estimates produced by N -mixture models were biased high and at times were biologically unrealistic in comparison to abundance estimates independently derived from spot mapping. Importantly, the magnitude of the difference between N -mixture model and spot mapping estimates of abundance was significantly greater at lower density study sites (Fig. 1). This systematic, density-associated bias in population estimation using N -mixture models suggests the possibility of a relationship between conspecific density and detectability (r) for these GCWA populations. In the research reported herein we test for

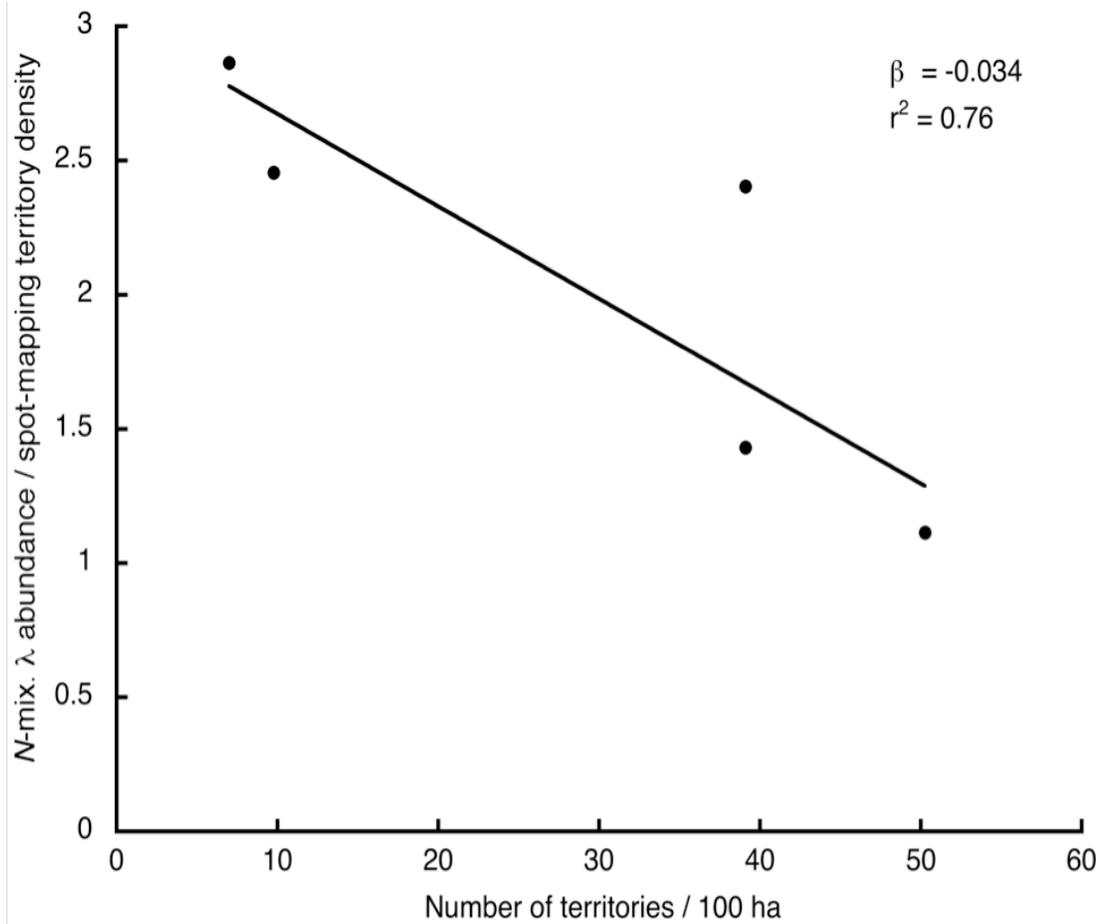


Figure 1. Comparison of abundance estimates in relation to male warbler density. Magnitude of difference between estimated abundance of male Golden-cheeked Warblers at six study sites (two study sites were estimated to have the same abundance) using *N*-mixture models (Hunt et al. In press) and estimates of territory density using spot mapping in 2009 (City of Austin 2010) in relation to territory density.

and examine the ecological and behavioral basis of detection (r) bias in these same populations.

Understanding the relationship between density and detectability (p or r) is facilitated by examination of the components of detection. Marsh and Sinclair (1989) and Johnson (2008) divided detection into elements that affect “perceptibility” versus “availability.” Perceptibility is influenced by factors affecting an observer’s ability to detect an animal, such as habitat attributes (Richards 1981) or weather conditions (Anderson and Ohmart 1977). In contrast, availability is largely determined by the behavior of the animal under study. An animal’s pattern of movement is a key component of availability as an animal must be present at a survey station while an observer is also present to be detected. Factors affecting perceptibility and availability have been investigated and techniques have been proposed to account for variability in many of these factors for selected taxa (summarized by Johnson 2008). However, our understanding of the mechanisms that underlie variation in availability and perceptibility and, importantly, the relationship between these components of detection, detection bias, and density remains underdeveloped for many taxa.

Behaviors linked to conspecific density are likely to affect the availability component of detection for passerine birds (Diel 1981, Bart and Schoultz 1984, Verner 1985). For instance, when present, a relationship between territory size and density (Morse 1976) affects the number of individuals available to be detected at a sample unit. Furthermore, as singing is vital to detection of many passerine species (Ralph et al. 1995), the presence of an individual at a sample unit may not be sufficient for the species or individual to be detected. In this sense availability may also be contingent on

behaviors that advertise presence, such as singing in birds. Thus to the extent that behaviors linked to availability are influenced by conspecific density, variation in density among sample units may lead to a density-detectability bias (Howell et al. 2004, Johnson 2008) in avian surveys. Such behaviors have the potential to bias estimates of density either through over- or underestimation by observers in the field (Howell et al. 2004) or through biased estimates of probability of detection (p or r) (Alldredge et al. 2007b).

Passerine birds are primarily enumerated by sound-based surveys (Mayfield 1981, Ralph et al. 1995). Thus, availability for detection of the species or individuals is dependent on song rate (i.e., the number of songs produced per unit time per individual bird or per survey unit), which translates into the number of opportunities for observers to detect an individual or a species at a sample unit during a point count. Not surprisingly, song rate has been shown to positively influence detection probabilities (p) (Mayfield 1981, Wilson and Bart 1985, McShea and Rappole 1997, Alldredge et al. 2007b) and many passerine species increase singing rates in response to an increase in conspecific density (Penteriani et al. 2002, Sillett et al. 2004, Chelén et al. 2005, Sexton et al. 2007, Laiolo and Tella 2008).

Herein we tested the key assumption of the Royle and Nichols (2003) model—that detection of one animal is independent of the detection of other animals at a sample unit (Royle and Nichols 2003). We also explored the ecological and behavioral basis of the relationship between density estimated both by spot mapping and N -mixture models and detectability of GCWA within the six GCWA populations examined by Hunt et al. (In press). Our goal was to understand the mechanisms behind the systematic bias in the

estimates of abundance for this endangered passerine species produced by N -mixture models.

METHODS

Study system.—We assessed the relationship between conspecific density and probability of detection in natural populations of the Golden-cheeked Warbler (GCWA), *Setophaga chrysoparia*. Conservation concern for this endangered species, endemic to south-central Texas (Pulich 1976) has led to strong interest in reliable population monitoring (City of Austin 1999, Anders and Dearborn 2004, Peak 2007, Watson et al. 2008, Collier et al. 2010, Morrison et al. 2010, Peak 2011, Hunt et al. In press, Weckerly and Ott unpublished). Variation in GCWA density across the study sites examined herein (City of Austin 2010, Hunt et al. In press) and across the species range (Wahl et al. 1990, Morrison et al. 2010) in conjunction with known relationships between song rate and conspecific density in other passerine species (Penteriani et al. 2002, Sillett et al. 2004, Laiolo 2008, Laiolo and Tella 2008) suggests the possibility that singing behavior and hence probability of detection (p or r) may be influenced by conspecific density in the GCWA.

The six study sites at which we examined the singing behavior of the GCWA are distributed throughout the Balcones Canyonlands Preserve (BCP) located in Travis County, Texas, USA. 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 GCWA and other endangered species (City of Austin and Travis County 1996). Descriptions of the six study sites are found in (City of Austin 1999, Hunt et al. In press).

Estimates of density.—We tested the hypothesis that the probability of detection for the GCWA is related to conspecific density using estimates of density independently derived from spot mapping and N -mixture models. The City of Austin (COA) has estimated the density of territorial male GCWAs within a 40.5 ha plot at each of the six study sites from 1998 through 2011 (City of Austin 1999, 2011) using the spot mapping technique (Bibby et al. 1992). In 2009, the season in which we examined the relationship of singing rate and density, COA estimates of territory density ranged from 2.5 to 18 per 40.5 ha across study sites (City of Austin 2010). Because both N -mixture model estimates of abundance and estimates of singing rate were based on a 113 ha grid (see below) we scaled the 40.5 ha spot-mapping estimates of territory number to 113 ha to assess the effect of territory density on song rate and to compare the relationship of singing rate and density among the two density estimation techniques.

N -mixture model estimates of the abundance of GCWAs per study site were estimated by Hunt et al. (In press). In 2008 Hunt et al. (In press) established a 1 km² point-count grid consisting of 36 survey stations equally spaced at 200 m intervals positioned to overlay the COA 40.5 ha spot-mapping plot on each of seven BCP properties (including the six sites examined herein). Detections of GCWAs were restricted to ≤ 100 m from the center of each survey station and thus, accounting for the area sampled on the outside rows of grids, each point-count grid surveyed 113 ha. Point-count surveys ($N = 4$), conducted at approximately weekly intervals, based on a 5 min survey period per survey station provided the data that Hunt et al. (In press) used to estimate the abundance of male GCWA per 113 ha at each study site using N -mixture models (Royle and Nichols 2003). Hunt et al. (In press) showed spot mapping-derived

territory densities to be more biologically realistic in comparison to abundance estimates derived through N -mixture models. Spot mapping has often been used as a standard method of estimating abundance with which to compare other methods (Verner and Ritter 1988, Verner and Milne 1990, Bibby et al. 1992, Buckland 2006, Chandler et al. 2011, Peak 2011, Hunt et al. In press). As such we compared the effect of the N -mixture model-derived abundance estimates and spot mapping-derived territory density estimates on GCWA song rate as a means of further testing the performance of N -mixture models.

The primary assumption of the Royle and Nichols (2003) model assessed here—the detection of one animal is independent of the detection of other animals at a sample unit—relates to the detection of an individual at a given sample unit, i.e. a survey station. Therefore we also compared song rate sampled per survey station to estimated local territory density. Just as at the level of the study site we did this using abundance estimates derived through spot mapping as well as N -mixture models. Using the COA spot mapping data from 2009 we estimated local territory density per survey station as the number of mapped territories overlapping a 100 m detection radius of each survey station. Specific information on the spatial relationships of GCWA territories was available for the subset of survey stations at each study site (range 3 to 6, total $N = 28$) that fell within the 40.5 ha COA spot mapping plot at each study site. This measure approximated the number of singing males available to be detected from each survey station given that Hunt et al. (In press) restricted detections to those made within 100 m. We also reanalyzed the count data collected by Hunt et al. (In press) to produce an estimate of the abundance (λ) of male GCWA per survey station (N_i) at each study site using N -mixture models in PRESENCE 3.1 (MacKenzie et al. 2002, Hines 2006). To do

this we replaced the “study site” λ covariate used by Hunt et al. (In press) to estimate λ per study site with a covariate for “survey station” to estimate λ per survey station. This approach required that individual models be run for each study site. Average λ estimates per survey station per study site obtained in this way were similar to those estimated by Hunt et al. (In press). Estimating local abundance in this way also allowed us to then test the significance of the correlation between λ per survey station and the number of territories that overlapped a 100 m radius of survey stations. A strong correlation may indicate the N -mixture models assessed here adequately estimated abundance of male GCWAs in comparison to spot mapping estimates.

Estimates of song rate.—To record the singing behavior of male GCWAs we deployed “SM1 Song Meter” autonomous recording units (ARU) (Wildlife Acoustics, Inc) at each of 14 randomly selected survey stations within each of the six 1 km² point-count grids established by Hunt et al. (In press). We had no previous knowledge of spot-mapping estimates of territory density at the level of the study site or survey station prior to placement of ARUs at survey stations. Therefore “blind” selection of the survey stations at which ARUs were positioned and the data subsequently collected mimics the random selection of survey stations and the data produced by point count surveys. Recordings were collected from 15 March through 3 May 2009 corresponding to the GCWA breeding season. 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 one-minute pause between recordings from approximate sunrise to approximate sunset (≈ 14 hrs/day) for two consecutive days. The 5 min recording intervals corresponded to the 5 min survey interval typically used in passerine point-count surveys

(Lynch 1995, Ralph and Droege 1995, Watson et al. 2008) and concurrently used at these same study sites and survey stations by Hunt et al. (In press). “Song Scope” software (Wildlife Acoustics, Inc.) provided a sonogram of avian vocalizations that was inspected to verify and count GCWA songs. This procedure provided an accurate, time-stamped record of GCWA vocalizations within the detection radius (see below) of the ARU at each survey station throughout each day during the seven-week study season.

For both Hunt et al. (In press) and this study we considered a song to be a discrete vocalization typically no longer than two seconds in duration. Two measures of song rate per survey station were computed based on the ARU recordings: the average number of individual songs per 5 min survey interval and the proportion of 5 min survey intervals containing ≥ 1 song. Importantly, the ARUs recorded the total number of songs produced by all male GCWAs vocalizing within the detection radius of each ARU. While recordings often distinctly showed that at least two males were singing at a survey station, individual songs could not be attributed to specific males. As a result, the total number of males contributing to the recordings at each station cannot be known due to the nature of the method. Thus to examine the relationship between song rate and warbler density, we measured song rate as the total number of songs available to a surveyor to detect the species or an individual at a survey station. We combined “A”- and “B”-type songs (Pulich 1976, Bolsinger 2000, Leonard et al. 2010) to estimate both measures of song rate since preliminary analyses found no difference in the ability of ARUs to detect A- and B-songs as a function of distance and no relationship between the density of GCWA and the ratio of A- and B-songs (Warren and Ott unpublished). Across all sites 8% of 5 min recordings were excluded due to weather exceeding USFWS survey

parameters (City of Austin 1999) or non-GCWA zoogenic or anthropogenic noise. After excluding these recordings we analyzed an average of 3,188 5 min samples from a minimum of 13 survey stations per study site. In total we analyzed 19,127 5 min samples across all survey stations and study sites.

Detection radii of ARUs.—The estimates of abundance computed at the level of the study site presented in Hunt et al. (In press) and the estimates of abundance computed at the level of the survey station within each study site developed here (see above) used only those aural detections of GCWA estimated by human observers to have been within 100 m from the center of each survey station. As the tests of hypotheses we conducted here involved variables based on the data gathered by human observers (Hunt et al. In press) and the ARUs employed in the current study, we estimated the detection radius of each ARU in a preliminary study to determine whether the area sampled per survey station was comparable between humans and ARUs. To estimate the maximum detection distance and verify consistency of ARUs we suspended the six ARUs side by side 1.5 m above the ground in an open field. We then played a one-minute recording of A- and B-songs calibrated to 55 dB at 6 m for both song types (the average volume of ten male GCWA singing in the wild on BCP properties at an average of 6 m) in calm weather conditions at distances of 5, 10, 30, 50, 75, 100, and 150 m. Based on inspection of sonograms both 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 data collected by ARUs were comparable with data collected by human observers (figure 2 in Hunt et al. 2011). We found no variation among ARUs in their ability to detect GCWA songs.

Study site-level warbler density and song rate.—Song rate data were collected per survey station, thus there were two ways in which the mean song rate per study site could be calculated; using data from all recorded survey stations and using only recorded survey stations wherein ≥ 1 GCWA song was recorded. Preliminary analysis showed that the relationship between mean song rate and territory density per study site did not differ between the two methods of calculating song rate thus we present results for all analyses using all recorded stations. To determine if significant variation existed in the song rate (the mean number of songs per 5 min and the proportion of 5 min recordings with ≥ 1 song) among study sites we used an ANOVA.

To test the hypothesis that average conspecific density assessed at the level of the study site influences song rate we first regressed the mean number of songs recorded per 5 min period on estimates of territory density per study site produced by spot mapping by means of linear mixed effects regression. Five linear mixed effects models were assessed (Table 1). Covariates included territory density, day of season, time of day (linear) and time of day (quadratic). Day of season and time of day were included as covariates to account for the possible confounding effect of these temporal factors. We assessed the full model as well as reduced models that included territory density and one of each temporal covariate.

We next tested the hypothesis that territory density per study site influences singing rate using the proportion of 5 min with ≥ 1 song as the response variable. We again used linear mixed effects regression and assessed two models wherein the full model included covariates for territory density and day of season and the reduced model included only territory density as a covariate. All models included study site as a random blocking

factor to account for unspecified site effects. Models were evaluated using the information-theoretical approach (Akaike 1973), with Akaike Information Criterion corrected for small sample size (AIC_c) (Sugiura 1978). We then regressed both measures of song rate on the estimates of density per study site produced by N -mixture models (Hunt et al. In press). We did not repeat the AIC analysis investigating the potential role of temporal factors using the N -mixture model derived estimates of density because these estimates are known to be biased. In addition, we found the estimate of abundance for one study site to be particularly erroneous. Therefore, we assessed the effect of N -mixture model-derived density on song rate both with and without the outlier site estimate.

Survey station-level warbler density and song rate.—To test the hypothesis that variation in the estimated density of male GCWAs per survey station influenced song rate we first regressed both the mean number of songs per 5 min and the proportion of 5 min recordings with ≥ 1 song recorded per survey station on the number of territories estimated to overlap each survey station. We then repeated this analysis using the estimates of density per survey station produced using N -mixture models calculated in the present study. Data were pooled across all study sites for this analysis.

An increase in the number of songs available to be detected at a survey station in response to an increase in local territory density per survey station alone does not indicate an effect of density on the detection of an individual at a sample unit. A significant effect of local territory density, either positive or negative, on average song rate per unit male GCWA, on the other hand, would indicate an effect of density on singing rate at the individual level. Thus we also conducted a test of the hypothesis that the detection of

individual male GCWAs at a survey station is dependent on the number of territories overlapping the detection radius of a survey station. To test this hypothesis we used linear regression to test for an effect of local territory density on the average song rate (both measures) divided by the number of territorial males with a 100 m radius of each survey station. This analysis was repeated using the N -mixture model-derived estimates of abundance (λ) per survey station. All analyses were conducted in R 2.9.2 (R

Development Core Team 2009

RESULTS

Variation in song rate.—Male GCWAs were detected by ARUs at all sampled survey stations sampled at three of the six study sites and at 76%, 85%, and 92% of survey stations at the other three study sites. The two study sites with the fewest number of stations at which the species was recorded also had the lowest estimated territory densities. Both the mean number of songs per 5 min ($F = 5.98$, $p < 0.001$) and the proportion of 5 min intervals with ≥ 1 song ($F = 11.997$, $p < 0.001$) varied significantly between study sites. The percent of 5 min intervals with ≥ 1 song per survey station at the study site with the lowest territory density (7 territories / 113 ha) ranged from 0.8% to 32% with a mean of 8.8% across all survey stations. This contrasts to the study site with the highest territory density (50 territories / 113 ha) where the percent of 5 min intervals with ≥ 1 song per survey station ranged from 12% to 80% with a mean of 51% across all survey stations. We recorded an average of 0.49 (± 0.17 SE) songs per 5 min at the study site with the lowest estimated territory density. In contrast at the highest density study site an average of 7.51 (± 1.8 SE) songs were detected per 5 min.

Study site-level warbler density and song rate.—The model assessing the mean number of songs detected per 5 min at each survey station as the dependent variable including territory density per study site and time of day (quadratic) was selected based on the lowest AIC_C value (Table 1). We also found a significant interaction between

Table 1. Test for a relationship between conspecific density, time of day, date and song rate using model selection of linear mixed effects models. Model selection statistics shown are Akaike Information Criterion corrected for small sample size (AIC_c), AIC_c weight (W), number of parameters (N.par) and twice the log likelihood (-2LL). Variables included territory density (Density), time of day (linear) (Time), time of day (quadratic) ($Time^2$), and date. Selected models are presented in bold.

Model	AIC_c	W	N.par	-2LL
<i>Mean number of songs / 5-min</i>				
Density X Time²	12253.71	0.53	6	12241.67
Density X Time	12260.28	0.38	6	12248.23
Density X Date	12290.87	0.08	6	12278.83
Density X Date X Time X Time ²	12345.05	< 0.001	18	12308.67
Density	12387.39	< 0.001	4	12379.37
<i>Proportion of 5-min with ≥ 1 song</i>				
Density X Date	-31.44845	0.73	4	-39.71
Density	-11.46926	0.37	6	-24.02

territory density and time of day (quadratic) on the mean number of songs detected per 5 min per survey station ($t = -6.98$, $p < 0.0001$). The mean number of songs detected per 5 min per survey station was greatest at higher territory density study sites at or near sunrise at all study sites. The effect of territory density on the mean number of songs detected per 5 min was greater later in the day. The selected model assessing the proportion of 5 min intervals with ≥ 1 song (included covariates for territory density and day of season) (Table 1) revealed a significant interaction between the effect of territory density and day of season ($t = -2.5$, $p = 0.013$) indicating that the effect of territory density was not uniform throughout the season and was greatest later in the season. The proportion of 5 min intervals with ≥ 1 song was greatest at higher territory density study sites early in the season at all study sites.

We found a significant effect of N -mixture model-derived abundance on the mean number of songs per 5 min per study site both with ($t = 9.99$, $p < 0.001$) and without the outlier site estimate ($t = 16.49$, $p < 0.001$) (Fig. 2 A). We also found a significant effect of N -mixture model-derived abundance on the proportion of 5 min intervals with ≥ 1 song per study site both with ($t = 6.52$, $p < 0.001$) and without the outlier site estimate ($t = 10.44$, $p < 0.001$) (Fig. 2 B). The relationship between song rate and territory density estimated by spot mapping was similar to that of song rate and N -mixture model-derived abundance only when the outlier site estimate was removed.

Survey station-level warbler density and song rate.—As expected both the mean number of songs detected per 5 min per survey station ($t = 8.72$, $p < 0.001$) and the

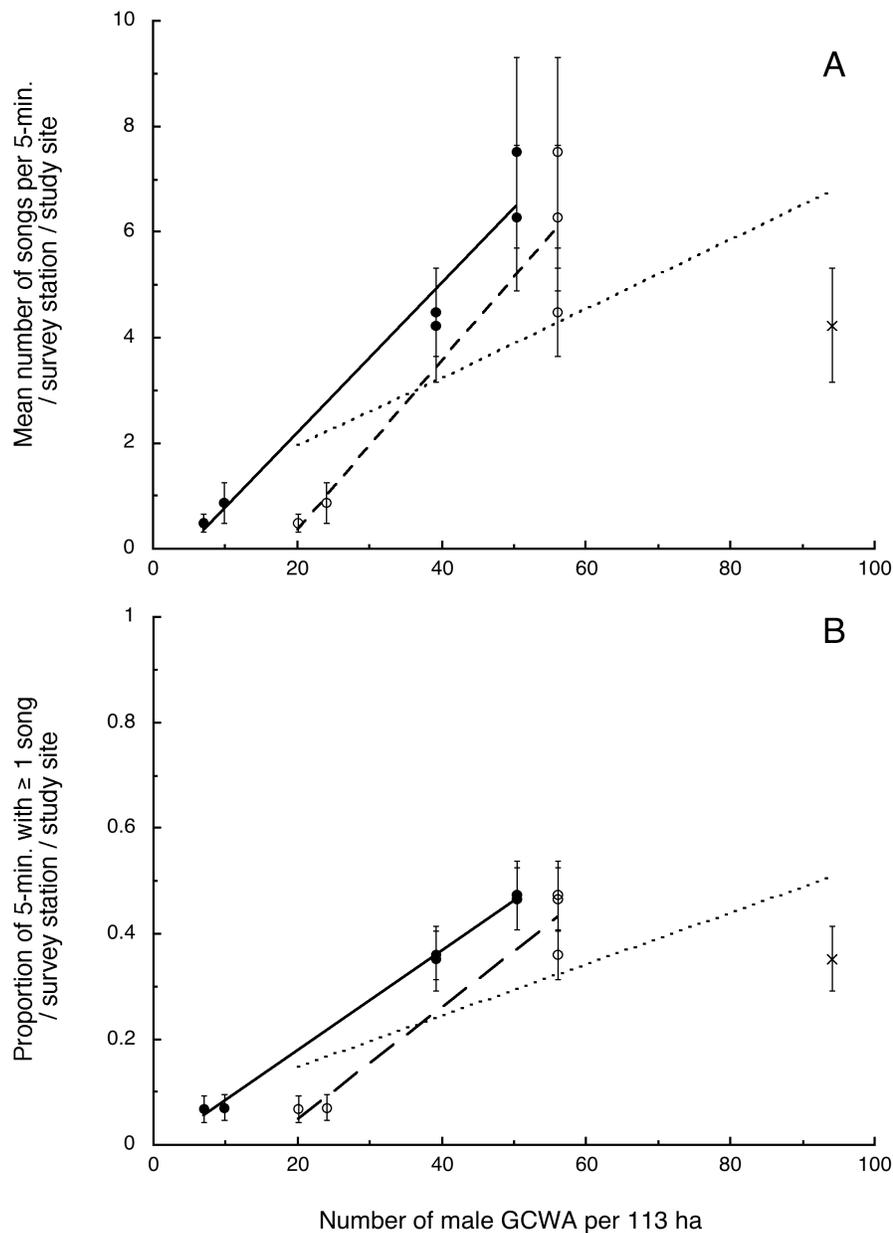


Figure 2. Mean song rate per survey station in relation to the number of male warblers per study site. Relationship of the (A) mean number of songs per 5 min (\pm SE) and the number of male GCWA per 113 ha and (B) the proportion of 5 min survey intervals with ≥ 1 song and the number of male GCWA per 113 ha. Song rate estimates based on a minimum of 2,874 5 min surveys across ≥ 13 survey stations per study site. Closed circles and solid line indicate mean song rate as a function of territory density estimated by spot mapping: [(A) $\beta = 0.142$, $r^2 = 0.96$; (B) $\beta = 0.0095$, $r^2 = 0.99$]. Open circles indicate mean song rate as a function of estimated abundance derived through N -mixture models (Hunt et al. In press). The 'x' value indicates song rate at an erroneous N -mixture model-derived estimated abundance at a single study site. The dashed line indicates the slope of mean song rate versus N -mixture model-derived estimated abundance without the erroneous site estimate [(A) $\beta = 0.159$, $r^2 = 0.88$; (B) $\beta = 0.011$, $r^2 = 0.95$], while the stippled line indicates the slope with all estimates of abundance per study site [(A) $\beta = 0.065$, $r^2 = 0.38$; (B) $\beta = 0.005$, $r^2 = 0.51$].

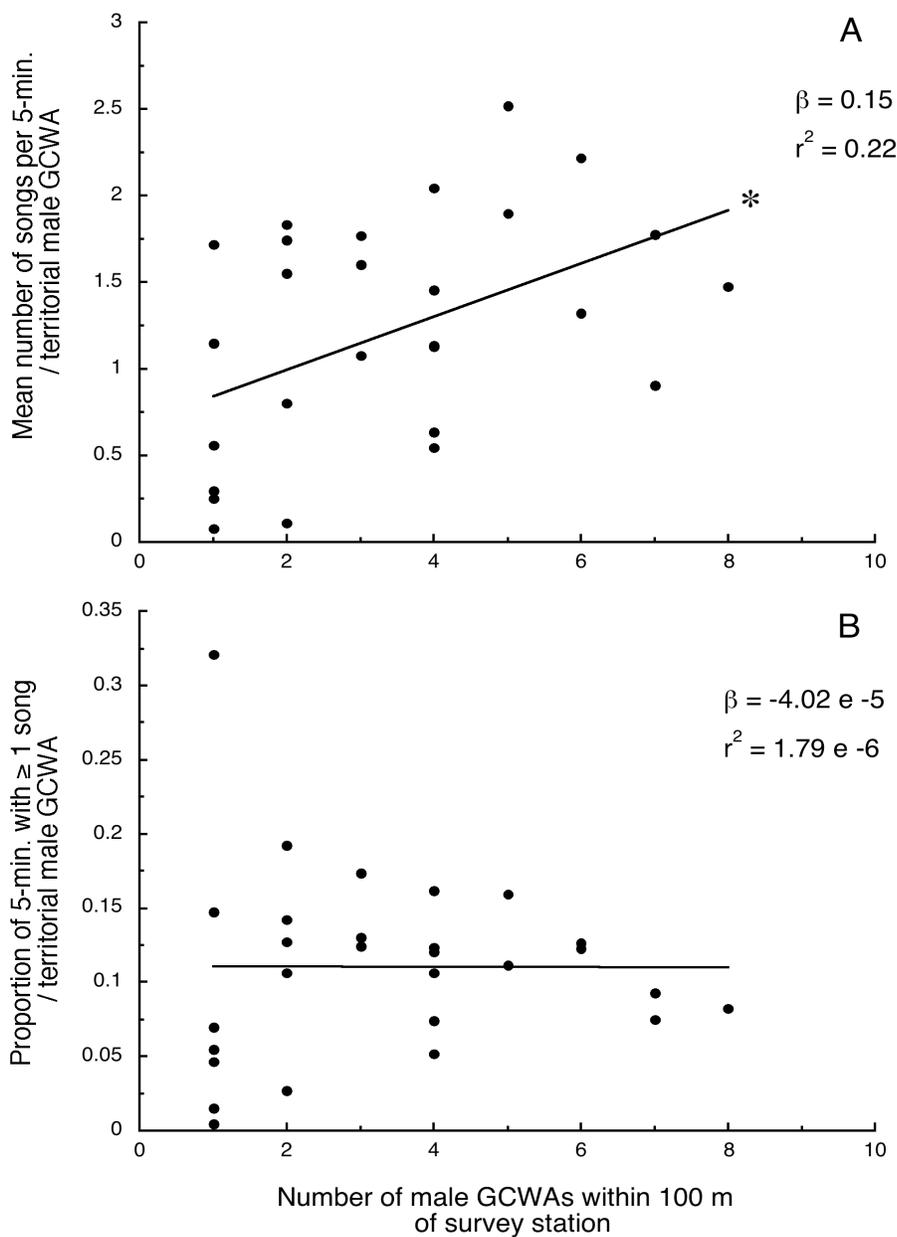


Figure 3. Mean song rate per male GCWA in relation to the number of spot mapped male warblers per survey station. Relationship between the mean number of songs per 5 min (\pm SE) / territorial male GCWA and the number of territories estimated through spot mapping to be within 100 m of each survey station (A) and (B) as the proportion of 5 min surveys intervals with ≥ 1 song / territorial male GCWA and the number of territories within 100 m of a survey station. An asterisk indicates a significant slope.

proportion of 5 min with ≥ 1 song per survey station ($t = 7.81$, $p < 0.001$) significantly increased with increasing number of territories within a 100 m radius of a survey station. Importantly, we found a significant effect of local territory density on the mean number of songs detected per 5 min per unit male ($t = 2.68$, $p = 0.013$) (Fig. 3 A). However, we did not find an effect of local density on the proportion of 5 min with ≥ 1 song per unit male ($t = -0.01$, $p = 0.995$) (Fig. 3 B).

Similarly, the mean number of songs detected per 5 min per survey station ($t = 5.97$, $p < 0.001$) and the proportion of 5 min with ≥ 1 song per survey station ($t = 6.59$, $p < 0.001$) significantly increased with increasing estimated λ (derived through N -mixture models) per survey station. Similar to the results found using local territory density as the independent variable, we also found a significant effect of estimated λ on the mean number of songs detected per 5 min per unit male ($t = 2.08$, $p = 0.041$) (Fig. 4 A) but no effect of estimated λ on the proportion of 5 min with ≥ 1 song per unit male ($t = 0.965$, $p = 0.338$) (Fig. 4 B).

Territory density and λ per survey station.—A comparison of the number of territories within 100 m and estimated λ per survey station revealed only a moderate correlation ($r = 0.398$) (Fig. 5). Further inspection of these data reveal that λ was underestimated at most survey stations in comparison to local territory density estimated through spot-mapping (indicated by values below the 1:1 line in Fig. 5). Interestingly, survey stations that were overestimated (indicated by values above the 1:1 line in Fig. 5) were limited to survey stations with less than four territories within 100 m.

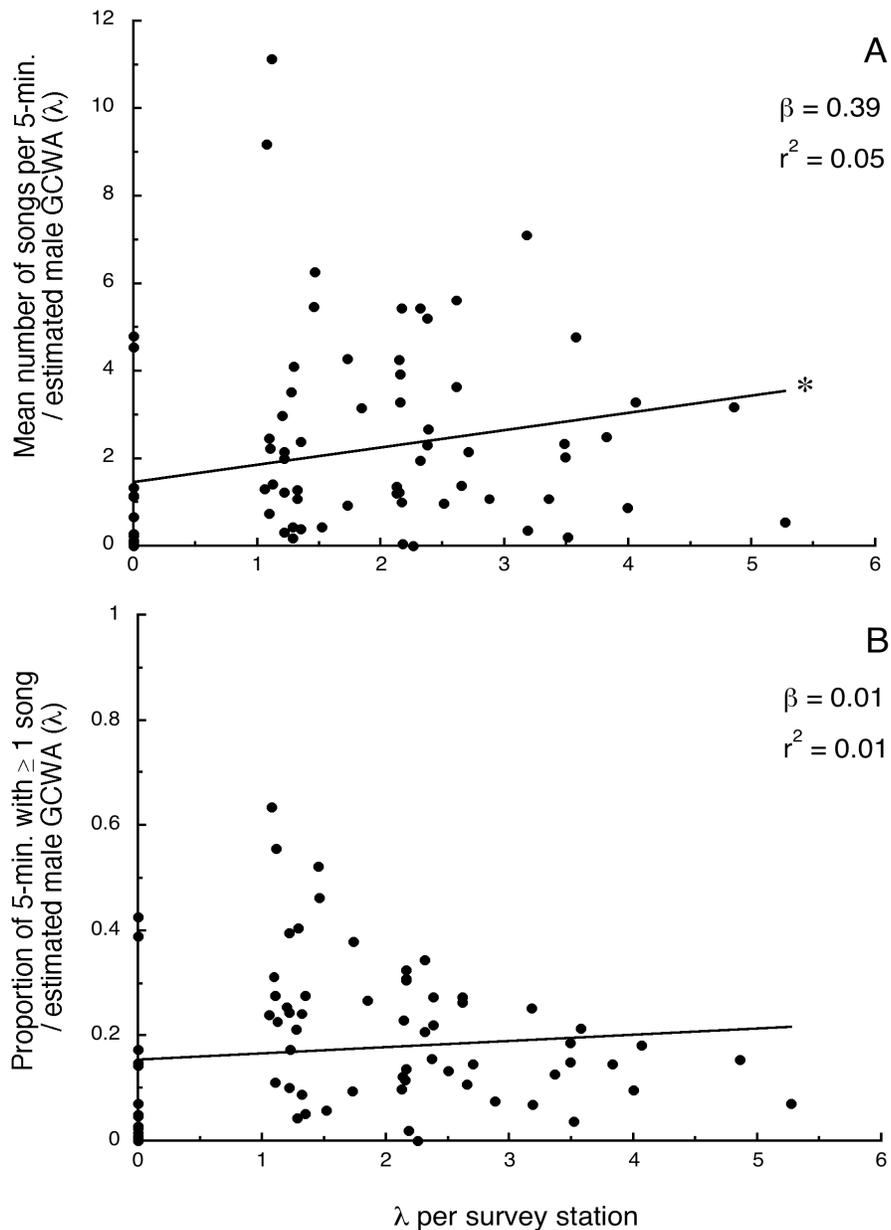


Figure 4. Mean song rate per male GCWA (λ) in relation to the number of estimated male warblers per survey station (λ). Relationship between the mean number of songs per 5 min (\pm SE) / estimated male GCWA (λ) (A) and (B) the proportion of 5 min recording intervals with ≥ 1 song / estimated male GCWA (λ) and estimated λ per survey station. Survey stations with estimated an $\lambda = 0$ and a $y > 0$ were possible because λ was estimated from four 5 min point counts (Hunt et al. In press) while song rate data estimated by extensive ARU sampling. An asterisk indicates a significant slope.

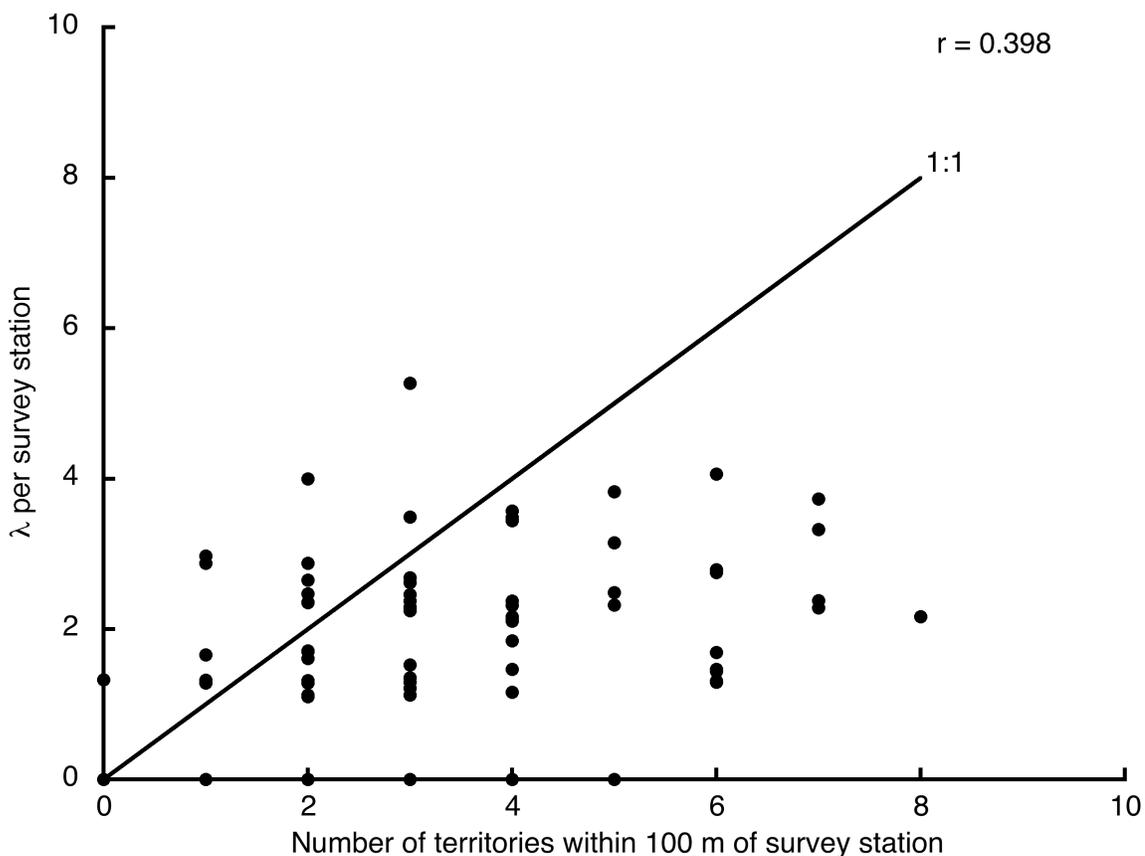


Figure 5. Correlation between estimated λ per survey station (using point count data from Hunt et al. In press) and the number of territories within 100 m of a survey station. ($r = 0.398$) Values above 1:1 slope (solid line) represent survey stations whose abundance (λ) was overestimated by N -mixture models while those below the line represent survey station underestimated by N -mixture models. Survey stations with a y-value = 0 and an x-value > 0 represent stations estimated to be absent by N -mixture models but within the detection radius of more than one male territory.

DISCUSSION

Since most detections of passerine birds are by sound during point count surveys (Ralph et al. 1995) song rate represents the number of opportunities available to detect a species of interest or an individual of the species at survey stations within a survey period (Alldredge et al. 2007b, Johnson 2008). We recorded the singing of all male GCWAs within the detection radius (max. < 100 m) of 80 survey stations distributed across six study populations that varied dramatically in the number of territorial males per hectare. We then asked if the song rate component of detectability is influenced by conspecific density in the GCWA. A significant effect of territory density per study site on song rate would indicate that territory density has an effect on the detection availability of this species. The results presented here indicate that indeed higher territory densities yield higher song rates at survey stations. However, an increase in the number of songs recorded per survey station is the expected outcome of an increase in the number of males at each survey station or study site. This pattern illustrates one obvious way in which territory density may influence the detection of the GCWA at the species level. This result indicates that the probability of detecting the species at a survey station is not independent of conspecific density. This adds to the growing body of evidence highlighting the need for accounting for imperfect detection when estimating abundance of passerines.

Because we designed our sampling scheme to mimic the standard 5 min point count survey interval we had the opportunity to inspect the true availability of a single species

to be detected audibly in all potential survey intervals across two days at a number of survey stations. Both measures of song rate considered here were influenced by territory density but may relate to detection availability in point count surveys differently. Given that a 5 min survey interval is standard among point count surveys for passerines (Ralph et al. 1995), the proportion of 5 min intervals with ≥ 1 song can be thought of as the availability of the species to be detected audibly using the standard survey interval throughout a day. Our results indicate that, as expected, the availability of the species to be recorded as present at a survey station during any given survey interval increases as conspecific density increases. At the study site with the lowest estimated territory density only 9% of 5 min intervals contained ≥ 1 GCWA song. This translates to the species being available to be detected on average during only 9 out of every 100 potential survey intervals. This provides a stark contrast to this same measure of song rate at the highest density study site where the species was available to be detected on average during 50% of potential survey intervals. Intriguingly the increase in the proportion of 5 min intervals with ≥ 1 song with territory density found here ($\beta = 0.008$) is similar to the increase in detection probabilities of the species with increasing abundance found by Hunt et al. (In press) ($\beta = 0.012$) during the same time period based on five-minute surveys per survey station sampled four times per season.

While the proportion of 5 min with ≥ 1 song may be considered the detection availability of the species in survey intervals throughout the day, the mean number of songs per 5 min may be considered the detection availability of the species within an average survey interval. Certainly, an average rate of ≥ 1 song per 5 min indicates that an observer has the opportunity to detect the species (i.e. available) during a survey interval

subject to perceptibility (i.e. the observer recognizes and records the species). Given imperfect detection perceptibility, e.g. observers may not always detect a species from a single opportunity (e.g. one song), an increase in the number of detection opportunities per survey interval, as shown here, likely would result in increased probability of detection (Mayfield 1981, Wilson and Bart 1985, McShea and Rappole 1997, Alldredge et al. 2007b). We recorded an average of less than one song per 5 min at the two study sites with lowest estimated territory densities. Thus, at these low-density study sites less than one song is available to be detected within an average survey interval. In contrast, higher density study sites yielded averages greater than four songs per 5 min indicating that the detection availability of the species may be more than four times greater within an average survey interval at these higher density study sites.

Higher song rates recorded per survey station in response to an increase in conspecific density alone do not indicate bias in detection of the individual within the model framework of OBMs. Bias in detection of individuals as a function of density would only come from a violation of one of the two implicit assumptions of OBMs; (1) all individuals are equally detectable and (2) the detection of one individual is independent of other individuals. In this study we examined the relationship between the number of GCWA territories overlapping a 100 m radius of a survey station (hereafter local territory density) and song rate measured as the mean number of songs per 5 min and the proportion of 5 min intervals with ≥ 1 song as a means of assessing the relative detection availability of the individual per survey station. We tested the hypothesis that if conspecific density affects the singing of individual male GCWAs we would see a significant effect of local territory density on the average song rate per unit bird (song

rate per survey station / local territory density). By selecting those 28 survey stations across the six study sites for which we had independent estimates of territory maps we formed a pool of 28 observations that allowed us to test this hypothesis with two measures of song rate. We found no effect of local territory density on the proportion of 5 min intervals with ≥ 1 song per unit bird. However, our results also indicated that the number of songs recorded per 5 min was significantly affected by local territory density. This provides indirect evidence that males contributed a greater number of songs to the mean captured by ARUs in response to increased local territory density. If so, the detection availability of individuals, as measured by the number of songs each male exhibits per 5 min, may not be independent of the detection of other individuals violating one of the implicit assumptions of OBMs. A violation of this assumption may lead to biased estimates of abundance as in Hunt et al. (In press). This is particularly troubling for species of concern such as the GCWA.

As a further test of the assumptions of OBMs we compared N -mixture model estimated abundance per survey station (λ) to the number territories within 100 m of a survey station, which we treat as a record of the number of known individuals (at some point within the breeding season) within the detection radius of a survey station. The fact that the correlation between estimated λ and the number of surrounding territories per survey station was weak ($r = 0.398$) appears to be largely the result of a systematic underestimation of abundance per survey station by N -mixture models (Fig. 5). Interestingly, the only survey stations whose abundance was overestimated were survey stations with few surrounding territories (i.e. 1-3). Such stations also fall primarily within low-density study sites and overestimation at the survey station level may translate to

overestimation per study site. Thus, it is possible that the systematic density associated bias at the population level shown in Figure 1 is the result of overestimation at low-densities as well as underestimation at high-densities.

We also assessed the effect of local density (per survey station) on song rate using estimated λ per survey station to further investigate the performance of N -mixture models in relation to spot mapping. Using the number of territories surrounding survey stations we saw that the detection of individuals is not independent of conspecific density as evidenced by a significant effect of local territory density on the mean number of songs per 5 min per unit bird. If N -mixture models produced unbiased estimates of abundance one would predict that the effect of λ per survey station on song rate would be similar to that of local territory density on song rate. Somewhat surprisingly, we found the same pattern using λ per survey station as the dependent variable as we found using local territory density as the dependent variable in that we saw a significant effect of local density on the mean number of songs per 5 min per unit bird but no effect on the proportion of 5 min intervals with ≥ 1 song per unit bird. In this respect, though the N -mixture model-derived estimates of abundance may be biased high, the model appears to perform adequately.

Our primary conclusion that detection availability of male GCWAs by song is dependent on conspecific density is in part dependent on both the accuracy of the COA (2009) territory density estimates and assumptions inherent in scaling territory density estimates up to 113 ha. The COA enumerates the number of territories per 40.5 ha but in order to make these estimates comparable to the ARU data and Hunt et al. (In press) abundance estimates collected within 1 km² grids we scaled up these estimates to 113 ha.

This assumes that the GCWA densities were homogenous within the 113 ha area subsuming each 40.5 ha plot. The COA selected the tracts for the placement of 40.5 ha plots in part because they represented some of the best habitat for GCWA (City of Austin 1999). In some cases the habitat immediately surrounding the COA spot-mapping plots is very similar to the habitat within, while others are surrounded by less suitable GCWA habitat.

Using the mean song rate across each study site to estimate detection availability per study site assumes that GCWA males are homogeneously distributed and that singing rate is homogenous across survey stations within each study site. However, low-density sites may support a limited number of birds due to a limited amount of suitable habitat that may also be heterogeneously distributed throughout a site. Such patchiness of suitable habitat may mean that the biologically relevant area sampled for the GCWA may not have been homogenous across study sites. To account for this we also examined the relationship between conspecific density and GCWA singing excluding data from stations that did not record any GCWA songs during the two-day recording period. Stations excluded on this basis, with one exception, were only within the two lowest density study sites. Excluding these survey stations ensured that stations placed in areas unoccupied by GCWAs did not bias estimates of average song rate per study site, particularly at low densities. However, excluding these survey stations did not alter the relationship between mean song rate and territory density appreciably thus we chose to present only the results of analyses including all recorded stations. In addition, though each of the six study sites was adequately sampled to estimate song rate, estimates of rate for only six study sites meant we could not reasonably assess potential nonlinear effects

in a regression of song rate versus territory density at the level of the study site. However, the range of territory density estimates among the study sites recorded in the current study represents the range of densities available within the BCP and these estimates are of wild populations.

Part of using ARUs in this capacity is that one cannot know if a bird was present at a station and not vocalizing or if was simply not present. Thus, the observed effect of territory density on the song rate found here could be explained by the singing behavior, average movements, singing, or combination of these behaviors at the level of each individual male GCWA. In a territorial bird the probability that an individual at a survey station is detected may be a function of the proportion of their territory that overlaps with the detection radius of a survey station in addition to their rate of singing. Thus the assumption that all individuals are equally detectable from a survey station may be violated if heterogeneity exists in the area that individual territories overlap the detection radius of a survey station. The assumption that the detection of individuals is independent of that of other individuals may be violated if the number of other males present at a survey station affects the singing behavior of other individuals. Moreover, the number of neighboring territorial males has been shown to affect individual male song rate in several passerines species (Chelén et al. 2005, Sexton et al. 2007, Laiolo et al. 2008) including one species of wood warbler (Silleet et al. 2004).

Because one of the main functions of passerine song is territorial defense (Morton 1977, Catchpole 1981, Searcy and Andersson 1986) an increase in the density of neighboring males may result in an increase in the rate of singing of individual males. However, the singing behavior of individual males alone may not explain the effect of

territory density on song rate per survey station. In territorial wood warblers, like the GCWA, resource availability or defensibility may limit the size of breeding territories or home ranges (Smith and Schulgart 1987, Anich et al. 2010). In this way conspecific density may influence the size of breeding territories (Morse 1976). By measuring the mean maximum distance between any two spot mapped observations per male estimated by the COA (2009) as a measure of territory size we found that territory size is negatively (albeit weakly) influenced by density ($t = -3.6$, $p < 0.001$, $r^2 = 0.12$), as has been seen in other wood warblers (Morse 1976). Thus, males in lower density areas may have larger territories and may spend less time on average at any given point within his territory, such as within the detection radius of a survey station. This effect could potentially translate to decreased song rates recorded per survey station and therefore lower detection availability of the species or of an individual at lower densities even without an effect of conspecific density on individual male song rate. We propose two, non-mutually exclusive hypotheses to explain the effect of territory density we observed on song rate. (1) An increase in the number of neighboring territorial males increases the stimulus for singing at the level of each individual male. (2) An increase in territory density results in smaller territories that overlap to a greater extent resulting in an increase in the potential for an observer to be within the detection radius of multiple individual males. These hypotheses are the focus of on-going research.

In conclusion, this study was designed to mimic the typical survey interval used in point count surveys for passerines (Ralph et al. 1995) with the main difference being that, through the use of ARUs, we expanded the survey effort to include all potential survey intervals throughout a day (130 5 min intervals / day). We then replicated this effort for

two days at each of 80 point count survey stations within six study sites known to vary in GCWA territory densities. This allowed us to examine the relationship between actual detection availability, as measured by song rate, and conspecific density. As expected we found a significant positive effect of territory density on song rate indicating that the detection availability of the species is influenced by density and underlining the need for abundance estimators that account for imperfect detection. Further, by looking at average song rate per unit bird as it relates to territory density we found indirect evidence that the detection availability of individual male GCWAs may be influenced by conspecific density. This violates the implicit assumption of OBMs that the detection of one individual is independent of the detection of other individuals at a sample unit. As such this study illustrates how the behavior of a territorial passerine may violate model assumptions and potentially lead to biased estimates of abundance. With this study we focused on a general issue with the N -mixture model using a particular case study focused on a single passerine species. However, the GCWA is certainly not alone in its territorial nature nor are the methods of detecting the species (by song) unique. Thus, the results of this study are likely to translate to other passerine species, particularly other wood warblers. Model-based abundance estimators, like the N -mixture model, that correct for imperfect detection are powerful tools that will continue to play a part in improving our ability to efficiently and accurately estimate population size. Nonetheless we urge careful attention to model assumptions particularly in relation to the biology and behavior of the species of interest.

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