



Research Article

# Occupancy and Abundance of Wintering Birds in a Dynamic Agricultural Landscape

MARK W. MILLER,<sup>1,2</sup> *Everglades Research and Education Center, University of Florida, 3200 E. Palm Beach Rd., Belle Glade, FL 33430, USA*  
 ELISE V. PEARLSTINE, *Everglades Research and Education Center, University of Florida, 3200 E. Palm Beach Rd., Belle Glade, FL 33430, USA*  
 ROBERT M. DORAZIO, *Southeast Ecological Science Center, U.S. Geological Survey and Department of Statistics, University of Florida, Gainesville, FL 32611-0339, USA*  
 FRANK J. MAZZOTTI, *Fort Lauderdale Research and Education Center, University of Florida, 3205 College Avenue, Fort Lauderdale, FL 33314-7799, USA*

**ABSTRACT** Assessing wildlife management action requires monitoring populations, and abundance often is the parameter monitored. Recent methodological advances have enabled estimation of mean abundance within a habitat using presence–absence or count data obtained via repeated visits to a sample of sites. These methods assume populations are closed and intuitively assume habitats within sites change little during a field season. However, many habitats are highly variable over short periods. We developed a variation of existing occupancy and abundance models that allows for extreme spatio-temporal differences in habitat, and resulting changes in wildlife abundance, among sites and among visits to a site within a field season. We conducted our study in sugarcane habitat within the Everglades Agricultural Area southeast of Lake Okeechobee in south Florida. We counted wintering birds, primarily passerines, within 245 sites usually 5 times at each site during December 2006–March 2007. We estimated occupancy and mean abundance of birds in 6 vegetation states during the sugarcane harvest and allowed these parameters to vary temporally or spatially within a vegetation state. Occupancy and mean abundance of the common yellowthroat (*Geothlypis trichas*) was affected by structure of sugarcane and uncultivated edge vegetation (occupancy = 1.00 [95% CĪ = 0.96–1.00] and mean abundance = 7.9 [95% CĪ = 3.2–19.5] in tall sugarcane with tall edge vegetation versus 0.20 [95% CĪ = 0.04–0.71] and 0.22 [95% CĪ = 0.04–1.2], respectively, in short sugarcane with short edge vegetation in one half of the study area). Occupancy and mean abundance of palm warblers (*Dendroica palmarum*) were constant (occupancy = 1.00, 95% CĪ = 0.69–1.00; mean abundance = 18, 95% CĪ = 1–270). Our model may enable wildlife managers to assess rigorously effects of future edge habitat management on avian distribution and abundance within agricultural landscapes during winter or the breeding season. The model may also help wildlife managers make similar management decisions involving other dynamic habitats such as wetlands, prairies, and even forested areas if forest management or fires occur during the field season. © 2011 The Wildlife Society.

**KEY WORDS** common yellowthroat, edge effects, Everglades Agricultural Area, palm warbler, point counts, site occupancy, sugarcane.

Statistical techniques developed within the last decade have enabled estimation of site occupancy and wildlife abundance using presence–absence or count data obtained via repeated visits to a sample of sites (MacKenzie et al. 2002, 2006; Royle and Nichols 2003, Royle 2004, Royle and Dorazio 2008). These methods usually assume that populations are demographically and geographically closed, meaning that animals do not give birth, die, emigrate from, or immigrate into study sites between visits during a field season, although some recent techniques allow for movement in or out of a site (Nichols et al. 2008, Rota et al. 2009). The closure assumption intuitively implies that habitat does not change sub-

stantially within a site during the field season or that wildlife abundance is independent of habitat. Existing occupancy models can readily handle the scenario in which habitat changes among seasons or concurrently in all sites within a season. However, many habitats are highly variable spatially and temporally over short periods. Such habitats include inland wetlands where water level can vary seasonally and within a season (Mitsch and Gosselink 1986). Prairie, wetland, shrubland, savannah, and forest vegetation also can be highly dynamic as a result of natural fires or controlled burns (Whelan 1995). Estimating wildlife population size in a rapidly changing ecological system ideally should account for changes in habitat at each sample area.

Agricultural lands are one example of a dynamic habitat, changing extensively over a short period as a result of cultivation and harvest activities. These landscapes are, or have the potential to be, important wildlife habitat. Agricultural intensification may be responsible for population declines of

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<sup>1</sup>E-mail: mark\_wayne\_miller@yahoo.com

<sup>2</sup>Present Address: 2006 NW 55th Avenue, G-8, Gainesville, FL 32653, USA.

many grassland and farmland bird species in North America and in Europe (Bethke and Nudds 1995, Krebs et al. 1999, Donald et al. 2001, Peterjohn 2003, Askins et al. 2007). Conversely, populations of these bird species may increase when agricultural areas are managed in a way that benefits wildlife, for example, through set-aside programs such as the United States Conservation Reserve Program (Best et al. 1997, Reynolds et al. 2006, Herkert 2007, Niemuth et al. 2007).

Uncultivated vegetation along field edges may provide nesting areas, refugia, and movement corridors for wildlife, as well as reduce soil erosion and associated runoff of fertilizers and pesticides (Best 1983, Marshall and Moonen 2002, Vickery et al. 2002). As such, management of field margins and other practices associated with agri-environment schemes may benefit birds and farmers, although documented success of such cases is limited (Vickery et al. 2004). Future evaluation of habitat management efforts in agricultural environments should benefit from a model that accounts for extreme spatio-temporal variation in vegetation.

Some species may follow an ideal free distribution (Fretwell and Lucas 1969, Fretwell 1972). Such species may be distributed across the landscape in proportion to availability of their preferred habitat. Other species may follow a despotic distribution in which territorial behavior by individuals in preferred habitat excludes others. The ideal free distribution predicts species that prefer unharvested sugar cane become less abundant in harvested fields and crowd into remnant unharvested fields as the harvest season progresses. Absence of such crowding would be consistent with the despotic distribution.

We developed a variation of existing occupancy and abundance models that allows for spatio-temporal habitat change, and resulting changes in animal abundance, among sites and between visits to a site during one field season. The model also allows occupancy and mean abundance to vary spatially and temporally within a habitat. We attempt to apply our model to address the ideal free distribution and the despotic distribution while studying the avian community in sugarcane fields in the Everglades Agricultural Area (EAA) of south Florida (Bottcher and Izuno 1994). The landscape in our study area was dominated by wetland and agricultural habitat containing substantial edge cover. Therefore, we also predicted avian species that prefer bare fields would be more common and more widespread in harvested areas and species that prefer edge habitat would be most common and most widespread in areas with unharvested sugarcane and tall, dense edge vegetation.

We included observer, habitat, and time-of-day effects in our model of detection probability (Sauer et al. 1994). High winds potentially can affect detection probability of birds by altering their behavior and can mask avian vocalizations by increasing background noise levels. In addition, some species sing or call frequently in early morning and less so later in the day seemingly regardless of weather conditions (Robbins 1981). Wind speed consistently increases in late morning in the EAA, and we predicted detection probability would be lower in late morning. Detection probability might be lower

along fields of tall, dense unharvested sugarcane because birds in such vegetation cover might be less visible to observers.

Estimation of population parameters can be problematic when a species is rare or uncommon or difficult to detect, resulting in sparse counts. We conducted a series of simulations to examine the utility of our model when studying such species.

## STUDY AREA

The EAA was a large agricultural area (280,000 ha) just south and east of Lake Okeechobee in south Florida (Bottcher and Izuno 1994). The EAA was located on former Everglades wetlands that were channelized and diked for agricultural and urban water management. Most of the area was sparsely populated by humans outside of a few small towns. There were few public roads, access to much of the area was restricted, and wildlife was abundant (Pearlstone et al. 2005).

The primary crop in the EAA was sugarcane, which was grown year round and harvested in late fall through early spring. Fields were 16 ha and bordered by ditches or canals. Each canal had an unimproved road on  $\geq 1$  side. Edges of fields, roads, and canals were vegetated by grasses and forbs. Trees were almost non-existent. The exotic Brazilian pepper (*Schinus terebinthifolius*) was the largest woody edge species.

Most sugarcane fields in the EAA were burned just before being harvested. Vegetation cover within a field changed from a 3–3.5-m-tall, dense grassland prior to harvest to a bare field within 1–2 days. Edge vegetation could be partially burned during harvest. At other times edges were often mowed or sprayed with an herbicide for control. All fields within an area may not have been harvested at the same time, although a group of adjacent fields could have been harvested over several days. Most harvests produced some stubble, which was generally left in the field. As a result of harvest the landscape changed from an extensive tall grassland to a fragmented mosaic of dense stands of unharvested sugarcane, almost unvegetated fields, and harvested sugarcane fields in various states of regeneration.

## METHODS

We included 245 sample locations in the study. Each location was a circle with a 50-m radius, centered on a small unpaved road along field edges and, as such, included portions of 2–4 fields as well as grasses and forbs along edges of the road and accompanying canals. Circles were grouped along transects and approximately evenly-spaced  $\geq 500$  m apart. Transects had 6–19 circles each and were 700–13,000 m apart, although one densely sampled area was effectively one transect with 29 sample circles. Our study design required a large percentage of circles to be within tall sugarcane during the initial survey visit. Initially we selected the first sample circle of a transect at random, however, as the harvest season progressed, unharvested sugarcane became increasingly difficult to find before we selected all sample locations, so we began actively placing the first circle of each transect within tall sugarcane.

We visited most sites 5 times. We made 1,181 site visits from 9 December 2006 to 3 March 2007. We started fieldwork approximately 15 min before sunrise and usually sampled for 3–4 hr. We sampled each site for 5 min, during which we counted all passerines, killdeer (*Charadrius vociferous*), and doves (family Columbidae) seen or heard except those flying through the site with no obvious connection to it. We included birds that flushed from or landed in a sample circle during a sample period. We also included swallows foraging within a sample circle. We excluded larger bird species, such as waterfowl, wading birds, and raptors from analysis out of concern they might range so widely that we could spot one individual at numerous sites. We determined the edge of a site using a Nikon ProStaff Laser 440™ rangefinder (Nikon Vision Co., LTD, Tokyo, Japan) and a Garmin GPS 12 receiver™.

Two observers (MWM and EVP) conducted all fieldwork and had decades of experience as recreational and professional birders. Prior to our study EVP conducted avian field research in the EAA for several years. The 2 field observers completed approximately 40 hr of fieldwork together establishing field sites and practicing species identification and sampling protocols prior to formal data collection.

We focused primarily on passerines and felt a priori that 500 m between centers of adjacent circles was adequate to ensure each circle was independent, at least for small resident bird species exhibiting territorial behavior. The common yellowthroat (*Geothlypis trichas*) is an abundant territorial resident in the study area. Estimates of home range of breeding common yellowthroats range from 0.1 to 2.9 ha (Guzy and Ritchison 1999), suggesting the home range of an individual bird was unlikely to encompass portions of adjacent circles.

We sometimes conducted sampling in high winds, but not during heavy rain. Wind speed increased >2 hr after sunrise, so we included a categorical time-of-day effect in the detection probability function as described below. Dense vegetation can potentially reduce an observer's ability to detect a species, so we also included a categorical effect of vegetation structure in the detection probability function. We also included a categorical observer effect.

We classified unharvested fields as tall cane. A recently harvested sugarcane field resembles fallow land with plants <15 cm tall in rows approximately 1 m apart. We classified such fields as short cane. A few harvested sugarcane fields were replanted with corn, beans, or other vegetables. We eliminated 5 sample circles entirely and 22 other site-visits from analysis upon detecting vegetables within a sample circle. Sugarcane is a grass and begins regrowing right after being cut. Once harvested sugarcane regrew to approximately 1.2–1.5 m tall, plants began to coalesce and form a canopy. At that point we classified a field as medium cane. On each visit to a site we recorded the percentage of short, medium, and tall cane. We classified grasses and forbs along field, road, and canal margins as short (<30 cm) or tall (≥30 cm) edge vegetation.

For analysis, we classified vegetation at a given site as tall cane if we recorded ≥67% of land cover as either tall cane or

medium cane in the field. All sites classified as tall cane were ≥50% unharvested sugarcane. We classified vegetation cover as short cane if ≥67% of land cover was short cane or fallow land. We classified all other sites as intermediate cane.

### Statistical Analysis

We estimated changes in abundance of birds at each sample location using a hierarchical model similar to that developed for estimating trend in harbor seal abundances (Royle and Dorazio 2008) and is an extension of the model developed by Royle (2004). In this approach a model of the population's dynamics is combined with a model of the observed point counts that accounts for sampling and errors in detection. In our case, however, the dynamical part of the model is considerably more complex than the model described by Royle and Dorazio (2008). Our models assumed changes in avian abundance at each site coincided with changes in vegetation cover (sugarcane state and edge state) and timing of these changes in cover differed among sites. We describe our specific modeling assumptions in the following sections.

*Model of population dynamics.*— Our initial most-general model included 6 parameters for mean abundance that corresponded to the 6 combinations of 3 sugarcane (c) states (tall [TC], intermediate [IC], and short [SC]) and 2 edge (e) states (tall [TE] and short [SE]). This initial model did not include spatial or temporal variation in mean abundance within a habitat state. Let  $N_{it}$  denote the abundance of birds present at site  $i$  during visit  $t$ . We assume  $N_{it} | \lambda_{it} \sim \text{Poisson}(\lambda_{it})$ , where mean abundance of birds  $\lambda_{it}$  depends on habitat state  $\mathbf{x}_{it}$  as follows:  $\log(\lambda_{it}) = \boldsymbol{\alpha}' \mathbf{x}_{it}$ . Here,  $\mathbf{x}_{it}$  is just a vector-valued, dummy variable used to codify one of the 6 elements of the parameter vector  $\boldsymbol{\alpha} = (\alpha_1, \dots, \alpha_6)$ . Each element of  $\boldsymbol{\alpha}$  corresponds to the mean abundance of birds (on the log scale) in a distinct habitat. Note that by estimating  $\lambda_{it}$ , we also estimate mean occurrence probability  $\psi_{it}$  because  $\psi_{it} = \Pr(N_{it} > 0) = 1 - \exp(-\lambda_{it})$  (Royle and Nichols 2003, Royle 2004, Dorazio 2007, Royle and Dorazio 2008).

An important aspect of this model is that it allows mean abundance and occurrence of birds at a site to change as the habitat  $\mathbf{x}_{it}$  at that site changes. If habitat does not change then mean abundance and occurrence does not change, and this population closure is what allows parameters to be estimated. For example, suppose the sequence 11221 corresponds to measurements of habitat state during 5 visits to a site. In our model the parameter  $\alpha_1$  corresponds to mean abundance of birds during visits 1, 2, and 5, whereas  $\alpha_2$  corresponds to mean abundance during visits 3 and 4. Mean abundance of the population is constrained constant on visits 1, 2, and 5 because habitat is the same on those visits; however, the habitat sequence 11221 includes 3 site-level abundance parameters:  $N_{i1}$ ,  $N_{i3}$ , and  $N_{i5}$ . In other words, in this example abundance at site  $i$  is fixed during 3 time periods: visits 1 and 2 ( $N_{i1} = N_{i2}$ ), visits 3 and 4 ( $N_{i3} = N_{i4}$ ), and visit 5 ( $N_{i5}$ ). However, abundance at site  $i$  need not be the same on visits 2 and 5 ( $N_{i2} \neq N_{i5}$ ) even though habitat is the same on visits 2 and 5. The design is somewhat analogous to a multi-season occupancy model

(MacKenzie et al. 2003) applied to one field season, but without estimating colonization and extinction when habitat changes. Our model easily accommodates sequences with missing observations because they make no contribution to the likelihood function.

As the harvest season progresses, birds may potentially crowd into remnant unharvested sugarcane. Continuing with the example habitat sequence 11221, mean abundance during the fifth visit might differ from mean abundance during visits 1 and 2 even though habitat at that site is the same on each of those 3 visits as a result of crowding into habitat 1 late in the season. We allowed for this possibility by subdividing the 5 visits into 2 periods ( $s$ ): an early period consisting of visits 1 and 2 and a late period consisting of visits 3–5. In this example, the parameter  $\alpha_1$  corresponds to mean abundance of birds during visits 1 and 2,  $\alpha_2$  corresponds to mean abundance during visits 3 and 4, and  $\alpha_3$  corresponds to mean abundance during visit 5 ( $\alpha_1 \neq \alpha_3$ ).

We allowed for spatial heterogeneity of mean abundance among sites by subdividing sample circles into 2 regions, a western region ( $n_{\text{circles}} = 121$ ) and a region encompassing circles in the northern and eastern portion of our study area ( $n_{\text{circles}} = 119$ ). We chose this a posteriori subdivision because our study area appeared to be divided by a swath containing the town of Belle Glade and several sod and vegetable farms. In regional models we allowed mean abundance to differ between the 2 regions ( $r$ ) even if habitat was the same in both regions ( $\alpha_{\text{west}} \neq \alpha_{\text{northeast}}$ ).

*Model of observations.*— We developed a model of the observed counts that depends on the set of latent abundances  $\{N_{it}\}$  (defined above) and on a set of site- and time-specific detection probabilities  $\{p_{it}\}$ . Specifically, we assumed that each of the  $n_{it}$  birds observed at site  $i$  during visit  $t$  was detected with probability  $p_{it}$ ; thus, we modeled the observed count  $n_{it}$  as a Binomial ( $N_{it}, p_{it}$ ) outcome. To specify differences in detection among sites and visits, we formulated the probability of detection (on the logit scale) as a linear combination of spatially and temporally varying covariates:

$$\text{logit}(p_{it}) = \beta' \mathbf{x}_{it} + \beta_7 \mathbf{d}_{it} + \beta_8 \mathbf{o}_{it},$$

where  $\mathbf{d}$  is a binary, dummy variable used to codify time of day (0 if <2 hr after sunrise; 1 otherwise) and  $\mathbf{o}$  is a binary, dummy variable used to codify each of 2 observers. We modeled each species separately, which allowed detection probability to differ among species.

We estimated model parameters  $\alpha$  and  $\beta$  by the method of maximum likelihood, as described by Royle and Dorazio (2008) using Program R (R Version 2.10.0, www.rproject.org, accessed 26 Oct 2009). As stated above, mean abundance and detection parameters were identifiable because our data included consecutive within-site visits wherein habitat remained fixed (see Results). For each common species we estimated total abundance among the 240 field sites during each visit by creating a Bayesian version of the best model of that species in Program WinBUGS (Lunn et al. 2000, Royle and Dorazio 2008).

Fitting our initial most-general model (without season or region effects in the mean abundance term) to the counts produced unrealistically high estimates of abundance and low estimates of detection. Therefore, we redefined vegetation state,  $x_{it}$ , in the detection probability function as a single binary, dummy variable,  $h_{it}$  (1 if  $\geq 50\%$  of sugarcane was tall or medium sugarcane; 0 otherwise). In other words, we reduced the number of intercept terms in the detection probability function of our initial most general model from 6 to 2. We fit a set of models wherein we assumed mean abundance differed among vegetation states and between regions or between seasons and we assumed detection either to differ by observer, vegetation state, and time of day or to be constant. These models reflect our prior belief that the primary source of variation in the counts was associated with changes in abundance induced by changes in vegetation state, not with changes in detectability of birds, as supported by that for each species the maximized log-likelihood ( $\log L$ ) associated with the most complex model in our subset was nearly equivalent to that obtained by fitting the original (more complex) model. For most species a model did not converge when we allowed mean abundance to differ among vegetation states, seasons, and regions.

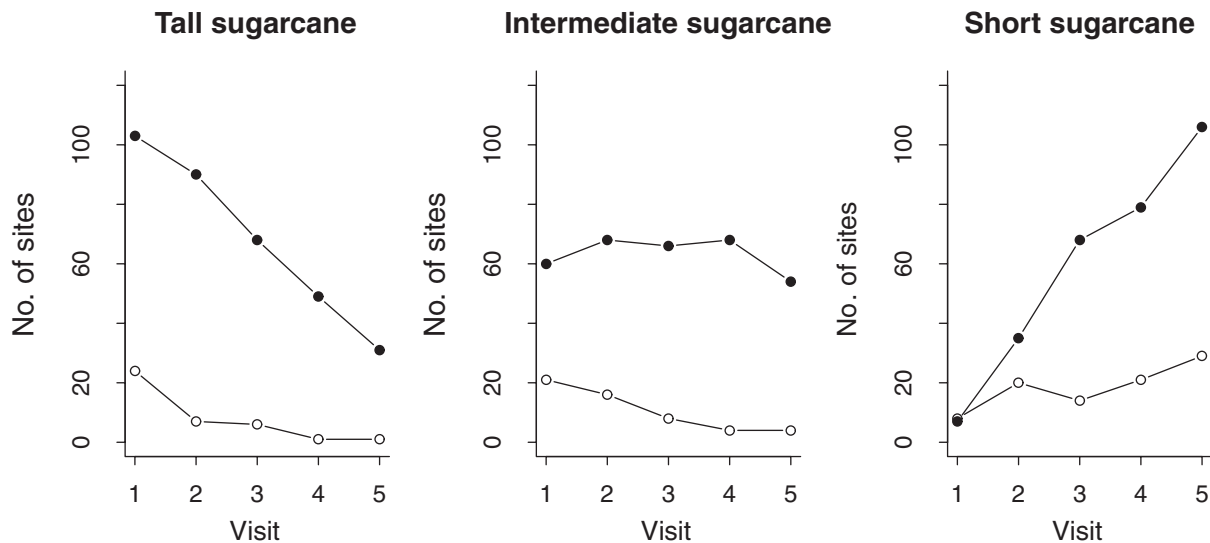
For common species we used parametric bootstrapping to estimate model fit,  $\hat{c}$ , of the most general model among those models with a constant detection probability (MacKenzie et al. 2006), and we used Akaike's Information Criterion (AIC or QAIC) to select the best model among this set (Burnham and Anderson 2002). A new model was created allowing detection probability in this best model to vary as a function of habitat, observer and time-of-day effects and AIC or QAIC was used to determine whether this new model was the best one for estimating species abundance. For uncommon species only two models were created: one with a constant detection probability and one allowing detection probability to vary as a function of habitat, observer and time-of-day effects. For these uncommon species  $\hat{c}$  was estimated for the latter model.

## Simulations

We ran 10 simulations to explore model performance for uncommon species with low detection probabilities. Most simulations involved 5 visits to 250 sites each containing 1 of 2 equally prevalent, randomly assigned habitats. Among simulations we varied number of sites, number of visits to each site, detection probability, number of habitats present in the landscape, and number of habitats recorded. For each simulation we generated 100 data sets and recorded the percentage of the 100 analyses in which the true value of mean abundance was contained within the 95% Bayesian credible intervals of the estimated mean abundance. We also recorded the mean width of the 100 Bayesian credible intervals of estimated mean abundance.

## RESULTS

The number of circles classified as tall sugarcane steadily decreased during the field season from 127 to 32 (53–13%), whereas the number of circles classified as short sugarcane



**Figure 1.** We counted doves and passerines in each of 240 field sites  $\leq 5$  times during the sugarcane harvest season in the EAA of south Florida during December 2006–March 2007. During each visit to each site we classified sugarcane as tall, intermediate or short and edge vegetation as tall or short. Here we show the number of sites of each vegetation state on each visit. The number of sites we classified as tall cane decreased during the field season, whereas the number of sites we classified as short cane increased. A solid circle represents sites with tall edge vegetation; an open circle represents sites with short edge vegetation.

increased from 15 to 135 (6–56%, Fig. 1). Changes in sugarcane and edge cover were also evident in the distribution of vegetation states per circle. The number of circles with  $y = 1, 2, 3, 4,$  and  $5$  vegetation states was  $n_y = 52, 119, 49, 19,$  and  $1,$  respectively, indicating that most circles experienced  $\geq 1$  change in vegetation cover.

We recorded 22 passerine species, killdeer, mourning dove (*Zenaidra macroura*), and common ground dove (*Columbina passerina*) within circles during sample periods (Table 1, Appendix). The 3 most common species we detected were the palm warbler (*Dendroica palmarum*), common yellowthroat, and red-winged blackbird (*Agelaius phoeniceus*).

For each of the 3 most widely-detected species AIC or QAIC decreased substantially when we added observer,

time-of-day, and vegetation effects to the model of detection probability, which we denoted by  $p_{o,d,h}$  (Table 2). These 3 models each had an Akaike weight of one. Consequently, we report estimates of mean occupancy and mean abundance for these 3 species based on fitting models with  $p_{o,d,h}$  to the counts (Table 3).

The palm warbler was the most widely detected species in our study (Table 1). Model fit ( $\hat{c} = 2.10$ ) was based on model  $\lambda_{c,e,r} p$ . For the palm warbler the model  $\lambda$  had the lowest QAIC among those models with a constant detection probability (QAIC = 1,246). However, QAIC decreased substantially when we added observer, time-of-day, and vegetation effects to the model of detection probability (QAIC = 1,173, Table 2). We estimated mean occupancy

**Table 1.** Naive estimates of mean occupancy by vegetation state for birds wintering in the Everglades Agricultural Area of south Florida during December 2006–March 2007. We divided number of known occupied sequences of a given vegetation state (left no. in each table cell) by total number of sequences of that vegetation state in 240 sample circles to obtain a naive estimate of mean occupancy (Naive occ, right no. in each table cell). A habitat sequence was  $\geq 1$  consecutive visit to a sample circle during which sugarcane and edge state remained constant. We list only species we detected during  $\geq 3$  site-visits. Total number of sequences of each vegetation state were: 121 tall cane (TC), tall edge (TE); 33 TC, short edge (SE); 135 intermediate cane (IC), TE; 39 IC, SE; 136 short cane (SC), TE; and 54 SC, SE.

Species	TC-TE		TC-SE		IC-TE		IC-SE		SC-TE		SC-SE	
	No.	Naive occ.	No.	Naive occ.	No.	Naive occ.	No.	Naive occ.	No.	Naive occ.	No.	Naive occ.
Killdeer	4	0.03	2	0.06	23	0.17	7	0.18	53	0.39	26	0.48
Mourning dove	1	0.01	0	0.00	0	0.00	0	0.00	5	0.04	1	0.02
Common ground dove	24	0.20	2	0.06	13	0.10	3	0.08	9	0.07	1	0.02
Eastern phoebe <i>Sayornis phoebe</i>	10	0.08	0	0.00	8	0.06	1	0.03	6	0.04	1	0.02
Tree swallow	4	0.03	2	0.06	17	0.13	1	0.03	23	0.17	11	0.20
Northern rough-winged swallow <i>Stelgidopteryx serripennis</i>	1	0.01	0	0.00	0	0.00	0	0.00	4	0.03	1	0.02
Common yellowthroat	90	0.74	13	0.39	68	0.50	8	0.20	32	0.24	6	0.11
Palm warbler	81	0.67	12	0.36	81	0.60	16	0.41	76	0.56	17	0.31
Yellow-rumped warbler <i>Dendroica coronata</i>	8	0.07	1	0.03	13	0.10	0	0.00	23	0.17	1	0.02
Red-winged blackbird	67	0.55	7	0.21	49	0.36	7	0.18	24	0.18	9	0.17
Boat-tailed grackle	4	0.03	0	0.00	3	0.02	0	0.00	14	0.10	10	0.19
Savannah sparrow	4	0.03	0	0.00	4	0.03	0	0.00	6	0.04	3	0.06
Song sparrow <i>Melospiza melodia</i>	0	0.00	0	0.00	0	0.00	0	0.00	2	0.01	1	0.02
Swamp sparrow	4	0.03	0	0.00	1	0.01	0	0.00	0	0.00	0	0.00

**Table 2.** Competing models of mean abundance ( $\lambda$ ) of common passerines wintering in sugarcane habitat in the Everglades Agricultural Area of south Florida during December 2006–March 2007. Models of  $\lambda$  included effects of sugarcane state (c, [tall, intermediate and short]), edge vegetation (e, [tall vs. short]), region (r, [NE vs. W]), and season (s, [early vs. late]). Akaike’s Information Criterion (QAIC for palm warbler and red-winged blackbird and AIC for common yellowthroat) decreased when we added observer (o), vegetation state (h, [“tall cane” if  $\geq 67\%$  of land cover was either tall cane or medium cane, otherwise “short cane”]), and time-of-day (d, [early morning was  $< 2$  hr after sunrise; otherwise late morning]) effects to the model of detection probability ( $p$ ).

Species	Model	No. parameters	AIC or QAIC	$\Delta$ AIC	Akaike weight
Palm warbler	$\lambda, p_{o,d,h}$	6	1,173	0	1
	$\lambda, p$	3	1,246	73	0
	$\lambda_{e,r} p$	4	1,248	75	0
	$\lambda_{c,r} p$	5	1,250	76	0
	$\lambda_{c,e,r} p$	8	1,253	79	0
	$\lambda_{c,e,s} p$	14	1,259	85	0
	$\lambda_{c,e,r} p$	14	1,261	87	0
	Common yellowthroat	$\lambda_{c,e,r} p_{o,d,h}$	16	1,550	0
$\lambda_{c,e,r} p$		13	1,646	96	0
$\lambda_{c,e} p$		7	1,657	107	0
$\lambda_{c,r} p$		4	1,661	111	0
$\lambda_{c,e,s} p$		13	1,661	111	0
$\lambda_{e,r} p$		3	1,722	172	0
$\lambda p$		2	1,734	184	0
Red-winged blackbird		$\lambda_{c,r} p_{o,d,h}$	8	370	0
	$\lambda_{c,r} p$	5	397	27	0
	$\lambda_{c,e,r} p$	8	400	29	0
	$\lambda_{c,e,r} p$	14	405	35	0
	$\lambda, p$	3	406	35	0
	$\lambda_{e,r} p$	4	407	37	0
	$\lambda_{c,e,s} p$	14	409	39	0

to be 1.0 regardless of sugarcane or edge state (Table 3). Estimated mean abundance was constant ( $\hat{\lambda} = 18$ , 95% CI = 1–270). Point estimates of intercepts in the function of detection probability suggested that  $p$  was slightly higher in tall cane than in short cane ( $\hat{\beta}_{TC} = -3.73$ , SE = 1.43;  $\hat{\beta}_{SC} = -3.89$ , SE = 1.41) although 95% CI of the intercepts broadly overlapped (95% CI =  $1.96 \times SE$ , Table 4). Point estimates of slopes suggested  $p$  was lower in late morning than in early morning ( $\hat{\beta}_d = -0.11$ ,

$SE = 0.13$ ) and differed among observers ( $\hat{\beta}_o = 1.05$ , SE = 0.13). The 95% CI of the observer effect did not overlap zero. Selected estimates of  $p$  are presented in Table 4. The highest  $\hat{p}$  for palm warblers was 0.06, 95% CI = 0.00–0.56, for observer 2 in tall cane in early morning.

In contrast, mean occupancy and abundance of common yellowthroats were strongly associated with cane state and edge vegetation. Our best model for this species was  $\lambda_{c,e,r}$

**Table 3.** Estimates of mean occupancy and mean abundance of common passerines wintering in sugarcane habitat in the Everglades Agricultural Area of south Florida during December 2006–March 2007. We obtained estimates using model  $\lambda, p_{o,d,h}$  for the palm warbler (o, observer; d, time-of-day; h, habitat state), model  $\lambda_{c,e,r} p_{o,d,h}$  for the common yellowthroat (c, sugarcane state; e, edge state; r, region), model  $\lambda_{c,r} p_{o,d,h}$  for the red-winged blackbird and model  $\lambda_{c,s} p_{o,d,h}$  (s, season) for common ground doves. Models accounted for extreme variation in vegetation cover among sample circles and between visits to a sample circle within one field season. We classified vegetation cover into the 6 categories associated with combinations of 3 sugarcane states (tall [TC], intermediate [IC], and short [SC]) and 2 edge (e) states (tall [TE] and short [SE]). For some models we divided the study area into 2 regions and the study period into 2 seasons.

Species	Region	Vegetation state	Occupancy 95% CI	Abundance 95% CI	
Palm warbler	Both	All	1.00 (0.69–1.00)	18 (1–270)	
Common yellowthroat	NE	TC, TE	1.00 (0.96–1.00)	7.9 (3.2–19.5)	
		TC, SE	1.00 (0.91–1.00)	6.9 (2.4–19.6)	
		IC, TE	0.99 (0.87–1.00)	5.1 (2.1–12.9)	
		IC, SE	0.84 (0.39–1.00)	1.8 (0.5–6.8)	
		SC, TE	0.42 (0.14–0.85)	0.54 (0.2–1.9)	
		SC, SE	0.20 (0.04–0.71)	0.22 (0.04–1.2)	
		W	TC, TE	1.00 (0.94–1.00)	6.9 (2.8–17.1)
	TC, SE	0.98 (0.70–1.00)	3.8 (1.2–12.2)		
	IC, TE	0.98 (0.80–1.00)	4.0 (1.6–10.0)		
	IC, SE	0.91 (0.51–1.00)	2.4 (0.7–8.0)		
	SC, TE	0.83 (0.43–1.00)	1.8 (0.6–5.8)		
	SC, SE	0.63 (0.19–0.99)	1.0 (0.2–4.6)		
	Red-winged blackbird	Both	TC	1.00 (0.52–1.00)	8.0 (0.7–89)
			IC	1.00 (0.46–1.00)	6.9 (0.6–76)
SC			0.98 (0.09–1.00)	4.2 (0.1–185)	
Common ground dove	Early	TC	0.89 (0.33–1.00)	2.25 (0.40–12.8)	
	Late	TC	0.90 (0.34–1.00)	2.32 (0.41–13.0)	
	Early	IC, SC	0.78 (0.23–1.00)	1.52 (0.26–8.9)	
	Late	IC, SC	0.46 (0.10–0.98)	0.61 (0.10–3.8)	

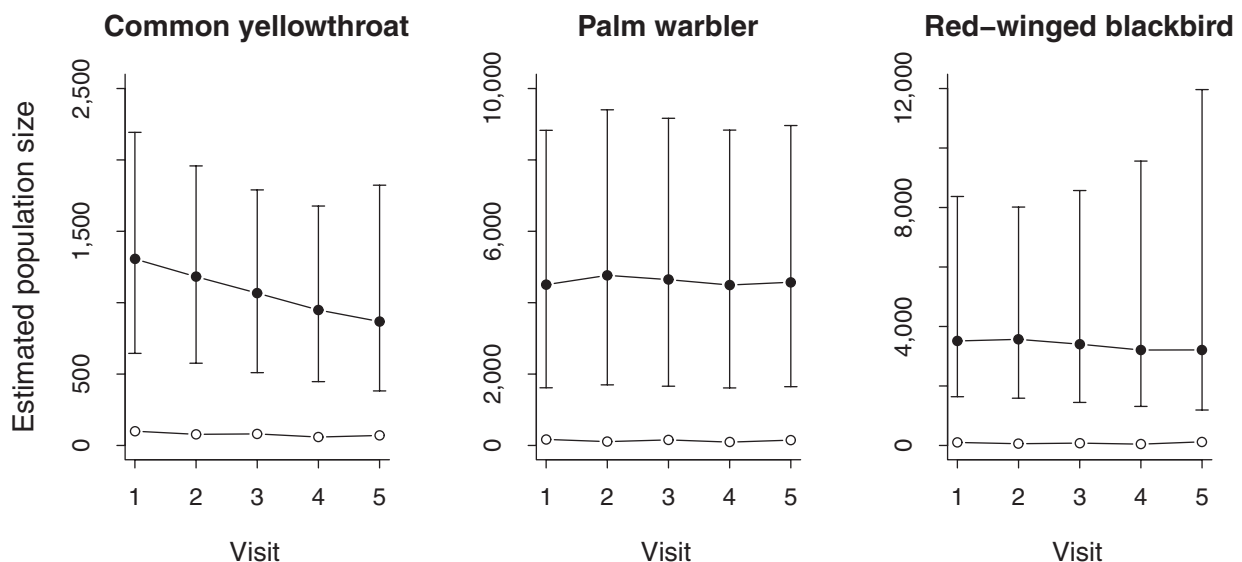
**Table 4.** Selected estimates of detection probability,  $\hat{p}$ , (and 95% CI) of birds wintering in the Everglades Agricultural Area of south Florida during December 2006–March 2007. The function of detection probability included a separate intercept for each of two vegetation classifications (“tall cane” if  $\geq 67\%$  of land cover was either tall cane or medium cane, otherwise “short cane”), a categorical observer effect (observer 1 vs. 2) and a time-of-day effect (early morning was  $< 2$  hr after sunrise; otherwise late morning).

Species	Tall cane, observer 1		Short cane, observer 1		Tall cane, observer 2		Tall cane, observer 1		Maximum detection probability	
	$\hat{p}$	Early 95% CI	$\hat{p}$	Early 95% CI	$\hat{p}$	Early 95% CI	$\hat{p}$	Later 95% CI	$\hat{p}$	95% CI
Mourning dove	0.12	0.02–0.47	0.12	0.02–0.47	0.12	0.02–0.47	0.12	0.02–0.47	0.12	0.02–0.47
Common ground dove	0.09	0.01–0.39	0.06	0.01–0.35	0.11	0.02–0.47	0.03	0.00–0.16	0.11	0.02–0.47
Tree swallow	0.15	0.01–0.70	0.15	0.01–0.70	0.15	0.01–0.70	0.15	0.01–0.70	0.15	0.01–0.70
Common yellowthroat	0.08	0.03–0.18	0.13	0.03–0.38	0.16	0.06–0.36	0.02	0.01–0.06	0.26	0.08–0.61
Palm warbler	0.02	0.00–0.28	0.02	0.00–0.25	0.06	0.00–0.56	0.02	0.00–0.26	0.06	0.00–0.56
Red-winged blackbird	0.06	0.00–0.45	0.03	0.00–0.60	0.16	0.01–0.76	0.01	0.00–0.12	0.16	0.01–0.76
Savannah sparrow	0.03	0.00–0.15	0.09	0.01–0.46	0.05	0.01–0.26	0.02	0.00–0.11	0.16	0.02–0.62

$p_{o,d,h}$  (AIC = 1,550;  $\hat{c} = 1.07$  based on model  $\lambda_{c,e,r} p$ ). Estimates of mean occupancy ranged from 0.20 (95% CI = 0.04–0.71) in short cane with short edge vegetation in the northeast portion of the study area to 1.00 in tall cane (Table 3). We estimated common yellowthroats to be most abundant in tall cane with tall edge vegetation and least abundant in short cane with short edge vegetation. Common yellowthroats seemed less widespread and less abundant in short cane in the northeastern than in the western portion of the study area. Point estimates of intercepts in the function of detection probability suggested that  $p$  was lower in tall sugarcane than in short sugarcane ( $\hat{\beta}_{TC} = -2.48$ ,  $SE = 0.50$ ;  $\hat{\beta}_{SC} = -1.86$ ,  $SE = 0.69$ ) although 95% CI of the intercepts overlapped each other. Point estimates of slopes suggested that  $p$  was lower in late morning than in early morning ( $\hat{\beta}_d = -1.27$ ,  $SE = 0.17$ ) and differed among observers ( $\hat{\beta}_o = 0.85$ ,  $SE = 0.14$ ). The 95% CI on these slope estimates did not encompass zero. The highest  $\hat{p}$  for this species was 0.26, 95% CI = 0.08–0.61, for observer 2 in short cane in early morning.

Cane state influenced mean abundance of red-winged blackbirds (best model  $\lambda_{c} p_{o,d,h}$ , QAIC = 370;  $\hat{c} = 5.57$  based on model  $\lambda_{c,e,r} p$ ). Red-winged blackbirds may have been more abundant in tall cane than short cane (Table 3). Point estimates of intercepts in the function of  $p$  suggested a higher  $p$  in tall sugarcane than in short sugarcane ( $\hat{\beta}_{TC} = -2.80$ ,  $SE = 1.33$ ;  $\hat{\beta}_{SC} = -3.53$ ,  $SE = 2.00$ ), although 95% CI of these intercepts overlapped. Point estimates of slope parameters suggested  $p$  was lower in late morning than in early morning ( $\hat{\beta}_d = -1.55$ ,  $SE = 0.43$ ) and differed among observers ( $\hat{\beta}_o = 1.11$ ,  $SE = 0.29$ ). The 95% CI on these slope estimates did not overlap zero. As with palm warblers and common yellowthroats, selected estimates of  $p$  for red-winged blackbirds suggested the observer effect was strongest (Table 4). The highest  $\hat{p}$  for this species was  $\hat{p} = 0.16$ , 95% CI = 0.01–0.76, for observer 2 in tall cane in early morning.

Estimated total abundances of common yellowthroats (at all 240 sample locations) decreased by 34% during the harvest season (Fig. 2). In contrast, total estimated abundance of



**Figure 2.** Estimated total population size (solid circle) and total counts (open circle) of 3 common passerine species wintering in 240 sites in sugarcane habitat in the Everglades Agricultural Area of south Florida during December 2006–March 2007. Estimated population size of common yellowthroats decreased during the sugarcane harvest, whereas estimated population size of palm warblers and red-winged blackbirds did not. Estimated 95% Bayesian credible intervals are also shown.

red-winged blackbirds and palm warblers exhibited no clear trend.

Convergence problems prevented us from fitting all models of mean abundance and detection to infrequently detected species. For tree swallows (*Tachycineta bicolor*) we redefined cane state as short cane versus other cane and removed edge effects. The best model for tree swallows was  $\lambda_c, p$  (QAIC = 163;  $\hat{c} = 14.24$  based on model  $\lambda_{c,r}, p$ ). Estimated occupancy and mean abundance were highest in short cane ( $\hat{\lambda} = 3.78$  [95% CI = 0.48–29.78],  $\hat{\psi} = 0.98$  [95% CI = 0.38–1.00]) and lowest in other cane ( $\hat{\lambda} = 0.90$  [95% CI = 0.11–7.35],  $\hat{\psi} = 0.59$  [95% CI = 0.10–1.00]). Estimated detection probability was 0.15 (95% CI = 0.01–0.70).

For the common ground dove we defined vegetation states as tall cane versus other cane and removed edge effects. This species was the only one for which we could create a model of mean abundance containing region and season effects. The best model for the common ground dove was  $\lambda_{c,s}, p_{o,d,h}$  (QAIC = 350;  $\hat{c} = 2.26$  based on model  $\lambda_{c,r,s}, p$ ). Estimated occupancy and abundance were highest in tall cane late in the field season and lowest in other cane late in the season (Table 3). Point estimates of intercepts in the function of  $p$  suggested a higher  $p$  in tall sugarcane than in short sugarcane ( $\hat{\beta}_{TC} = -2.32$ ,  $\text{SE} = 0.95$ ;  $\hat{\beta}_{SC} = -2.70$ ,  $\text{SE} = 1.06$ ), although 95% CI of these intercepts overlapped. Point estimated of slope parameters suggested  $p$  was lower in late morning than in early morning ( $\hat{\beta}_d = -1.28$ ,  $\text{SE} = 0.47$ ) and differed among observers

( $\hat{\beta}_o = 0.22$ ,  $\text{SE} = 0.36$ ). The 95% CI on the time-of-day effect did not overlap zero. The highest  $\hat{p}$  for common ground doves was  $\hat{p} = 0.11$ , 95% CI = 0.02–0.47, for observer 2 in tall cane in early morning.

For 2 species, we fitted less complex models of mean abundance wherein  $\lambda$  was fixed. The savannah sparrow (*Passerculus sandwichensis*) was the most frequently detected sparrow. The best model was  $\lambda, p_{o,d,h}$  (AIC = 223;  $\hat{c} = 1.00$  based on model  $\lambda, p_{o,d,h}$ ). Estimated mean abundance and mean occupancy were  $\hat{\lambda} = 0.5$  (95% CI = 0.10–2.6) and  $\hat{\psi} = 0.40$  (95% CI = 0.09–0.93). Point estimates of intercepts in the function of  $p$  suggested a lower  $p$  in tall sugarcane than in short sugarcane ( $\hat{\beta}_{TC} = -3.59$ ,  $\text{SE} = 0.94$ ;  $\hat{\beta}_{SC} = -2.27$ ,  $\text{SE} = 1.09$ ), although the 95% CI of the intercepts overlapped. Point estimates of slopes in the detection function suggested  $p$  was lower in late morning than in early morning ( $\hat{\beta}_d = -0.52$ ,  $\text{SE} = 0.54$ ), and differed among observers ( $\hat{\beta}_o = 0.63$ ,  $\text{SE} = 0.46$ ), although for both covariates the 95% CI overlapped zero. The highest  $\hat{p}$  for savannah sparrows was 0.16, 95% CI = 0.02–0.62, for observer 2 in short cane in early morning.

The best model for the mourning dove (*Zenaidura macroura*) was  $\lambda, p$  (QAIC = 94;  $\hat{c} = 1.83$  based on model  $\lambda, p_{o,d,h}$ ,  $\hat{\lambda} = 0.12$  [95% CI = 0.03–0.53],  $\hat{\psi} = 0.11$  [95% CI = 0.03–0.41],  $\hat{p} = 0.12$  [95% CI = 0.02–0.47]).

Results of simulations indicated that estimates of mean abundance generally were possible with 5 visits to 250 sites each containing 1 of 2 equally prevalent habitats on any given visit when detection probability was low (Table 5). Model

**Table 5.** Simulations evaluating ability of a dynamic occupancy and abundance model to estimate mean abundance of uncommon birds wintering in the Everglades Agricultural Area of south Florida during December 2006–March 2007. Each simulation involved analysis of 100 data sets. We present the percentage of those 100 analyses in which true mean abundance ( $\hat{\lambda}$ ) was contained within 95% Bayesian credible intervals of the estimated mean abundance ( $\hat{\lambda}$ ), and the mean width of 95% credible intervals (95% CI) of estimated mean abundance. Results generally suggest 5 visits to 250 sites in a landscape containing 2 equally common habitats will enable estimation of habitat-specific mean abundance of uncommon species with low detection probabilities. Simulation results suggest model performance improves with additional sites (simulation 6 vs. 1), additional visits (simulation 4 vs. 1), or by increasing detection probability (simulation 7 vs. 1). Estimates of  $\lambda$  were better for one habitat and worse for another when habitat affected mean abundance, but habitat type was constrained constant in the model (simulations 8 and 9 vs. 1). Model performance was weakest when habitat affected  $\lambda$  but habitat type was not recorded in the field (simulation 9 vs. 10).

Simulation	No. of sites	No. of visits	Parameters used to generate data	Parameters estimated in model	$\lambda$ Within 95% CI	Mean 95% CI width
1	250	5	$\lambda_1 = 0.20, p_1 = 0.15$ $\lambda_2 = 0.10, p_2 = 0.20$	$\lambda_1, p_1$ $\lambda_2, p_2$	Habitat 1 = 76% Habitat 2 = 86%	Habitat 1 = 2.07 Habitat 2 = 1.38
2	250	5	$\lambda_1 = 0.10, p_1 = 0.20$ $\lambda_2 = 0.10, p_2 = 0.20$	$\lambda_1, p_1$ $\lambda_2, p_2$	Habitat 1 = 77% Habitat 2 = 75%	Habitat 1 = 1.61 Habitat 2 = 1.25
3	250	5	$\lambda_1 = 0.10, p_1 = 0.20$ $\lambda_2 = 0.10, p_2 = 0.20$	$\lambda, p$	87%	0.64
4	250	10	$\lambda_1 = 0.20, p_1 = 0.15$ $\lambda_2 = 0.10, p_2 = 0.20$	$\lambda_1, p_1$ $\lambda_2, p_2$	Habitat 1 = 83% Habitat 2 = 89%	Habitat 1 = 0.82 Habitat 2 = 0.56
5	250	5	$\lambda = 0.10, p = 0.20$	$\lambda, p$	95%	0.23
6	500	5	$\lambda_1 = 0.20, p_1 = 0.15$ $\lambda_2 = 0.10, p_2 = 0.20$	$\lambda_1, p_1$ $\lambda_2, p_2$	Habitat 1 = 86% Habitat 2 = 82%	Habitat 1 = 1.02 Habitat 2 = 0.60
7	250	5	$\lambda_1 = 0.20, p_1 = 0.30$ $\lambda_2 = 0.10, p_2 = 0.40$	$\lambda_1, p_1$ $\lambda_2, p_2$	Habitat 1 = 86% Habitat 2 = 94%	Habitat 1 = 0.62 Habitat 2 = 0.32
8	250	5	$\lambda_1 = 0.20, p_1 = 0.15$ $\lambda_2 = 0.10, p_2 = 0.20$	$\lambda_1, p_1, p_2$	Habitat 1 = 83% Habitat 2 = 65%	Habitat 1 = 0.92 Habitat 2 = 0.58
9	250	5	$\lambda_1 = 0.20, p_1 = 0.15$ $\lambda_2 = 0.10, p_2 = 0.20$ (habitat type recorded in the data set)	$\lambda, p$	Habitat 1 = 85% Habitat 2 = 71%	Habitat 1 = 1.04 Habitat 2 = 0.62
10	250	5	$\lambda_1 = 0.20, p_1 = 0.15$ $\lambda_2 = 0.10, p_2 = 0.20$ (habitat type not recorded in the data set)	$\lambda, p$	Habitat 1 = 36% Habitat 2 = 0%	Habitat 1 = 2.22 Habitat 2 = NA



performance improved with increasing number of sites (simulation 6 vs. 1, mean width of 95%  $\text{C}\hat{\text{I}}$  was reduced by approximately 53%; in this paragraph we use  $\text{C}\hat{\text{I}}$  to mean Bayesian credible intervals), number of visits (simulation 4 vs. 1, percentage of 95%  $\text{C}\hat{\text{I}}$  containing  $\lambda$  increased by approximately 6% and mean width of 95%  $\text{C}\hat{\text{I}}$  was reduced by approximately 60%), or detection probability (simulation 7 vs. 1, percentage of 95%  $\text{C}\hat{\text{I}}$  containing  $\lambda$  increased by approximately 11% and mean width of 95%  $\text{C}\hat{\text{I}}$  was reduced by approximately 73%). Model performance also improved by increasing the number of consecutive visits to a site during which habitat was constant (simulation 5 vs. 3, percentage of 95%  $\text{C}\hat{\text{I}}$  containing  $\lambda$  increased by 9% and mean width of 95%  $\text{C}\hat{\text{I}}$  was reduced by 64%). When habitat affected mean abundance and habitat was recorded in the field but not included in the model (simulations 8 and 9 vs. 1),  $\hat{\lambda}$  for one habitat was improved by approximately 10%, but was reduced by approximately 20% for the other habitat; mean width of 95%  $\text{C}\hat{\text{I}}$  was reduced by approximately 55%. In simulation 9 we recorded habitat type in the data set but constrained it to be constant in the model (example habitat sequences in the data: 12212, 21221, 12121). Model performance was weakest when habitat affected mean abundance but was not recorded in the field (simulation 10 vs. 9), resulting in each site having a habitat sequence of 11111 in the data set (percentage of 95%  $\text{C}\hat{\text{I}}$  containing  $\lambda$  decreased by approximately 80% and mean width of 95%  $\text{C}\hat{\text{I}}$  increased by 113%).

## DISCUSSION

The avian species we detected generally are associated with wetland, edge, or agricultural habitat, the 3 dominant habitats in the EAA. Each of these land cover types can be dynamic in nature, and we believe our dynamic version of Royle's (2004) model was invaluable in estimating effects of vegetation structure on avian population parameters. The EAA was largely an artificial grassland, however, we detected few grassland species. Modeled species generally responded to variation in vegetation structure in ways we a priori expected based on known life history traits (Yasukawa and Searcy 1995, Wilson 1996, Guzy and Ritchison 1999).

Model estimates of mean abundance and occupancy matched our perceptions in the field. The palm warbler is migratory and appeared to be a habitat generalist in winter (Wilson 1996). We feel our point estimates of abundance for this species are reasonable as our maximum count for this species was 16 birds and we detected  $\geq 5$  birds on 15 site visits.

We detected no evidence of birds crowding into remnant unharvested sugarcane as the harvest season progressed. The common ground dove was the only species for which a seasonal model was selected as best. The common yellowthroat is a resident and breeds in the study area. Males sang, often vigorously, in the early morning throughout the sample period, although we saw no physical evidence of breeding during the field season. Territorial behavior is consistent with the despotic distribution. Additional visits

or samples during each season may allow for creation of models containing season and region effects for more species in future studies, thus enabling more rigorous tests for crowding.

Common yellowthroats may not have dispersed from count circles between visits in the absence of habitat change because of territorial behavior. However, estimates of total  $N$  indicated that common yellowthroats became less common as the harvest season progressed. Prior to harvest of a sugarcane field we usually detected common yellowthroats in the sugarcane itself or in adjacent dense edge vegetation. Following harvest, we usually observed common yellowthroats along canal edges or in ditches. We heard common yellowthroats singing from harvested sugarcane fields after plants had grown to a height of approximately 1.2 m, suggesting that some birds recolonized harvested sugarcane fields once suitable vegetation structure regenerated. Edge vegetation may have served as forage habitat for yellowthroats prior to sugarcane harvest and as both forage habitat and refugia after sugarcane harvest. Regional differences in edge or canal management may have been responsible for common yellowthroats occupying a greater proportion of short cane sites in the western portion of the study area. Perhaps as the harvest progressed yellowthroats in the NE region were more likely to disperse out of the study area into natural areas bordering the EAA while yellowthroats in the western region were more likely to persist within canals and ditches in the EAA itself. Our study was not designed to examine that possibility, which could be a topic for future research.

MacKenzie et al. (2003) developed a multi-season occupancy model that incorporated colonization and extinction parameters between field seasons. Perhaps our dynamic occupancy and abundance model can be expanded to include colonization and extinction parameters, perhaps by following a robust design (Nichols et al. 2008, Rota et al. 2009). Such a model would be substantially more complex than the model we present and would include a potentially large number of colonization and extinction parameters. Such a model might also require more sites and more visits, or at least more samples per site visit, than in our study.

Flocks of some species, including egrets, herons, and the boat-tailed grackle (*Quiscalus major*) followed sugarcane harvest machinery from field to field to forage on prey items exposed by harvest activity. Such transient flocking behavior violates the assumption of closure. Killdeer sometimes congregated in recently planted sites, also violating the closure assumption. Transient flocking behavior resulted in large spikes in counts of killdeer and boat-tailed grackles and these spikes also prevented models from converging. Swallows and red-winged blackbirds may have been temporarily attracted to recently harvested sites to a lesser degree, which might be responsible for the large estimated  $\hat{c}$  for these species. Estimation of abundance of transient flocking species might require aerial surveys perhaps combined with a double-observer approach (Nichols et al. 2000) or perhaps use of the robust design (Nichols et al. 2008, Rota et al. 2009).

Our study was not designed to estimate how avian populations respond to habitat fragmentation (Harris 1984,

Herkert et al. 2003, Guénette and Villard 2005, Betts et al. 2007, Villard et al. 2007). However, future studies could build upon our modeling approach to address questions of colonization and extinction among habitat patches (MacArthur and Wilson 1967, MacKenzie et al. 2003). Combining our model with capture–recapture techniques allowing estimation of other population vital rates might enable study of how population dynamics vary temporally and spatially in a heterogeneous habitat (Van Horne 1983, Pulliam 1988, Pulliam and Danielson 1991, Johnson 2004, Runge et al. 2006).

Detection probability of birds is well known to vary among observers and during the day (Robbins 1981, Sauer et al. 1994, Diefenbach et al. 2003). Wind speed is also a common factor of consideration in avian field surveys. A reduction in  $\hat{p}$  in late morning for 5 species likely reflected reduced singing rates of common yellowthroats and red-winged blackbirds, as well as increased background noise and vegetation movement associated with increased wind speed. The same observer had the higher  $\hat{p}$  for each of these 5 species.

Although our results generally matched our expectations we acknowledge that our study design had several flaws. We conducted only one-field season, used broad definitions of sugarcane and edge structure, and all of our plots were located next to roads (Bart et al. 1995). These aspects of our study design weaken ecological inferences that can be drawn from our results. Nevertheless, we feel our results appear ecologically reasonable, albeit with large credible intervals for abundance of some species.

We only estimated mean abundance and occupancy for a few species in the EAA. However, we were able to estimate mean abundance and occupancy for 50% of the species we detected during  $\geq 3$  site-visits (Table 1). We excluded other species from analysis because they were too scarce, detected too infrequently or ranged too widely. For example, we detected a swamp sparrow (*Melospiza georgiana*) in 5 sites, but never detected this species in the same site on  $>1$  visit making parameter estimation problematic. Breeding birds might be more sedentary than wintering birds, making occupancy and abundance estimation in dynamic habitats more logistically feasible during the breeding season.

Our simulations suggested 5 visits to 250 sites each containing one of 2 equally prevalent habitats might be adequate to obtain habitat-specific estimates of mean abundance of uncommon species or species detected infrequently. If more habitats are to be considered, as was the case here, then more sites or visits should be considered if rare or uncommon species are of interest. Perhaps our modeling approach can be combined with double-observer, removal or robust design methods (Allredge et al. 2007, Nichols et al. 2008, Rota et al. 2009) to obtain precise estimates of uncommon species more efficiently.

We used a site radius of 50 m. Heaping occurs when observers round distances to a convenient values such as increments of 5 or 10 (e.g., 5 m, 10 m, 50 m, or 100 m, Buckland et al. 2001). Heaping can occur at any distance, even at 1,000 m. In our case heaping could occur if we

recorded birds as inside the sample area when those birds were actually outside of the sample area. We made a concerted effort to exclude birds if we were unsure whether they were inside the sample area, and we made use of laser range finders and handheld Global Positioning System (GPS) devices when making those decisions. We cannot say no birds were erroneously included in our counts but we think we took adequate precautions to minimize that possibility. Future studies could consider using a radius such as 54 m if future researchers wish to use circles roughly the same size as ours (Buckland et al. 2001).

We do not feel the above issues detract from the value of our modeling approach. The occupancy and abundance model we describe was very useful in analyzing avian point count data within a dynamic agricultural landscape in the EAA. We suggest this modeling approach will be useful in other habitats exhibiting extreme spatio-temporal variation within a short period such as prairies and wetlands. Even forested areas can change extensively over a short period if timber management activities or fires occur during the field season. Accounting for such habitat dynamics when monitoring populations to evaluate management action or landscape variation could ultimately help achieve conservation goals.

## MANAGEMENT IMPLICATIONS

Tall edge vegetation appeared to increase occupancy and abundance of common yellowthroats substantially in the EAA and perhaps may benefit other species. However, woody plants are actively eliminated in the EAA, partially to control blackbirds, which damage rice and corn crops (Yasukawa and Searcy 1995). Herbaceous edge vegetation is also removed to control rodent populations (Lefebvre et al. 1985) and to reduce risk of fields being colonized by unwanted grasses. Nevertheless, if herbaceous edge vegetation were allowed to persist in some areas, perhaps on a rotational basis, abundance of some wintering passerines and possibly even the northern bobwhite (*Colinus virginianus*) might increase. Herbaceous edge vegetation might also benefit sugarcane growers by helping to control soil erosion and runoff of agricultural pesticides and fertilizers while reducing money spent on fuel and machinery repair. Whether such benefits can be realized, and outweigh costs of additional crop damage by blackbirds, rodents and grasses would require additional study.

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**Appendix:** Wintering passerine species and selected non-passerines we detected during <3 site visits or that we detected outside of a sample period in sugarcane habitat in the EAA of south Florida during December 2006–March 2007. Species detected within a count circle during the count period are marked with an “a”.

Species	Common name
<i>Falco sparverius</i>	American kestrel
<i>Colinus virginianus</i> <sup>a</sup>	Northern bobwhite
<i>Gallinago delicata</i> <sup>a</sup>	Wilson’s snipe
<i>Megaceryle alcyon</i> <sup>a</sup>	Belted kingfisher
<i>Troglodytes aedon</i> <sup>a</sup>	House wren
<i>Poliopitila caerulea</i> <sup>a</sup>	Blue-gray gnatcatcher
<i>Turdus migratorius</i> <sup>a</sup>	American robin
<i>Dumetella carolinensis</i> <sup>a</sup>	Gray catbird
<i>Dendroica discolor</i>	Prairie warbler
<i>Quiscalus quiscula</i>	Common grackle
	Eastern meadowlark
<i>Spizella passerina</i> <sup>a</sup>	Chipping sparrow
<i>Melospiza lincolni</i>	Lincoln’s sparrow
<i>Ammodramus savannarum</i> <sup>a</sup>	Grasshopper sparrow
<i>Pipilo erythrophthalmus</i> <sup>a</sup>	Eastern towhee
<i>Passerina cyanea</i>	Indigo bunting