



## Original Article

# Tree Stocking Affects Winter Bird Densities Across a Gradient of Savanna, Woodland, and Forest in the Missouri Ozarks

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**ABSTRACT** Savanna and woodland were historically prevalent in the midwestern United States, and managers throughout the area are currently attempting to restore these communities. Better knowledge of the responses of breeding and non-breeding birds to savanna and woodland restoration is needed to inform management. We surveyed abundance of winter resident birds across a gradient of tree stocking encompassed by savannas, woodlands, and non-managed forests in the Missouri Ozark Highlands, USA, and assessed the effect of stocking on bird densities. We conducted point counts at 560 locations along 42 transects on 10 sites across 2 winters between December and February, 2009–2011. We estimated detection probabilities and densities of birds using hierarchical, distance-based abundance models that incorporate covariates into estimation of both detection probabilities and densities. We fit models for 12 species with >49 detections and met model assumptions. Detection probabilities were affected by observer, temperature, wind speed, and stocking, and there was some level of support of the effects of stocking on the densities of all 12 species. Densities of black-capped plus Carolina chickadees (*Poecile atricapillus*, *P. carolinensis*), brown creeper (*Certhia americana*), golden-crowned kinglet (*Regulus satrapa*), and red-bellied woodpecker (*Melanerpes carolinus*) increased with stocking; whereas, densities of eastern bluebird (*Sialia sialis*), hairy woodpecker (*Picoides villosus*), and northern flicker (*Colaptes auratus*) were greatest at intermediate values of stocking. Although densities of 7 of the 12 species varied substantially across the range of stocking, all species used all 3 communities across a wide range of stocking. We provide winter densities of 12 of the most common overwintering bird species in the Missouri Ozarks; the relationships between their densities and stocking can be used to guide management where managers have bird-species-specific objectives. © 2013 The Wildlife Society.

**KEY WORDS** bird abundance, detection probability, distance sampling, forest, restoration, savanna, winter, woodland.

Savanna and woodland are natural communities that were historically prevalent in the midwestern United States. Savanna is generally defined as grassland with open-grown, scattered trees and shrubs (Nuzzo 1986, McPherson 1997, Nelson 2002), while woodlands have greater and more consistent canopy cover, a sparse understory, and an herbaceous ground layer consisting of forbs, grasses, and sedges as a result of fire (Nelson 1985, Packard and Mutel 1997, Anderson et al. 1999). Criteria for distinguishing savanna, woodland, and forest vary regionally, but in Missouri, USA, desired structure for savanna is 10–30% canopy cover and <30 ft<sup>2</sup>/acre (1 ft<sup>2</sup> = 0.2296 m<sup>2</sup>/ha) basal area; woodland, 50–80% canopy cover and 30–90 ft<sup>2</sup>/acre basal area; and forest, >80% canopy cover and >80 ft<sup>2</sup>/acre

basal area (Nelson 2002, U.S. Department of Agriculture Forest Service 2005). Forest communities generally have a shade-tolerant understory and midstory and sparse ground cover because of less frequent fire and lack of sunlight reaching the forest floor (Nelson 2002). Oak savanna covered 11–13 million ha of the Midwest prior to European settlement, but only 2,607 ha remained by 1985 (Nuzzo 1986). Various land-use changes associated with the arrival of settlers and prolonged fire suppression led to forest succession that degraded most oak savanna within 20–40 years (Nuzzo 1986, Peterson and Reich 2001). Multiple land-management agencies are restoring savanna and woodland; approximately 22,000 ha of an estimated 971,000 ha of degraded oak woodland in the state of Missouri are being restored by the Missouri Department of Conservation, the Missouri Department of Natural Resources, and The Nature Conservancy (K. Borisenko, Missouri Department of Conservation; K. McCarty, Missouri Department of Natural Resources; D. Ladd, The Nature

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Conservancy; personal communication). An estimated 24,700–49,400 ha of restorable oak savanna maintain floristic diversity to justify preservation in Missouri (Currier 1993). Common management tools for savanna and woodland restoration include mechanical tree thinning and prescribed fire. Mechanical thinning reduces tree stocking and opens the canopy to allow sunlight to reach ground vegetation. Prescribed fire kills small-diameter woody species and encourages growth of grasses and forbs, resulting in decreased tree density and basal area (Peterson and Reich 2001). Restoring savanna and woodland can promote biodiversity and may provide more suitable communities for some species that now occupy forest or grassland (Davis et al. 2000).

Savanna and woodland restoration can increase breeding season avian diversity and densities. Burned savanna sites in Minnesota, USA, had an average of 31 bird species and  $6.95 \pm 1.26$  birds/ha, while unburned savanna sites had an average of 20 species and  $3.82 \pm 0.065$  birds/ha (Davis et al. 2000). In Indiana, USA, fire frequency in savannas and woodlands was positively correlated with species diversity and density of the most-threatened species (Grundel and Pavlovic 2007a). However, less is known about the effects of restoration efforts on winter bird communities. Grundel and Pavlovic (2007a, b) determined bird abundance during winter, both spring and autumn migrations, and the breeding season across a gradient ranging from open savanna to forest in northwestern Indiana, USA; however, this is the only study of which we are aware that estimates winter densities across a restoration gradient. Most winter studies took place in non-temperate overwintering habitat (Gutzwiller 1991, Cox and Jones 2009), used focal species to illustrate the effects of mid- to high-severity fire (Kreisel and Stein 1999, Covert-Bratland et al. 2006, Cox and Jones 2009), or considered different habitats (Zeller and Collazo 1995). There is little information on the effects of restoration on non-breeding bird communities in savanna or woodland. Because winter residents may depend on different resources than do breeding migrants, it is important to understand how winter residents respond to restoration management in addition to breeding birds.

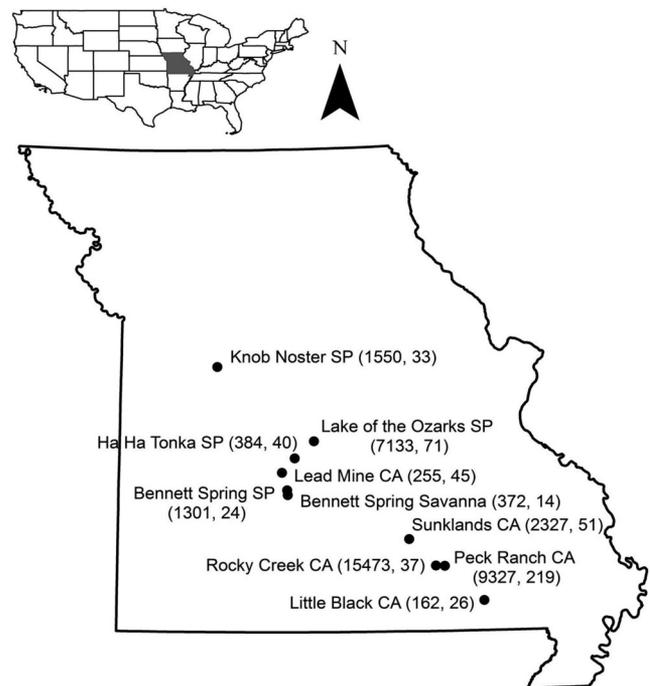
We estimated densities of winter-resident bird species across a range of tree cover in savanna, woodland, and forest communities across the Missouri Ozarks using hierarchical, distance-based abundance models that incorporate covariates into both detection probabilities and density estimates. We hypothesized that densities of individual species would vary with percent tree stocking based on the needs of each species. In general, we expected densities of bark-gleaning species (including brown creeper [*Certhia americana*], downy woodpecker [*Picoides pubescens*], hairy woodpecker [*Picoides villosus*], pileated woodpecker [*Dryocopus pileatus*], red-bellied woodpecker [*Melanerpes carolinus*], and white-breasted nuthatch [*Sitta carolinensis*]) would increase with stocking because trees provide foraging substrate and roost sites, and birds associated with open or early successional habitats (including eastern bluebird [*Sialia sialis*], northern flicker [*Colaptes auratus*], and Carolina wren [*Thryothorus*

*ludovicianus*]) would decrease with stocking because of a decrease in ground or shrub cover associated with greater tree density and canopy cover.

## STUDY AREA

We studied birds in the Ozark Highlands of Missouri. The region was equally divided between steep and rolling hills and gently rolling plains, ranging in elevation from 100 m to 600 m (McNab and Avers 1994). The region included mosaics of oak (*Quercus* spp.)–hickory (*Carya* spp.) and oak–hickory–pine (*Pinus* spp.) forest, bluestem (*Andropogon gerardii*, *Schizachyrium scoparium*) prairie, and eastern red cedar (*Juniperus virginiana*) glades (McNab and Avers 1994). Forest on upland and mesic slopes included post oak (*Q. stellata*), blackjack oak (*Q. marilandica*), shortleaf pine (*Pinus echinata*), white oak (*Q. alba*), northern red-oak (*Q. rubra*), bitternut hickory (*Carya cordiformis*), and flowering dogwood (*Cornus florida*; McNab and Avers 1994).

We selected 10 study areas across the Missouri Ozark Highlands owned by the Missouri Department of Conservation (conservation areas), the Department of Natural Resources (state parks), and The Nature Conservancy (Bennett Spring Savanna; Fig. 1). We selected sites by contacting managers and asking for examples of managed savannas or woodland that had largely achieved desired conditions and had areas of non-managed mature forest on similar landforms within 1 km. The total managed and unmanaged area of study sites ranged from 162 ha to 15,473 ha. We acknowledge the subjective nature of site selection, but essentially we used all sites suggested to us that met our criteria. Thus, inferences from our study should only



**Figure 1.** Location of study sites (total site area in ha, no. of points surveyed) on which we surveyed bird abundance in the Missouri Ozarks, USA, during winter 2009–2010 and 2010–2011.

be extended to the likely response of these species to future management with similar objectives and methods in the region.

## METHODS

### Point Counts

We surveyed bird abundance with point counts from 15 December 2009 to 22 February 2010 and 12 December 2010 to 10 January 2011. We randomly placed a grid of points 250-m apart over the entire managed or non-managed stand and randomly selected a starting point and direction for each transect. We then selected 9–14 points that were >50 m from the edge of the site. The number of points per transect and per stand was determined by the size of the stand up to a maximum of 14 points, so that a transect could be surveyed in a morning and to spread effort among as many stands as possible. Peck Ranch Conservation Area had more points than other sites because of its large size and the large area managed; however, points sampled in each year were from different restored and non-managed portions of the area. Rocky Creek Conservation Area was the largest site but had fewer points because it is more fragmented and therefore difficult to place point grids in it.

We conducted 10-minute unlimited-radius point counts in all temperatures and weather, except when raining or if winds were >13 km/hour. We performed all counts between sunrise and noon, except for 2 transects that we conducted after noon because of time and travel constraints. We measured the distance to each bird or a reference object near the bird with a Bushnell Yardage Pro laser range-finder (Bushnell, Overland Park, KS) to 1 m, but sometimes had to estimate distances when we could not focus the rangefinder on or near the bird because of vegetation or topography. We recorded the time of each detection, and temperature, wind speed, cloud cover, and precipitation at the beginning of each count. We measured temperature with a thermometer and measured wind speed as 0–3 on the Beaufort scale. Two observers conducted all surveys with nearly equal effort among savanna, woodland, and forest. We surveyed each point once throughout the study so we could maximize the number of points and study areas.

### Vegetation Measurements

We recorded diameter at breast height and species of all trees in an 11.3-m-radius circle around each point and calculated percent tree stocking (hereafter, stocking) based on trees of >4 cm diameter at breast height. We used the equation for estimating stocking for upland oaks and hickories in Ohio, Kentucky, Missouri, and Iowa (percent tree stocking =  $-0.00507N + 0.01698D + 0.00317D^2$ , where  $N$  is trees per acre,  $D$  is the sum of tree diam. [in in.], and  $D^2$  is basal area [in ft<sup>2</sup>/acre] divided by 0.005454; Gingrich 1967). We considered stocking as a continuous covariate because the amount of tree cover is the dominant structural feature defining savannas, woodlands, and forest; it is affected by the dominant management practices in savannas and woodlands (i.e., tree thinning and prescribed fire); and is the best measure of the amount of growing space occupied by

trees (Johnson et al. 2009). It is essentially a measure of the percent of a site covered by tree canopies, as estimated from tree diameters. Basal area is not as good a measure of growing space occupied because it continues to increase with stand age as tree volume increases, whereas stocking increases and then reaches an asymptote when the growing space is fully occupied. On average, stocking is 100% in mature undisturbed stands, but stocking can be greater or lesser depending on stand history. Desired savanna, woodland, and forest structure have been defined based on basal area but not stocking (U.S. Department of Agriculture Forest Service 2005). Therefore, we related our continuous measure of stocking to desired conditions for savanna and woodlands by equating stocking values to basal area (i.e., savanna was <30 ft<sup>2</sup>/acre basal area and <30% stocking). This approach worked for our application because there is an approximate 1:1 relationship between stocking (%) and basal area (ft<sup>2</sup>/acre) for typical midwestern oak–hickory stands (Gingrich 1967; J. Kabrick, United States Department of Agriculture Forest Service, personal communication).

### Data Analyses

We estimated detection probabilities and bird densities across a range of stocking using distance sampling. Distance sampling estimates density based on distance to detected individuals by assuming detectability decreases with increasing distance from the observer (Buckland et al. 2001). We used the R package *unmarked* (R Foundation for Statistical Computing, Vienna, Austria) to fit hierarchical models that account for imperfect detection while considering covariate effects on species density (Royle et al. 2004, Fiske and Chandler 2011). We used hierarchical models that included a detection function based on distance sampling and a Poisson regression model that considered covariate effects on density. The model uses a site-specific likelihood for data gathered at each point as a function of local abundance around that point, abundance is treated as a random effect, and analysis is based on the integrated parameters of the detection function, density, and density covariates (Royle et al. 2004).

We ran analyses for species with >49 detections and that met the assumptions of distance models. A sample of 60–80 detections is generally desirable for distance sampling (Buckland et al. 2001). We included 2 species with <60 detections (brown creeper and eastern bluebird) because histograms of the distribution of detections by distance indicated they met the following model assumptions: 1) objects at a distance of zero are always detected; 2) objects are detected at their initial location (no movement in response to the observer or other influences); and 3) distances are measured accurately (Buckland et al. 2001). We excluded observations with distances >90th percentile for each species to minimize effects of outliers (Buckland et al. 2001).

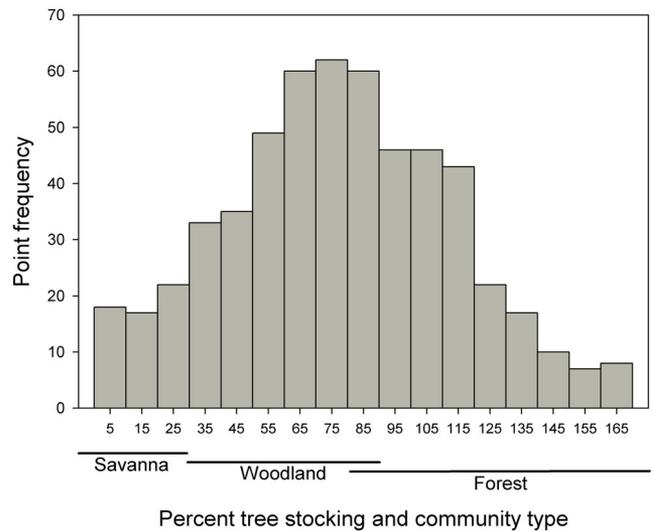
We fit models in a 3-stage process for each species and evaluated model support at each step with Akaike's information criterion adjusted for small sample sizes (AIC<sub>c</sub>). First, we determined whether a uniform, half-

normal, or hazard-rate key function was the most-supported for the detection function; these are standard functions used in distance sampling that we used to relate the probability of detection to the distance to detections of each species (Buckland et al. 2001). Identifying the most-supported key function in the first step simply reduced the model combinations we had to consider with detection and density covariates. We used the most-supported key function to evaluate candidate models with effects of observer, temperature, wind, and stocking on detection probability. We considered these effects singly and in all additive combinations (15 models), because there was no *a priori* reason to exclude any combinations. We then included the most-supported detection covariates and evaluated support for 3 models predicting density for each species: 1) a null model with no effect of stocking on species density, 2) a linear effect of stocking, and 3) a quadratic effect of stocking, which would be supported if density was higher or lower at intermediate stocking than at high and low stocking. We then assessed the fit of the most-supported model with a Freeman–Tukey test based on a parametric bootstrap of the top-ranked model (Fiske and Chandler 2011; the exception was eastern bluebird, for which the Freeman–Tukey procedure would not converge, probably because of sparse data). We estimated density of each species over the range of observed stocking by model-averaging predicted densities from the 3 bird-density models to account for model selection uncertainty (Burnham and Anderson 2002) and plotted predicted densities and 95% confidence intervals as a function of stocking. Support for the effects of stocking can be inferred by comparing the Akaike weights for models with stocking to the null model and from the change in density across stocking levels.

## RESULTS

Two observers surveyed 291 and 269 points across a gradient of stocking (Fig. 2) in the winter of 2009–2010 and 2010–2011, respectively, from 12 December to 22 February and detected 38 species. Across the days and points surveyed, mean temperature was  $-3.24^{\circ}\text{C}$  (range =  $-20^{\circ}\text{C}$  to  $20^{\circ}\text{C}$ ), mean wind speed 1 (range = 0–3 Beaufort scale), and mean stocking 79.3% (range = 10–170%). Across all sites, we detected 1–222 individuals of 38 species and fitted distance models for 12 species that had >49 detections (Tables 1 and 2). Brown creeper and eastern bluebird had less than the recommended minimum sample size of 60–80 detections (Buckland et al. 2001). Aural detections made up the majority of detections (i.e., 75% and 84% of detections for 2 of our most common species, golden-crowned kinglet (*Regulus satrapa*) and white-breasted nuthatch, respectively); however, this is probably a lower percentage than for many breeding season surveys (S. W. Kendrick and F. R. Thompson, personal observation).

We detected covariate effects on detectability and these effects varied by species. Distance models for 6 species were best fit with a hazard-rate key function and 6 species were best fit with a half-normal key function. The top-ranked detectability models included covariate effects of observer,



**Figure 2.** Distribution of sampled points across a gradient of percent tree stocking in the Missouri Ozarks, USA, during winter 2009–2010 and 2010–2011.

temperature, wind, or stocking (Table 1). Observer was included in the top-ranked models for brown creeper, golden-crowned kinglet, hairy woodpecker, pileated woodpecker, tufted titmouse (*Baeolophus bicolor*), and red-bellied woodpecker. Temperature had a positive effect on detection probability for brown creeper, black-capped plus Carolina chickadees (*Poecile atricapillus*, *P. carolinensis*; combined throughout analyses and hereafter called chickadees), eastern bluebird, and white-breasted nuthatch, and a negative effect on golden-crowned kinglet and northern flicker. Wind had a negative effect on the detectability of brown creeper, Carolina wren, downy woodpecker, eastern bluebird, pileated woodpecker, tufted titmouse, and white-breasted nuthatch. Stocking had a positive effect on brown creeper detection probability and a negative effect on the detection probabilities of chickadees, golden-crowned kinglet, and tufted titmouse. Detection probabilities averaged 0.518 and ranged from 0.067 to 0.756 (Table 1) across all modeled species in both years.

There were strong to weak relationships between stocking and density for all 12 species. A linear or quadratic effect of stocking on density was in the top-ranked model for 6 species (Table 2). The null model with no effect of stocking was the top-ranked habitat model for the remaining 6 species; however, the second-ranked model for these species included a linear effect of stocking with  $\Delta\text{AIC}_c = 0.10\text{--}1.73$ , indicating some support for stocking (Table 2). There was no evidence of lack of fit for the most-supported model ( $P > 0.05$  for all species; Table 2), but the Freeman–Tukey test would not converge for eastern bluebird because of sparse data.

Model-averaged estimates of density of brown creeper, chickadees, downy woodpecker, golden-crowned kinglet, pileated woodpecker, red-bellied woodpecker, tufted titmouse, and white-breasted nuthatch increased over the range of stocking 75%, 252%, 13%, 91%, 4%, 102%, 42%, and 17%,

**Table 1.** Covariates and detection probability from the most-supported detection model portion of hierarchical models estimating density of birds in the Missouri Ozarks, USA, during winter 2009–2010 and 2010–2011 from point counts.

Species	Detection covariates <sup>a</sup>	Detection <i>P</i>	Truncation distance (m) <sup>b</sup>
Red-bellied woodpecker	Obs	0.67	97
Downy woodpecker	Wind	0.42	97
Hairy woodpecker	Obs	0.55	100
Northern flicker	Temp	0.76	106
Pileated woodpecker	Obs + Wind	0.64	200
Black-capped + Carolina chickadees	Temp + Stock	0.53	85
Tufted titmouse	Obs + Wind + Stock	0.54	86
White-breasted nuthatch	Temp + Wind	0.55	96
Brown creeper	Obs + Temp + Wind + Stock	0.07	56
Carolina wren	Wind	0.56	120
Golden-crowned kinglet	Obs + Temp + Stock	0.35	65
Eastern bluebird	Temp + Wind	0.58	102

<sup>a</sup> Obs is observer, Temp is temperature, Wind is wind speed, Stock is percent tree stocking.

<sup>b</sup> Observations > truncation distance were excluded from analysis, truncation distance = 90th percentile of distances to detections for a species.

**Table 2.** Support for candidate models for the Poisson regression portion of hierarchical models estimating density of birds in the Missouri Ozarks, USA, during winter 2009–2010 and 2010–2011 from point counts, based on differences in Akaike's information criterion adjusted for small sample sizes relative to the most-supported model ( $\Delta AIC_c$ ) and Akaike weights ( $w_i$ ).

Species	Density model covariates <sup>a</sup>						<i>P</i> -value <sup>b</sup>
	Null		Stock		Stock + Stock <sup>2</sup>		
	$\Delta AIC_c$	$w_i$	$\Delta AIC_c$	$w_i$	$\Delta AIC_c$	$w_i$	
Red-bellied woodpecker	4.04	0.08	0.00	0.64	1.66	0.28	0.54
Downy woodpecker	0.00	0.52	1.07	0.30	2.14	0.18	0.40
Hairy woodpecker	3.24	0.15	4.26	0.09	0.00	0.76	0.52
Northern flicker	3.06	0.14	1.96	0.24	0.00	0.63	0.54
Pileated woodpecker	0.00	0.63	1.73	0.27	3.67	0.10	0.55
Black-capped + Carolina chickadees	6.10	0.02	0.00 <sup>c</sup>	0.49	0.00	0.49	0.44
Tufted titmouse	0.43	0.32	0.00	0.43	0.72	0.28	0.41
White-breasted nuthatch	0.00	0.45	0.22	0.40	2.20	0.15	0.39
Brown creeper	0.00	0.37	0.15	0.35	0.58	0.28	0.36
Carolina wren	0.00	0.56	1.18	0.31	2.83	0.14	0.47
Golden-crowned kinglet	3.74	0.10	0.00	0.63	1.68	0.27	0.18
Eastern bluebird	0.00	0.40	0.10	0.38	1.26	0.21	

<sup>a</sup> Covariates in the Poisson regression portion of hierarchical models estimating density; null indicates an intercept-only model, stock is percent tree stocking; the detection portion of the hierarchical model included the most-supported covariates affecting detectability for each species.

<sup>b</sup> *P*-values > 0.05 indicate no evidence of lack of fit based on parametric bootstrap Freeman–Tukey goodness of fit test. The Freeman–Tukey procedure would not run for eastern bluebird, presumably because of sparse data.

<sup>c</sup> 0.00005.

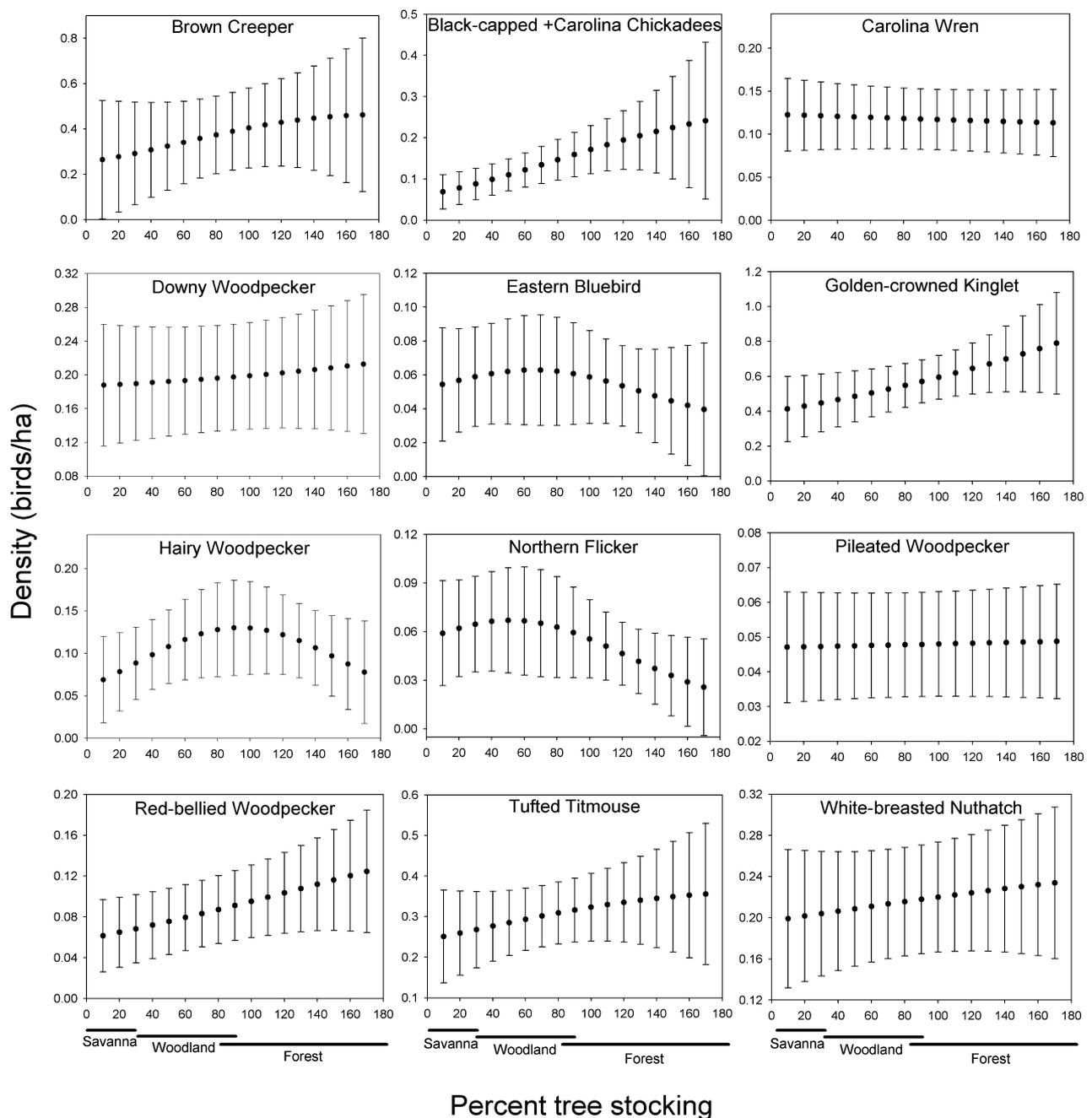
respectively (Fig. 3). Carolina wren decreased 8% over the range of stocking (Fig. 3). Densities of eastern bluebird, northern flicker, and hairy woodpecker peaked at intermediate stocking levels that were 58%, 160%, and 89% greater, respectively, than their lowest density (Fig. 3).

## DISCUSSION

Detection probabilities were affected by one or more factors for all species. Most prior studies that used distance models to estimate bird densities were done during the breeding season (Selmi and Boulinier 2003, Heltzel and Leberg 2006, Thompson and LaSorte 2008, Reidy et al. 2011) when birds are more vocal because of territory and mate defense. However, the winter detection probabilities we estimated (0.07–0.76) were similar to breeding-season detection probabilities from distance models applied to similar species in the same region as our study (range = 0.1–0.7; Thompson

and LaSorte 2008, Reidy et al. 2011). We expected winter detection probabilities to be lower than breeding season detection probabilities because of decreased audible territorial singing or calling in the winter; however, the lack of foliage may make birds more visible or audible at longer distances. Birds may also be more detectable in winter because fewer species and cues are present to compete for the observer's attention.

Effects of observer, temperature, wind, and stocking on detectability varied among species. Temperature had a positive effect on 4 species and a negative effect on 2 species. Winter birds may be more active and vocal in warmer temperatures, especially compared with some of the very cold temperatures we observed (<–20° C). However, detectability of golden-crowned kinglets and northern flickers was negatively affected by temperature, implying they were more vocal or active in cold temperatures. The effect of wind was



**Figure 3.** Model-averaged winter bird densities and 95% confidence intervals across a range of percent tree stocking in savanna, woodland, and forest in the Missouri Ozarks, USA, during winter 2009–2010 and 2010–2011 based on hierarchical models that incorporated covariates affecting detection probability and density.

always negative when supported, likely because wind made birds harder to hear. Stocking had a negative effect on detection probability for 3 species, likely because increased tree density and size made species more difficult to detect. The exception to this was brown creeper, for which detectability and species density increased with stocking; perhaps detectability increased with stocking because abundance increased with stocking.

The linear or quadratic form of stocking was in top-ranked models for 6 species and in the second-ranked model for the

remaining 6 species, indicating some support for an effect of stocking on all 12 species' densities. Model-averaged estimates of density varied substantially across the range of stocking for 7 species; densities of brown creeper, eastern bluebird, golden-crowned kinglet, and hairy woodpecker varied by >50%, and chickadees, northern flicker, and red-bellied woodpecker varied by >100%. Three bark-gleaning species increased with stocking as hypothesized (red-bellied woodpecker and brown creeper) or peaked at high but not maximum stocking (hairy woodpecker). However, densities

of downy woodpecker, pileated woodpecker, and white-breasted nuthatch did not vary substantially with stocking. Patterns of early successional or open-country birds were more consistent with our predictions and results of other studies. Eastern bluebird and northern flicker had high densities at low levels of stocking, but Carolina wren density did not vary with stocking. Some species' patterns of abundance among varying community types, which were heretofore unknown for winter months, were similar to those reported for the breeding season. Grundel and Pavlovic (2007a) also found tufted titmouse at greatest abundance in forest along a gradient of open to forest communities; and patterns in abundance of northern flicker, white-breasted nuthatch, and chickadees are similar to those observed in savanna, woodland, and forest in Illinois, USA (Brawn 2006). Comparable abundances between breeding and overwintering seasons give us confidence in this winter sampling method because we did not produce overly inflated or low estimates.

Our winter bird-density estimates were generally similar to the few other estimates of winter densities that exist, as well as to breeding season densities. Our estimates of golden-crowned kinglet winter density were close to previous estimates of 0.10–0.74 (Grundel and Pavlovic 2007a, Swanson et al. 2012). Our densities of white-breasted nuthatch were slightly greater than previous winter estimates of 0.12–0.19 birds/ha (Grubb and Pravosudov 2008). Breeding season densities overlapped our winter estimates for downy woodpecker (0.14–0.34 birds/ha; Jackson and Ouellet 2002), tufted titmouse (0.12–0.76 birds/ha; Grundel and Pavlovic 2007a), and pileated woodpecker (0.005–0.07 M birds/ha; Bull and Jackson 2011). Breeding densities of hairy woodpecker (0.003–0.075 birds/ha; Jackson et al. 2002) nearly overlapped our estimates. Our Carolina wren winter densities were less than previously reported breeding densities of 0.45–1.08 M birds/ha (Haggerty and Morton 1995).

Making inferences about abundance from uncorrected count data requires assumptions of equal or constant detectability across species, habitat, and other factors that could affect detectability, such as wind or temperature. Indices of abundance, such as counts, may not be ideal when comparing abundance across habitats or species, because detectability may vary among habitats and species (Rosenstock et al. 2002, Johnson 2008), of which we saw evidence in our study. Analysis of simple count data failed to detect an effect of stocking on abundance of chickadees, brown creeper, and tufted titmouse (Kendrick 2012); however, when we accounted for detectability using distance models, there was a strong relationship between stocking and density for all 3 species (Fig. 3). Further, we found support for effects of covariates on detectability for all of the 12 species we modeled, and we suggest investigators address detectability in future bird surveys through some combination of methods that include model-based estimation of the probability of detection and abundance or density, model-based analyses of counts that include covariates to account for factors contributing to variation in detectability, and good study

design-based methods. However, uncorrected count data may provide a way to examine abundances of species when the number of detections is too small for other model-based approaches if certain assumptions or design-based control of factors affecting detectability are applied (Johnson 2008).

## MANAGEMENT IMPLICATIONS

Winter bird densities varied across the range of tree stocking in restored savannas and woodlands and non-managed forest; therefore, we believe restoration management that affects stocking will affect winter bird densities in species-specific ways. However, because all species were present across a wide range of stocking, these species can likely be sustained in winter across a range of landscapes with various compositions of savanna, woodland, and forest, albeit at different abundances. We provide managers with winter densities of 12 of the most common overwintering species in the Missouri Ozarks, and the relationships between their densities and stocking can be used to guide management where managers have bird-species-specific objectives.

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