Using Pointing Dogs and Hierarchical Models to Evaluate American Woodcock Winter Occupancy and Densities

DANIEL S. SULLINS,[1,2] Arthur Temple College of Forestry and Agriculture, Stephen F. Austin State University, *Nacogdoches, TX 75962, USA*

WARREN C. CONWAY, Department of Natural Resources Management, Texas Tech University, *Lubbock, TX 79409, USA*

DAVID A. HAUKOS, U.S. Geological Survey, Kansas Cooperative Fish and Wildlife Research Unit, Division of Biology, Kansas State University, *Manhattan, KS 66506, USA*

CHRISTOPHER E. COMER, Arthur Temple College of Forestry and Agriculture, Stephen F. Austin State University, *Nacogdoches, TX 75962, USA*

ABSTRACT: Use of dogs has increased for multiple wildlife research purposes ranging from carnivore scat detection to estimation of reptile abundance. Use of dogs is not particularly novel for upland gamebird biologists, and pointing dogs have been long considered an important research tool. However, recent advances in Global Positioning System (GPS) technology and the development of hierarchical modeling approaches that account for imperfect detection may improve estimates of occupancy and density of cryptic species such as the American woodcock (*Scolopax minor*; hereafter, woodcock). We conducted surveys for woodcock using a trained pointing dog wearing a GPS collar during the winters of 2010–2011 and 2011–2012 in East Texas, USA. We surveyed 0.5-km-radius circular plots (*n* = 24; survey sites) randomly placed along secondary roads in Davy Crockett National Forest and on private timber property. Surveys lasted 1.5 hrs and were repeated 3–5 times each winter. We estimated woodcock occupancy and density using multiple modeling approaches at the survey site and forest stand scales within survey sites. Woodcock occupied 88% (21/24) of survey sites and 48% (39/82) of forest stands (i.e., unique cover types) within sites. Using a modified distance sampling technique, we estimated an average density of 0.16 birds/ha (SE = 0.13) throughout both study areas. We describe the first attempt to blend use of pointing dogs with hierarchical modeling approaches to derive estimates of regional diurnal woodcock occupancy and density, and describe relationships between these estimates of abundance and habitat covariates. Although forest stand occupancy estimates had the lowest coefficients of variation, our estimates of density provided the most useful inference of habitat use. Surveys using pointing dogs paired with hierarchical models of occupancy and density may provide a cost-efficient and effective approach to estimate habitat abundance at broad spatial scales.

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The use of pointing and flushing dogs in upland gamebird research in North America has an extensive history as an aid in collecting field specimens, documenting life history events, and banding (Audubon 1839, Bendire 1889, Reeves 1966). More recently, use of very high frequency (VHF) transmitters and Global Positioning System (GPS) telemetry to evaluate wildlife habitat use has become prominent (Millspaugh et al. 2012, Daw et al. 1998, Powell et al. 2005,

1 email: sullins@ksu.edu

2 current address: Kansas Cooperative Fish and Wildlife Research Unit, Division of Biology, Kansas State University, Manhattan, KS, USA

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Peterson et al. 2015). The same technological advancements that have made it possible to monitor marked individuals in fine detail have also allowed for expanded use of dogs into nontraditional realms of wildlife research (Dahlgren 2012). For example, the development of GPS tracking collars for dogs can improve the utility of dogs in wildlife research (Dahlgren 2012). Dogs have been used to detect wildlife mortalities related to wind turbines, among many other uses (Arnett 2006, Dahlgren et al. 2012), and advances in technology provide an opportunity to revisit the use of pointing dogs for estimating habitat use for cryptic webless migratory gamebird species such as the American woodcock (*Scolopax minor*; hereafter, woodcock).

In addition to technological advances, recently developed analytical methods allow for accounting of nuisance variables that can increase the error of occupancy and density estimates. Hierarchical models integrate detection and related covariates to estimate "true" occupancy or density of wildlife (Royle et al. 2004, Mackenzie et al. 2006). Hierarchical models account for imperfect detection using multiple repeat surveys, as in occupancy modeling, or by quantifying the relationship of detection with distance from the observer, as in distance sampling (Mackenzie et al. 2006, Buckland et al. 1993). The replicate surveys that some hierarchical models require introduce logistical constraints that limit the spatial extent of survey efforts and, therefore, the scale of inference. However, it may be more feasible to survey a broad geographic area multiple times than to capture, mark with transmitters, and monitor individuals over the same geographic extent.

Hierarchical models that account for detection probability can provide biologically relevant estimates of wildlife occupancy or density, allowing a clearer understanding of relationships between unmarked animals and habitat-related covariates, especially when detection probability covaries with habitat variables (Gu and Swihart 2004). The true values of occupancy and/or density adjusted for detection probability may be of less interest to land managers and conservationists than the relationships among habitat variables. Both occupancy and density estimates are products of the underlying point process pattern, and both can provide inference on habitat use (Kery and Royle 2016). Using occupancy or density to assess habitat use through evaluating models including habitat-related covariates may aid in guiding management decisions. A carefully designed study is needed to estimate occupancy and density of woodcock, which can occupy 9.2-ha diurnal winter home ranges (Horton and Causey 1979), make within-season movements ≥500 m in response to changes in precipitation and daily temperature (Doherty et al. 2010), and exhibit varied use of cover types both within and among winters (Krementz et al. 1994). Guidelines for designing such studies are needed to ensure that inference on woodcock ecology can be gleaned in the most cost-effective manner when using pointing dogs and hierarchical models.

Other tools that can improve estimates of occupancy and density include the advancement of Geographic Information Systems (GIS). Dog collars with GPS tracking capabilities make it straightforward to record, save, and analyze the track of a searching dog using GIS. Location errors for currently available dog-tracking devices are typically <20 m (Sepulveda et al. 2015). Information from GPS collars can provide spatially explicit information on survey efforts, including estimates of distances covered and time spent during surveying specific cover types when combined with GIS. Advances in GIS can make traditional pointing-dog surveys highly informative when dog tracks are georeferenced and overlaid on remotely sensed land-cover data. Linking woodcock habitat use to GIS layers would be beneficial for estimating the distribution of diurnal habitat for woodcock, which has been identified as a priority information need (Case and Case 2010).

We assessed the utility of conducting surveys for woodcock with pointing dogs in combination with hierarchical modeling and GIS tools to estimate diurnal occupancy and density on a portion of their wintering distribution in East Texas, USA. Specifically, we present methods using pointing dogs and hierarchical models to evaluate woodcock habitat use (occupancy and density) among land-cover types and in relation to habitat characteristics as a case study for use in future monitoring and research efforts.

Study Area

We conducted surveys for woodcock at 2 study areas representative of typical land-cover types in East Texas, USA. Campbell Unit #106 (hereafter, the Campbell Unit) was a 2,400-ha private timber site in San Augustine County and was managed for loblolly pine (*Pinus taeda*) timber-production. Our other study area was the 65,529-ha Davy Crockett National Forest (hereafter, DCNF) in Houston and Trinity counties (Fig. 1). The DCNF was managed on longer rotations for multiple uses including wildlife and timber production. However, timber harvest was greatly restricted at this study area (Van Kley 2006). The study areas were within the West Gulf Coastal Plain Bird Conservation Region (WGCP BCR), which was comprised mostly of loblolly pine (38%) and mixed-pine/hardwood forests (Krementz et al. 2008). The East Texas portion of the WGCP BCR was heavily forested and even-aged loblolly pine plantations were common. Our study areas were comprised of various soil types, with excessively drained sandy upland soils and poorly drained floodplain soils interspersed across the landscape (Van Kley 2006). Ultisol and Alfisol soil orders dominated uplands, although some Vertisols and Entisols were also present. Upland topsoils were typically a light-brown to reddish sandy loam, loam, or clay loam, medium to strongly acidic, and nutrient poor, whereas alluvial Entisol and Inceptisol soils dominated river floodplains (Van Kley 2006).

Methods

FIELD COLLECTED DATA

Survey site selection Within our study areas, we selected 24 0.5-km-radius sites to conduct woodcock surveys using a stratified random sampling design: 18 in DCNF and 6 in the Campbell Unit. We selected the centers of woodcock survey sites by placing evenly spaced points 1 km apart on secondary roads throughout each study area. We then created 0.5-km buffers in ArcMap 10 (ESRI 2010) around each point to create adjacent circles along all secondary roads in both study areas. We stratified sampling on soil type, as soil type has been used to characterize winter habitat suitability for woodcock (Cade 1985; see supplemental material).

Forest stand delineation Within the 2 study areas (Campbell Unit and DCNF), we evaluated woodcock habitat use at the 1) survey site and 2) stand scales. The survey site scale included the total area (78.5 ha) within each 0.5 km-radius survey site (see supplemental material for a summary of survey site habitat use via occupancy modeling). The stand scale was based upon the extent of land-cover types (stands) within each survey site, which varied among survey sites. We classified stands based on land-cover classifications from Diamond and Elliott (2009) and measured the area (in ha) of each stand within survey sites. We used land-cover types as both individual and aggregated categories in occupancy and density models. We classified stands into 8 land-cover types including grassland, streamside management zones (SMZ), upland deciduous forest, mature pine forest, mesic mixed pine/hardwood forest, pine forest 1–3 m tall, pine plantation >3 m tall, and riparian forest (see Diamond and Elliott 2009; more details in supplemental material).

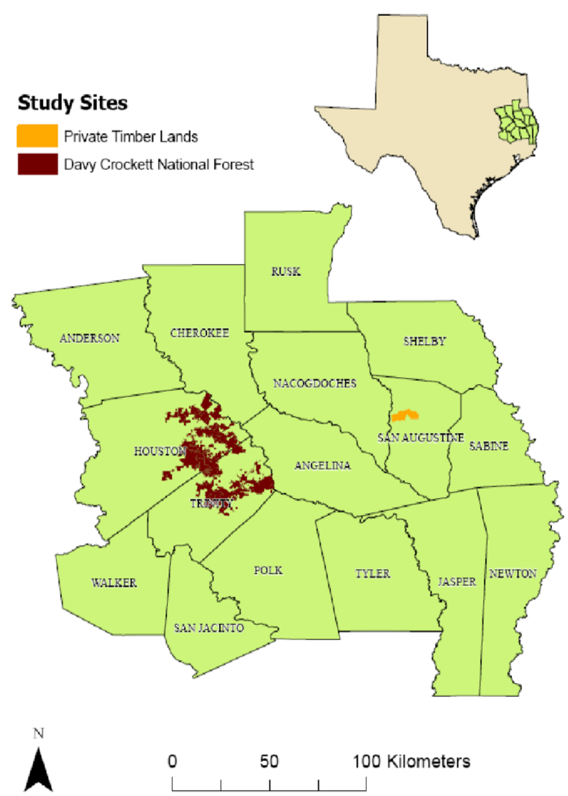

Figure 1. Counties and location of Davy Crockett National Forest and private industrial timberlands (Campbell timber Unit #106) surveyed for American woodcock during the winters of 2010–2011 and 2011–2012 in East Texas, USA.

Vegetation covariates within stands We measured structural vegetation characteristics at 416 random points after completing woodcock surveys. We randomly distributed points throughout all survey sites (Sullins 2013) using Hawth's Analysis (Beyer 2004) tools in ArcGIS 9.2 (ESRI, Redlands, CA). All random points were ≥200 m apart to ensure adequate coverage of each survey site. At each random point we measured percent vegetation cover (%) at 2 strata—<30 cm tall, and >0.5 m and <5 m tall—using the line-intercept method in each cardinal direction beginning at each random point (Hays et al. 1981). We measured vegetation cover <0.3 m tall along 2-m transects, and measured vegetation 0.5–5 m tall along 5-m transects (Hays et al. 1981). We measured stem density of trees >5.0 m tall within a 5-m radius of each random point following Hays et al. (1981).

Woodcock surveys We conducted multiple woodcock surveys at each site using the same trained pointing dog during the winters of 2010–2011 (31 December 2010–12 February 2011) and 2011–2012 (8 November 2011–3 March 2012). The trained pointing dog was a Llewellin Setter that was 1 year old when surveys began in 2010 (Fig. 2A). We began each survey at the center of each 0.5 km-radius survey site and proceeded in a manner that ensured complete coverage of potential diurnal woodcock habitat within each survey site. We remained within survey site boundaries by setting a handheld GPS to navigate to the center of the survey site throughout each survey, even though we were not navigating to the center, which allowed us to monitor if we were within 500 m of center of the site throughout the survey. Each survey lasted 1.5 hr, and we surveyed each site 3–4 times in 2010–2011 and 4–5 times in 2011–2012. No individual site was surveyed twice in the same day. Typically, and at most, we conducted 3 individual surveys (on different sites) on a given day, between 0700 and 1400 CST. We separated repeat visits on the same survey site by ≥2 days to ensure independence among visits. We randomized the order in which we surveyed sites so that each site would be surveyed first, second, and third during morning surveys, respectively.

We outfitted the pointing dog with a Garmin DC 40 GPS collar (Garmin International, Inc., Olathe, KS, USA) to record its movements through the survey site. We downloaded and saved the tracked movements of the pointing dog at the end of every day that we conducted surveys (Fig. 2A–B). Upon flushing a woodcock during a survey, we marked the location where the woodcock flushed using a handheld Garmin Astro 320 GPS. We recorded the flight direction of each flushed woodcock to minimize chances of recording the same woodcock multiple times. We followed procedures outlined in Gutzwiller (1990) and Dahlgren et al. (2012) in that we used the same dog for all surveys, surveyed each site at least once during all time intervals, and standardized search efforts by having only 1 dog handler (DSS) during all surveys. We attempted to minimize the influence of temperature, wind, precipitation, and barometric pressure on the probability of detecting woodcock by conducting all surveys during similar conditions (Gutzwiller 1990, Dahlgren et al. 2012). We also included weather-related covariates in initial candidate model sets to assess their effects (see below).

For use in estimating the effective area searched by the dog, we measured the point-to-flush distance (PFD) for each woodcock located by the pointing dog using a hip chain from where the dog first went on point to where the woodcock flushed (Guthery and Mecozzi 2008). We assumed the pointing behavior of the dog immediately occurred upon detection of a woodcock (Guthery and Mecozzi 2008). If the dog flushed a bird without pointing, we recorded the PFD as 0 m. We recorded locations of woodcock incidentally flushed by the dog handler, for future measurements of habitat variables, but we did not use these encounters to estimate occupancy and density.

Survey weather We obtained weather data from Weather Underground (weatherunderground.com) using data from stations that were closest to each survey site. We downloaded temperature (°C), humidity (%), and precipitation (cm) data for each day we conducted surveys. We used total rainfall in the 7 days prior to each date we conducted a survey as a precipitation covariate in occupancy and density models. We expected that weather-related variables may influence the detection of woodcock.

HIERARCHICAL MODELING AND MODEL SELECTION

We conducted occupancy modeling and distance sampling using the woodcock detections and PFDs acquired from surveys using pointing dogs during the winters of 2010–2011 and 2011–2012 in East Texas. We modeled occupancy at 2 spatial scales (survey site and stand scale) whereas we used distance sampling models to estimate density at only the stand scale. Survey site occupancy methods and results are included in the supplemental material. For models of woodcock occupancy and density, we only used count data from 3 repeat surveys occurring between 31 December 2010 – 6 February 2011, during the first season, and from 14 December 2011– 6 February 2012, during the second season. We did not use counts from surveys occurring in November and later in February when woodcock have not yet completed migration or have already started northward migration (Tappe et al. 1989, Olinde and Prickett 1991, Roberts 1993, Krementz et al. 1994, Moore and Krementz 2017).

STAND-SCALE OCCUPANCY MODELING

We estimated occupancy based on detection histories (present, Y_{ij} = 1; absent, Y_{ij}= 0) of survey sites ($_i$,) among multiple visits ($_j$; Mackenzie et al. 2006, Royle and Dora-

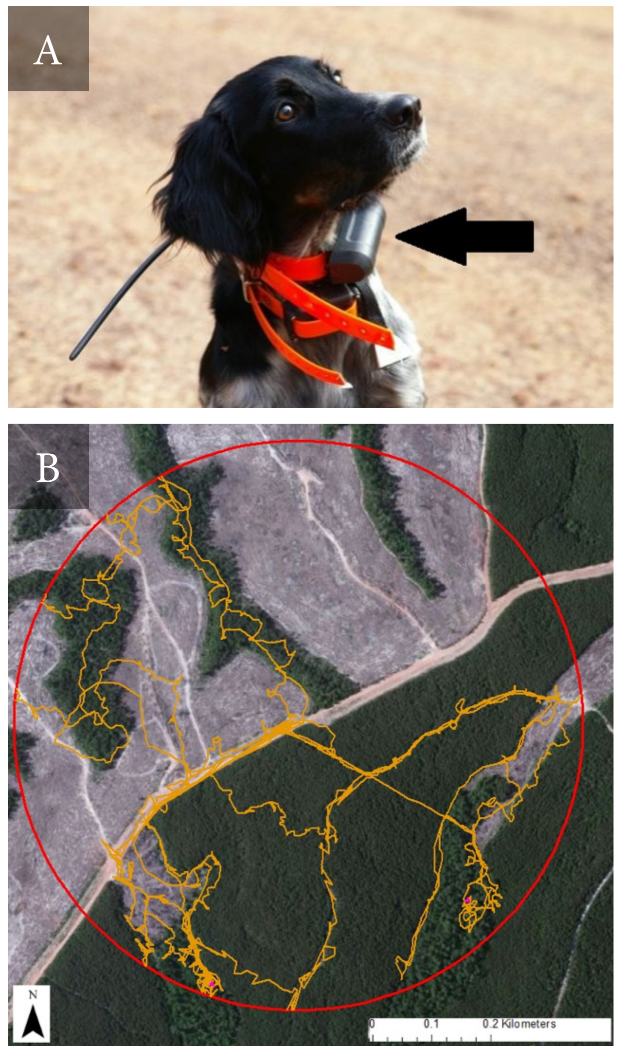

Figure 2. Trained pointing dog wearing a Garmin DC 40 GPS collar during American woodcock surveys in East Texas, USA during winters of 2010–2011 and 2011–2012. The black arrow points to the GPS collar (A). An example of a 0.5-km-radius survey site, outlined in red, on the Campbell timber unit in East Texas, USA and the dog track recorded by the GPS collar is displayed in gold (B).

zio 2008). Occupancy modeling estimates the probability of a site being occupied [$\psi = \Pr(Z_i = 1)$] while accounting for imperfect detection using a hierarchical model (Mackenzie et al. 2006). The hierarchical model is based on the Bernoulli joint distribution of the observation conditional on the latent occupancy state and incorporates an estimated probability of detection (ρ) where

$$Z_i \sim Bernouli(\psi)$$
$$(Z_{i\rho}) \sim Bernouli(\psi)$$

We estimated the probability of a site (ψ), or stand, being occupied and the detection probability (ρ) using hierarchical models with maximum likelihood estimators (Mackenzie et al. 2006). We used a logit link to generalize the model and likelihood to assess occupancy and detection probability as a function of covariates.

Observation Process We developed *a priori* candidate models to 1) explain latent woodcock occupancy and 2) identify factors related to detection as part of the observation process based on previously published information (Cade 1985). First, we identified top-ranked univariate detection models for each season by holding occupancy constant. We estimated stand-scale occupancy (ψ) and detection probabilities (ρ) using the function occu() in the package unmarked in R (Mackenzie et al. 2006, Fiske and Chandler 2011, R Development Core Development Team 2016).

We held occupancy constant while fitting models with covariates to explore relationships between detection probability and area searched within a stand (ha), average daily temperature (degrees C), survey specific detection, and percent canopy cover <0.3 m tall. We estimated the area searched within each stand by buffering each dog track in ArcGIS10 with the estimated ESW that we modeled using distsamp within the R package unmarked (Fiske and Chandler 2011, see distance sampling modeling methods below). We then intersected the polygon of area searched by the dog with the polygons of individual stands to quantify the area searched within each stand. We identified the best-supported univariate candidate model to predict detection probability using Akaike's Information Criterion adjusted for sample size (AIC_c; Burnham and Anderson 2002).

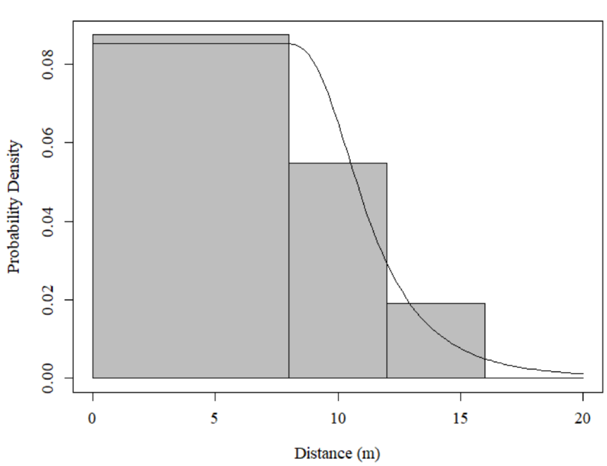

Figure 3. Estimated probability density function derived from the frequency of point-to-flush distances of American woodcock during winter in East Texas, USA at 0–7.9 m, 8–11.9 m, 12–14.9 m, 15–17.9 m, and 18–21 m away from the transect. Black line depicts the hazard rate function fit to the detection curve.

Occupancy covariate modeling We then used the covariate in the top-ranked detection model to control for nuisance variation in the observation process when fitting all occupancy models. We assessed latent occupancy using 2 groups of models. The first group included categorical descriptors of each stand, or *land-cover type*. The second group included covariates related to *vegetation structure* within stands that are described above and are hypothesized to influence diurnal habitat abundance during winter (Cade 1985): percent canopy cover 0.5–5.0 m tall and stem density of trees >5 m tall (trees/ha). For the land-cover type model group, we derived land-cover-type covariates, which were all categorical except for patch size (ha; patchsize), from Diamond and Elliott (2009). We directly assessed occupancy in the 8 cover types we delineated (see Forest Stand Delineation, above). We also evaluated occupancy in young pine forests 1–3 m tall (Ypine), mature pine forests (Mpine), and forested wetland/streamside riparian cover types (Wet), which were aggregates of multiple cover types (see Forest Stand Delineation and supplemental material). We defined patch size as the area (ha) of each surveyed forest stand.

We developed candidate models within the *land-cover type* and *vegetation structure* groups using single covariates and all possible combinations of covariates as interactive and additive models. We evaluated the best-supported candidate model, within and among groups, to predict woodcock occupancy using AIC_c (Burnham and Anderson 2002), model weights (w), and precision of coefficient estimates (SE). We reported coefficients (β) ± SE in the results section of the manuscript for candidate models of interest. We considered models informative if 85% confidence intervals of the untransformed coefficients did not contain zero (Arnold 2010). We assessed goodness-of-fit of global occupancy models in each year using 500 bootstrap simulations. We refit data sets from the model to "perfect" data and estimated a fit statistic using χ^2 (Fiske and Chandler 2011). We also estimated $\hat{c}$ using the AICcmodavg package following Mackenzie and Bailey (2004).

STAND-SCALE DENSITY ESTIMATES

We used a hierarchical distance sampling approach from Royle et al. (2004) that was modified for use in surveys conducted by a pointing dog (Guthery and Mecozzi 2008). Similar to occupancy modeling, distance sampling incorporates the observation process to estimate a latent state variable; however, distance sampling results in estimates of density instead of occupancy. Hierarchical distance sampling uses a multinomial Poisson mixture model where N_t is the latent abundance on transect $_t$ and π is the vector of cell probabilities among distance intervals that correspond to the vector of counts Y_t. In distance sampling, the vector of cell probabilities is the product of the probability of detection and the probability of occurrence based on the distance of the organism from the observer (Royle et al. 2004, Fiske and Chandler 2011) where

$$N_t \sim Poisson(\lambda)$$
$$(N_t) \sim Multinomial(N_t, \pi)$$

The hierarchical distance sampling method allows for covariate modeling using a log link (Royle et al. 2004).

We modified the distance sampling approach to quantify the area searched by the pointing dog and estimate densities of woodcock following Guthery and Mecozzi (2008). To estimate total area searched within each survey site, we established a line transect from each GPS track and a corresponding effective strip width (ESW) that we estimated using PFDs (Guthery and Mecozzi 2008). To estimate the ESW, we truncated the greatest 5% of all PFDs and fit remaining PFDs to a hazard rate key function, to model the detection rate as a function of distance from the pointing dog transect for this study (Buckland et al. 1993). In addition, we buffered each line transect by its estimated ESW using ArcGIS 10, and used the resulting estimated area as the total area (ha) searched as a detection covariate in multi-visit hierarchical models of occupancy (see above). We visually assessed detection-curve shape within stands, survey sites, and study areas using PFD histograms. We then pooled PFDs across surveys because there was not a consistent difference in detection-curve shape among stands, survey sites, or study areas (i.e., the pointing dog detected birds similarly at all sites).

We binned all PFDs within the first 8 m from the transect together and used a hazard rate key function to model detection probability as a function of distance. By creating a large first bin for the multinomial Poisson mixture model from Royle et al. (2004), we were able to model detection in a domain where it decreased as distance increased. The hazard rate key function also provided a good description of the detection function and can be used when the detection function has a wide shoulder of equal detection probability (Marques et al. 2011).

Distance sampling operates under the assumptions that detection is perfect at the center of the transect line [g(0) = 1] and that animals are detected at their initial location (Buckland et al. 1993). Further assumptions of the methods outlined in Guthery and Mecozzi (2008) include: that PFD measurements are accurate, woodcock are only counted once, each flushing observation is an independent event, the probability of detection is independent of clustering, the creation of transect lines does not influence the spatial distribution of woodcock, PFDs are an adequate surrogate to perpendicular distances from the line transect, and the random selection of survey sites outweighed any bias resulting from having nonrandom transects within survey sites and stands.

Observation Process We estimated woodcock density using the distsamp() function in the R package unmarked (Royle et al. 2004, Fiske and Chandler 2011, R Development Core Team 2016). We binned multiple survey transects and distance data (PFD) with breakpoints at 0, 8, 12, 16, and 20 m to estimate detection probability as a function of distance (Royle et al. 2004). To remove redundantly searched portions of dog tracks, where the dog circled back onto its original track, we buffered all surveys by an ESW estimated from the hazard rate detection model in ArcGIS 10. We estimated transect lengths from buffered GPS dog tracks by subtracting πESW2, dividing by 2ESW, and finally adding 2ESW. We then converted the area searched estimates back to t`ransect length estimates. The resulting transect length estimates did not contain redundantly searched areas and were therefore appropriate for use in the Royle et al. (2004) model.

We fit multinomial-Poisson mixture models to detections and distances (Royle et al. 2004). We first modeled the observation process and examined the influence of average daily temperature (degrees C), percent canopy cover <0.3 m tall, and effect of a first survey on the distance at which we detected woodcock using hazard rate, half-normal, and uniform functions (Buckland et al. 1993). Similar to the multi model approach we used for occupancy models, we included each covariate and functions as separate candidate models and assessed the rank of each model based on AIC_c (Burnham and Anderson 2002). We included a first-survey effect to assess whether there was a difference in detection between first and repeat surveys. Hazard rate key function models were best-supported based on AIC_c and we used the hazard rate key function to examine habitat covariate influence on abundance (λ) estimates.

Density covariate modeling To allow for comparison to occupancy estimates, we used the same covariates, candidate models, and modeling approach described above for occupancy models. We grouped covariates in land-cover type and vegetation structure hierarchical model sets to assess habitat use differences among both stand types and the available cover within stands. We estimated densities in the 8 land-cover types and aggregated cover types delineated previously for occupancy models (see Forest Stand Delineation above). We evaluated the best-supported candidate model, within and among groups, to predict woodcock densities using AIC_c, *w* (Burnham and Anderson 2002), and precision of coefficient estimates (SE). We reported coefficients (β) ± SE in the results section of the manuscript for candidate models of interest. We considered models informative if 85% confidence intervals of the untransformed coefficients did not contain zero (Arnold 2010). We used parametric bootstrapping to assess goodness-of-fit of distance sampling data pooled among years using 500 bootstrap simulations. We refit data sets from the model to "perfect" data and estimated a fit statistic using χ^2 (Fiske and Chandler 2011). Similar to occupancy models, we considered a model to fit these data if the observed value was >0.05% of the reference distribution (Sillett et al. 2012). Finally, we used the best-supported detection model with constant density to estimate density pooled among all survey sites and winters.

COMPARISON OF OCCUPANCY AND DENSITY ESTIMATES

We estimated occupancy and density for each cover type to evaluate the use of each approach for comparing habitat use among stands. We reported coefficients of variation (CV) to provide a relative estimate of error among all models and model approaches.

Results

During 185 surveys, the pointing dog traversed 1,596 km, we flushed woodcock 283 times, and we detected 300 individual woodcock. Woodcock were sparsely distributed throughout the survey sites ($\underline{x}$ = 1.65 flushes per survey) and occupied 83% and 71% of the 78.5-ha survey sites during the winters of 2010–2011 and 2011–2012, respectively. In 2010–2011, we flushed an average of 1.70 (SD = 2.06) woodcock per survey on both study areas combined, and in 2011–2012, we flushed an average of 1.60 (SD = 2.21) woodcock on both study areas combined. The mean area of all stands that woodcock occupied was 23.14 ha (SD = 21.50) and we estimated the highest woodcock density in stands classified as pine forests 1–3 m tall (Fig. 5).

STAND-SCALE OCCUPANCY

We identified 82 unique stands within survey sites that were on average 22.9 (SD = 21.50) ha in size. We detected woodcock at least once in 32% of stands (naïve ψ = 0.34; site-by-land-cover-type polygons) in 2010–2011, and in 35% of stands (naïve ψ = 0.35) in 2011–2012. The constant single-season occupancy model produced estimates of ρ = 0.53 (SE = 0.07) and ψ = 0.39 (SE 0.06) in 2010–2011 and ρ = 0.58 (SE = 0.05) and ψ = 0.38 (SE 0.06) in 2011–2012. The estimated probability of not detecting a woodcock when woodcock were present was 0.10 and 0.03 in 2010–2011 and 2011–2012, respectively. Both single-season models exhibited adequate goodness-of-fit (2010–2011 $\hat{c}$ = 0.36, P = 0.80, 2011–2012 $\hat{c}$ = 0.79, P = 0.51).

Observation process We held state variables (occupancy and density) constant using intercept-only stand-scale models to estimate detection probabilities based on stand and survey site covariates (Table 1). For occupancy models, the proportion of area searched (areasearched) within each stand was related to detection in 2010–2011 but not in 2011–2012 (Table 1). The best-supported detection probability model for 2010–2011 included the proportion of stand surveyed as a covariate (Table 1) and was the only candidate model with more support (based on AIC_c, *w* = 0.67) than the intercept-only model (*w* = 0.11). All relationships that follow are reported as the coefficient (β) ± SE. The proportion of stand surveyed was positively related

Table 1. Candidate hierarchical models of American woodcock detection and single-season occupancy in East Texas during the winters of 2010–2011 and 2011–2012. Single-season occupancy models were constructed using the R package unmarked (Mackenzie et al. 2006, Fiske and Chandler 2011).

Winter 2010–2011					**Winter 2011–2012**				
Model[1,2]	**k**	**AICc**	**ΔAICc**	***w***	**Model[1,2]**	**k**	**AICc**	**ΔAICc**	***w***
ψ(.),ρ(areasearched)	3	213.23	0.00	0.67	ψ(.),ρ(.)	2	211.54	0.00	0.34
ψ (.),ρ(.)	2	216.83	3.60	0.11	ψ(.),ρ(areasearched)	3	213.02	1.48	0.16
ψ (.),ρ(firstsurvey)	3	217.59	4.36	0.08	ψ(.),ρ(firstsurvey)	3	213.38	1.84	0.14
ψ (.),ρ(30cm)	3	218.10	4.87	0.06	ψ(.),ρ(julian)	3	213.54	2.00	0.13
ψ (.),ρ(julian)	3	218.50	5.27	0.05	ψ(.),ρ(30cm)	3	213.61	2.07	0.12
ψ (.),ρ(temp)	3	218.85	5.62	0.04	ψ(.),ρ(temρ)	3	213.69	2.15	0.12

1 k = no. of parameters, AIC_c =Akaike's Information Criterion adjusted for sample size, ΔAIC_c = difference in AIC_c relative to smallest value. Model symbols included ψ = occupancy probability, and ρ = detection probability for multiple-visit models.

2 Covariates represent estimated proportion of survey site searched each survey by the dog (areasearched), estimation of a second detection probability for the first survey (first survey), canopy cover <30 cm tall (<30cm), days since the first survey (julian), and temperature (temp).

with detection probability in 2010–2011 (β = 0.81 ± 0.37), and its 85% confidence interval did not contain zero. In 2011–2012, proportion of stand surveyed was not related to detection (β = 0.41 ± 0.47, w = 0.16) and was not competitive with the intercept-only model (w = 0.34).

Occupancy covariate modeling After accounting for detection, we modeled relationships of occupancy with habitat covariates within the land-cover type and vegetation structure model groups. Within the land-cover type model group, occupancy in 2010–2011 was better predicted by quadratic patch size of the timber stands than by land-cover-type category, and the quadratic effect of patch size (β_1 = 1.24 ± 0.44, β_2 = -0.47 ± 0.40; w = 0.19) was the best predictor of occupancy (Table 2). In 2011–2012, occupancy was best predicted by the model including categorical land-cover types (w = 0.25).

Within the vegetation structure model group, canopy cover 0.5–5 m tall was the best predictor of occupancy in both 2010–2011 (β = 0.97 ± 0.39, w = 0.62) and 2011–2012 (β = 0.80 ± 0.31, w = 0.60; Table 2) and did not contain zero in the 85% confidence interval. The highest occupancy rates were associated with percent canopy cover 0.5–5 m tall >60% (Fig. 4), and we estimated a canopy cover threshold of 50% (i.e., stands with <50% canopy cover 0.5–5 m tall were likely to be occupied by woodcock). At least 50% of the stands with >50% canopy cover 0.5–5 m tall were occupied by woodcock.

STAND-SCALE DENSITY ESTIMATES

We estimated an ESW of 10.03 m based on a hazard rate detection function (Buckland et al. 1993). Our estimate of density for both winters pooled was 0.16 woodcock/ha (SE = 0.13) and the goodness-of-fit was adequate (χ^2=1,999, P = 0.331). Woodcock density was higher in 2010–2011 ($\underline{x}$ = 0.27 woodcock/ha [SE = 0.12]) than in 2011–2012 ($\underline{x}$ = 0.13 woodcock/ha [SE = 0.02]) when estimated using the intercept-only density model.

Observation process Detection-related covariates did not improve the parsimony of models of woodcock density. However, we did assess the shape of the detection curve (e.g., half-normal, uniform, or hazard rate function) separately for PFDs from each year of the study. We measured PFD at 221 locations where we flushed woodcock during both winters of the study. The best-supported detection model included a hazard rate key function and carried 91% of the model weight (w = 0.91) when compared to half-normal and uniform models.

Within the land-cover-type model group, the model including land cover was the best-supported model in 2010–2011 and 2011–2012 (w = 1.0 in 2010–2011 and 2011–2012). Overall, pine forests 1–3 m tall supported the greatest woodcock density (Fig. 5).

Within the vegetation structure model group, densities were best predicted by canopy cover 0.5–5 m tall (Table 2). In both years of the study, models of density that included canopy cover 0.5–5 m tall were the best-supported (w= 0.62 in 2010–2011 and w = 0.60 2011–2012) and had β-coefficients (2010–2011= 0.28 ± 0.10, 2011–2012 = 0.57 ± 0.09) with 85% confidence intervals that did not contain zero (Fig. 4).

COMPARISON OF OCCUPANCY AND DENSITY ESTIMATES

In 2010–2011, density of woodcock in pine forest 1–3 m tall was greater than in pine plantations >3 m tall, mature pine forests, and disturbed/tame grassland based on 85% confidence intervals (Table 3; Fig. 5). In 2011–2012, densities in pine forest 1–3 m and SMZ areas were greater than at all other cover types except pine plantation >3 m based on 85% confidence intervals. Occupancy models had an average CV of 3.8%, and density models based on distance sampling had an average CV of 37% (Table 3, Fig. 5).

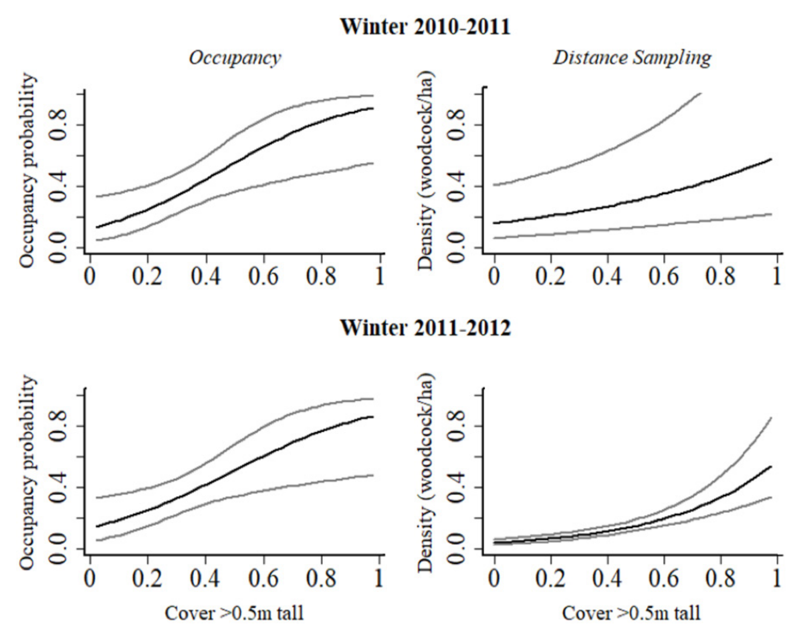

Figure 4. Relationships from best-supported models predicting American woodcock occupancy and density during winter in East Texas, USA as a function of the percent canopy cover of vegetation 0.5–5.0 m tall. Plots are from single-season occupancy models (left) and models of density based on distance sampling (right).

Discussion

Understanding woodcock population response to global and local change necessitates the use of cost-effective monitoring that can identify differences in habitat use among land-cover types and variably distributed resources at broad geographic scales (Morrison 2001, Grimm et al. 2008, Keith et al. 2008, Ellwood et al. 2013). We evaluated the combined use of pointing dogs, hierarchical models, and GIS analysis to characterize woodcock winter habitat use at the survey-site and stand scales (Guthery and Mecozzi 2008, Fiske and Chandler 2011, Diamond and Elliott 2009). Woodcock in East Texas occupied diurnal sites in forest stands having >50% canopy cover 0.5–5 m tall. Additionally, we found that relationships between occupancy and specific land-cover types (stands) differed between years but density of woodcock was consistently higher in pine forest 1–3 m tall. We implemented a modified distance sampling approach to estimate density and compare habitat use among stands with different forest cover types (site-by-land-cover polygons). Effect sizes of factors related to density estimated using distance sampling were greater compared to occupancy modeling and an N-mixture modeling approach described by Sullins (2013), whereas occupancy estimates had lower CVs. Although lower CVs indicated that occupancy estimates were more precise, the greater differences in estimated density among stands may make our distance sampling approach more useful when comparing habitat use among forested cover types or management practices.

Within occupied survey sites, mean stand area was 23.14 ha (SD = 21.50), which is >2X the average diurnal home-range size estimate for wintering woodcock in Alabama ($\underline{x}$ = 9.2 ha, SD = 2.3; Horton and Causey 1979). Although most forested stands had similar occupancy estimates, our occupancy modeling approach that used surveys conducted with trained pointing dogs highlights a potential tool that may aid future surveys for woodcock. In particular, occupancy surveys using pointing dogs could assist in monitoring populations during the winter when they are more difficult to detect than displaying males in spring, and for which limited information exists regarding habitat use and land-cover associations. The simplicity of occupancy estimates limits bias while also maintaining high precision; it is more likely to correctly predict presence or absence as opposed to density (Table 3, Walther and Moore 2005). We observed no use of disturbed or tame grassland and deciduous forest cover types by woodcock during the day on wintering areas in East Texas. The absence of woodcock in deciduous forest stands was likely a result of all forest cover types dominated by hardwoods occurring in drier upland areas on our study areas. The xeric nature of upland deciduous forest combined with drought during our study period likely made this land-cover type unsuitable. We did observe woodcock using more traditional bottomland hardwood forest, but most of these areas included some component of coniferous (*Pinus* spp.) forest cover and were therefore classified as mixed pine/hardwood forest. Disturbed and tame grasslands in our classification system included grasslands and recent clear-cuts. Although the limited use of grasslands by woodcock during the daytime has been previously reported, woodcock in East Texas

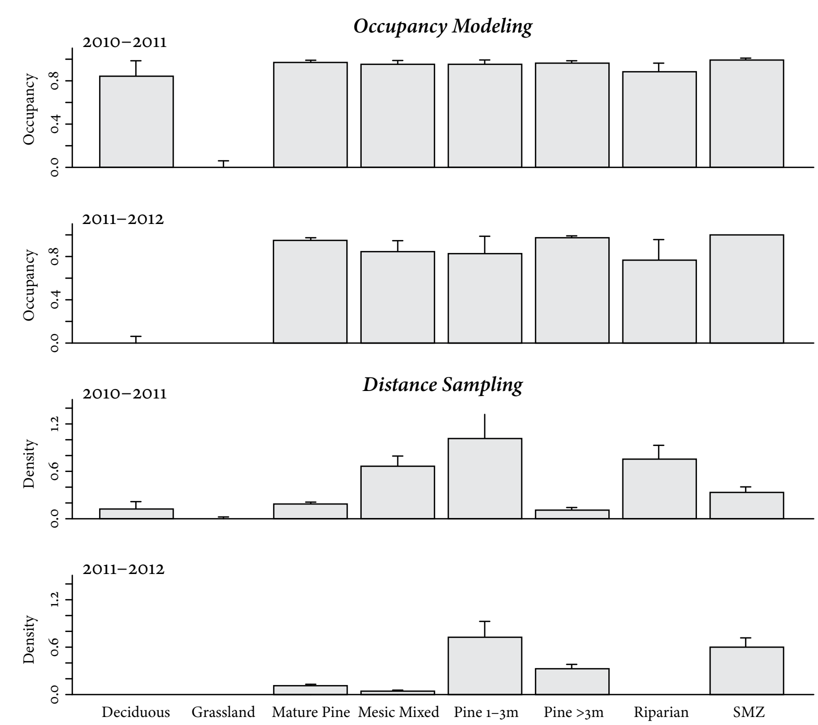

Figure 5. Predicted occupancy and density of American woodcock in 8 land-cover types (stands) in East Texas, USA during winter of 2010–2011 and 2011–2012. The 8 land-cover types were deciduous forest (Deciduous), disturbance/tame grassland (Grassland), mature pine forest (Mature Pine), mesic mixed pine/hardwood forest (Mesic Mixed), pine forest 1–3 m tall (Pine 1–3m), pine plantation >3 m tall (Pine >3m), forest wetland/riparian area (Riparian), and streamside management zones (SMZ). See Methods for description of forest stand delineation and details on classification.

were historically known to use recent clear-cuts when forest management incorporated piling debris in windrows (Whiting 2001), suggesting the availability or suitability of this cover type may have changed with changing forest management practices.

Best-supported models of both occupancy and density included canopy cover 0.5–5 m tall, indicating the importance of dense thicket habitat for woodcock in the winter. The probability of occupancy of stands by woodcock increased with percent canopy cover of vegetation 0.5–5 m tall. This relationship with occupancy exhibited a threshold where at ~50% canopy cover of vegetation 0.5–5 m tall the probability of occupancy of woodcock was ~0.5. We also found a more exponential relationship between percent canopy cover of vegetation 0.5–5 m tall with woodcock density (Fig. 4). The information provided from occupancy modeling related to canopy cover covariates may be of greater use to land managers who need to make discrete, yes-or-no decisions when setting specific habitat-related goals (Mavrommati et al. 2016). For questions related to habitat abundance and habitat connectivity, the coarse but precise estimates from the occupancy modeling may be especially useful.

Table 2. Hierarchical models (3 highest ranking and intercept-only) used to estimate American woodcock occupancy and density at survey sites in East Texas in winter during 2010–2012. We constructed single-season occupancy models and models of density based on distance sampling in the R package unmarked (Mackenzie et al. 2006, Royle et al. 2004, Fiske and Chandler 2011).

Winter 2010–2011 Model[1,2]	k	AICc	ΔAICc	*w*	Winter 2011–2012 Model[1,2]	k	AICc	ΔAICc	*w*
OCCUPANCY									
Vegetation structure									
ψ(>0.5m),ρ(.)	4	204.97	0.00	0.62	ψ(>0.5m),ρ(.)	3	204.86	0.00	0.60
ψ(>0.5m+Sdense),ρ(.)	5	206.02	1.05	0.37	ψ(>0.5m+Sdense),ρ(.)	4	205.78	0.92	0.38
ψ (.),ρ(.)	3	213.23	8.26	0.01	ψ(.),ρ(.)	3	213.02	8.16	0.01
Landcover									
ψ(PS²),ρ(.)	4	208.22	0.00	0.19	ψ(Ltype)ρ(.)	9	200.90	0.00	0.25
ψ(Ypine+PS²),ρ(.)	5	209.23	1.01	0.11	ψ(Wet+Mpine+Ypine+PS)	8	201.81	0.91	0.16
ψ(Ltype),ρ(.)	10	212.80	4.58	0.02	ψ(Mpine+Wet*PS)ρ(.)	8	202.49	1.59	0.11
ψ(.),ρ(.)	3	213.23	5.01	0.02	ψ(.)ρ(.)	4	212.92	12.02	0.00
DENSITY									
Vegetation structure									
haz(.)λ(>0.5m)	4	442.16	0.00	0.70	haz(.)λ(>0.5m)	4	480.27	0.00	0.68
haz(.) λ(>0.5m+Sdense)	5	444.28	2.12	0.24	haz(.)λ(>0.5m+Sdense)	5	481.80	1.53	0.32
haz(.)λ(.)	3	447.12	4.96	0.06	haz(.)λ(.)	3	515.35	35.08	0.00
Landcover									
haz(.)λ(Ltype)	10	391.85	0.00	1.00	haz(.)λ(Ltype)	10	421.14	0.00	1.00
haz(.) λ(Mpine+Ypine+Wet)	6	405.66	13.81	0.00	haz(.)λ(Mpine*PS)	8	457.38	36.24	0.00
haz(.)λ(Ypine+Wet)	5	406.72	14.87	0.00	haz(.)λ(Wet*PS)	8	477.85	56.71	0.00
haz(.)λ(.)	3	447.12	55.27	0.00	haz(.)λ(.)	3	515.35	94.21	0.00

[1] k = no. of parameters, AIC_c =Akaike's Information Criterion adjusted for sample size, ΔAIC_c = difference in AIC_c relative to smallest AIC_c value. Model symbols included ψ = occupancy probability, ρ = detection probability for multiple-visit models, haz = hazard rate key function used to model detection distance, and λ = abundance parameter.

[2] Covariates represent canopy cover 0.5–5 m tall (>0.5m), stem density of trees >5 m tall (Sdense;trees/ha), area of land-cover stands within survey sites (PS), pine plantation >3 m tall and mature pine forest (Mpine), forest wetland and riparian land-cover types (Wet), young pine forest 1–3 m tall (Ypine), and 8 categorical land-cover types created from Diamond and Elliott (2009; Ltype). The estimated area searched based on distance sampling was used as a probability of detection covariate for all occupancy models.

Our detection curves derived through distance sampling were similar to those reported by Guthery and Mecozzi (2008) for flushes of >7 northern bobwhites (*Colinus virginianus*). Both northern bobwhites and woodcock showed a peak in frequency of detections away from the center of the survey transect, likely due to using PFDs instead of perpendicular distances from a transect that was a straight line. Namely, PFD was not always equivalent to the perpendicular distance because, upon detection, the pointing dog typically stopped ~5 m from the woodcock even when the woodcock would have been directly on the transect (i.e., a perpendicular distance of 0 m). The estimation of detection curves in distance sampling is contingent on probability of detection decreasing as distance from the transect line increases. To meet the assumption of detection decreasing with distance it is important to consider how distance intervals are binned (Buckland et al. 1993). The first bin will likely need to encompass a larger area when surveying wildlife with pointing dogs compared to traditional distance sampling with a human visual observer.

One potential drawback of the distance sampling method we used is that, although the starting points were randomly generated, the paths followed were not completely random. A potential solution to this issue is to generate random, straight-line transects that the dog handler walks while the pointing dog roams freely (Warren and Baines 2011). In this approach, the detection distance is the perpendicular distance from the straight-line transect (i.e., where the handler walks) to where birds flush (Warren and Baines 2011). The Warren and Baines (2011) method was developed in treeless areas where observing flushes is possible at great distances. In contrast, visually monitoring a pointing dog at distances >50 m is not feasible in densely stocked 5-m-tall pine plantations. Although our transects were not completely randomly located we did survey all cover types within survey sites during each visit and the handler stayed <50 m away from the pointing dog to ensure detection of woodcock that flushed unexpectedly.

Table 3. Estimates, standard errors (SE), and coefficients of variation (CV) of occupancy and density of American woodcock in 8 land-cover types derived from Diamond and Elliot (2009) in East Texas. We constructed single-season occupancy models and models of density using distance sampling using the R package unmarked (Mackenzie et al. 2006, Royle et al. 2004, Fiske and Chandler 2011).

	Occupancy			Density		
Land-cover type	**Estimate**	**SE**	**CV**	**Estimate**	**SE**	**CV**
2010–2011						
Deciduous	0.84	0.15	18	0.11	0.11	100
Grassland	0.00	0.06	N/A	0.00	0.00	N/A
Mature Pine	0.96	0.02	2.2	0.18	0.03	16
Mesic Mixed	0.95	0.04	3.8	0.65	0.15	23
Pine 1–3m	0.94	0.05	5.6	1.01	0.33	32
Pine >3m	0.96	0.03	2.8	0.10	0.04	36
Riparian	0.87	0.09	10	0.74	0.18	25
SMZ	0.99	0.01	1.4	0.32	0.09	28
2011–2012						
Deciduous	0.00	0.06	N/A	0.00	0.00	N/A
Grassland	0.00	0.00	N/A	0.00	0.00	N/A
Mature Pine	0.95	0.02	0.02	0.10	0.02	16
Mesic Mixed	0.85	0.10	0.12	0.02	0.02	100
Pine 1–3m	0.83	0.16	0.19	0.71	0.21	30
Pine >3m	0.97	0.02	0.02	0.33	0.05	16
Riparian	0.76	0.20	0.26	0.00	0.00	N/A
SMZ	1.00	0.00	<0.001	0.59	0.12	20

[1] Land-cover type abbreviations are for deciduous forest (Deciduous), disturbance/tame grassland (Grassland), mature pine forest (Mature Pine), mesic mixed pine/hardwood forest (Mesic Mixed), pine forest 1–3 m tall (Pine 1–3m), pine plantation >3 m tall (Pine >3m), forest wetland/riparian area (Riparian), and streamside management zones (SMZ).

COMPARISON OF OCCUPANCY AND DENSITY ESTIMATES

Density and occupancy are inherently related (Kery and Royle 2016, Miller et al. 2016). Occupancy and density are linearly related when species are rare and local abundance is low. In contrast, when a species is common, density can provide more inference on relationships between abundance and habitat-related variables (Kery and Royle 2016). In East Texas during winter, woodcock were common throughout almost all forest cover types, and density estimates improved inference of habitat use among forest cover types (Table 3) compared with occupancy estimates. Occupancy estimates within forest cover types, excluding deciduous forests in 2011–2012, ranged from 0.76–1.00, whereas density estimates ranged from 0.02–1.00 woodcock/ha. If the goal of future research or monitoring is to evaluate differences in habitat use among categorically defined patches—whether land-cover type, as in this example, soil type, or management practice—the distance-sampling approach has the greatest potential value. Quantifying differences in habitat use among sites using occupancy may be most effective when the proportion of occupied sites approaches 0.5 (Kery and Royle 2016).

Management Implications

Effective monitoring is a necessary step for the adaptive management of landscapes for woodcock. Using pointing dogs to monitor woodcock populations provides an option for estimating abundance of woodcock outside of breeding season when Singing Ground Surveys are conducted, and may provide an effective means of evaluating management on the wintering grounds and at migratory stopover sites. Our monitoring of woodcock occupancy and densities indicated that current forest management practices in East Texas provided habitat for woodcock at broad scales, and that use of cover types varies among years with greatest densities in pine forests 1–3 m tall. Therefore, forest management that maintains a heterogeneity of forested cover types on the landscape may be ideal. We advise future winter monitoring efforts to survey between 15 December – 31 January if possible, based on known arrival and departure dates on wintering grounds. Finally, a stratified random sampling design to distribute starting points among categorical land-cover covariates is appropriate when differences in occupancy or densities among cover types is the question of interest. Our survey protocol was not extravagant and, therefore, field work could be replicated with limited funding when matched with the proper personnel ($300–700 for a GPS collar and handheld unit).

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Supplemental Material

METHODS

Stratified random sampling of survey sites based on soil suitability We derived digital soil suitability following Cade (1985) using SSURGO (Soil Survey Geographic Database) soil maps to stratify sampling and identify survey sites (Sullins 2013, Soil Survey Staff 2017). Soil suitability scores were based on the texture and drainage characteristics of soil types, and we used them to evaluate the Cade (1985) woodcock wintering habitat suitability index model in a concurrent research project (Sullins 2013). Soil suitability scores ranged from 0–1, where a soil suitability score of 0 indicated unsuitable soils for woodcock and a score of 1 indicated optimal soils (Cade 1985). In DCNF, we randomly selected 6 survey sites within 3 different classes of soil suitability scores: 0–0.39, 0.4–0.85, and 0.86–1.0. At the Campbell Unit, we randomly selected survey sites within 2 classes of soil suitability scores (0–0.85, and 0.86–1.0), because there were fewer soil types present and they were less variable than those at DCNF. We selected survey sites only if the assigned soil suitability class comprised ≥40% of its area.

Landcover classification and aggregation Pine forest 1–3 m tall included both pine plantations and naturally regenerating pine forest. We delineated the SMZ classification and land-cover classification corrections for timber stands harvested after publication of Diamond and Elliott (2009) using satellite imagery provided as a basemap in ArcGIS 10 (imagery provided by ESRI, i-cubed, USDA FSA, USGS, AEX, GeoEye, Getmapping, Aerogrid, and IGP). Streamside management zones were typically mixed pine/hardwood or hardwood forest, and included areas within 30–80 m of ephemeral streams. We combined stands of pine plantation >3 m tall and mature pine forest land-cover classifications from Diamond and Elliott (2009) to estimate proportion of mature pine forest (Mpine). We grouped all wetland, SMZ, and stream/riparian cover types together to estimate proportion of wet cover (Wet) because woodcock are thought to select young forest cover types with moist soil (Straw et al. 1994, Berry et al. 2006).

Survey site occupancy We estimated woodcock occupancy (ψ) and detection probabilities (ρ) at the survey site scale using the package unmarked (Fiske and Chandler 2011) in R (R Development Core Team 2016) and following Mackenzie et al. (2006). We estimated naïve occupancy for each winter (i.e., 2010–2011 and 2011–2012) as the ratio of sites having ≥1 detection to those with zero woodcock detections. We modeled detection at the survey site scale and included covariates for study area, percent mature pine forest (Diamond and Elliott 2009), percent vegetation cover <0.3 m tall, percent vegetation cover 0.5–5 m tall, average daily temperature (degrees C), ordinal date (0 + median survey date each winter), and precipitation (mm accumulated in 7 d leading up to survey). After obtaining the top-ranking detection model based on AIC_c, we kept the detection portion of the model constant, using the covariate from the top-ranked detection model, and fit models with the same covariates list immediately above to predict the latent occupancy process.

We tested goodness-of-fit of the global model using 1,234 bootstrap samples and considered models overdispersed if $\hat{c} > 1.0$ (Burnham and Anderson 2002, Mackenzie and Bailey 2004). When models were overdispersed (i.e., $\hat{c} > 1.0$), we used $QAIC_c$ for model selection and inflated parameter standard error estimates by $\sqrt{\hat{c}}$ (Burnham and Anderson 2002, Mackenzie et al. 2006). We estimated the probability of not detecting a woodcock at a site where it was actually present using:

$$(1- \rho)^n,$$

where n was the number of surveys per survey site (Mackenzie et al. 2006).

RESULTS

Survey Site Occupancy In winter 2010–2011, most (77%; 14/18) 0.5-km radius survey sites at DCNF and all (6/6) survey sites at the Campbell Unit were occupied by ≥1 woodcock. The total proportion of survey sites occupied (naïve ψ) in 2010–2011, not adjusted for detection probability, was 0.83. In 2011–2012, 3 survey sites occupied the prior winter were not occupied, and 1 previously unoccupied survey site was occupied at DCNF. There was no change in occupancy at survey sites at the Campbell Unit, as we detected woodcock during ≥1 survey at all survey sites during both winters. For both study areas combined, in 2011–2012, the naïve occupancy estimate was 0.71 (17/24 survey sites). In the winter of 2011–2012, we detected ≥1 woodcock at all Campbell Unit survey sites and 61% of DCNF survey sites. For both winters combined, we detected woodcock at least once on 87% of survey sites, detected 1–3 woodcock at 50% of occupied survey sites, and detected a maximum of 8 woodcock during a single survey.

The best-supported detection probability model for both years did not include any covariates and we used the intercept-only model to estimate detection as $\rho = 0.61$ (SE = 0.07) in 2010–2011 and $\rho = 0.75$ (SE = 0.05) in 2011–2012. Overall ψ was 0.89 (SE = 0.09) and 0.71 (SE = 0.09) in 2010–2011 and 2011–2012, respectively. The estimated proportion of survey sites where woodcock were present but not detected during our surveys (i.e., false negative) was 0.06 (2010–2011) and <0.01 (2011–2012). Model goodness-of-fit estimated from 1,234 bootstrap simulations provided evidence of slight overdispersion in 2010–2011($\hat{c}$ = 1.39, p = 0.23) and no overdispersion in 2011–2012 ($\hat{c}$ = 0.62, p = 0.88).

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