The Journal of Wildlife Management 79(6):917–926; 2015; DOI: 10.1002/jwmg.903

Research Article

Site Occupancy of Brown-Headed Nuthatches Varies With Habitat Restoration and Range-Limit Context

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ABSTRACT Knowledge about species' responses to habitat restoration can inform subsequent management and reintroduction planning. We used repeated call-response surveys to study brown-headed nuthatch (*Sitta pusilla*) patch occupancy at the current limits of its apparently expanding range in an area with active habitat restoration. We fit a probit occupancy model that accounted for spatial autocorrelation using restricted spatial regression. Nuthatch occupancy was related to patch-level vegetation structure and range-extension context, i.e., latitude, but not prescribed fire history. Latitude and percent tree stocking had a negative relationship with occupancy (coefficients and 95% credible intervals: −1.07 [CI: −1.63, −0.67] and −0.63 [CI: −0.97, −0.350]). The density of recently killed and well-decayed snags had positive associations with occupancy (coefficients and 95% credible intervals: 0.57 [CI: 0.17, 1.16] and 0.37 [CI: 0.05, 0.72]). Neither grassy herbaceous cover nor percent of stocking in pine were associated with occupancy. We found that restoration efforts created suitable stand structure for brown-headed nuthatches, but many restored sites in the range-extension zone appeared to be vacant. Occupied habitats in the range-extension zone had fewer snags, less frequent fire, and more shrub cover than occupied sites where the species was established. Release from conspecific competition may have permitted nuthatches in the range-extension zone to exploit habitats that would otherwise have been marginal. Alternatively, nuthatches may be restricted to such sites although there are more suitable sites tens of kilometers away. Experimental translocations and reintroductions could determine how habitat structure and nuthatch density affect the quality of restored sites in the range-extension zone and enable those sites to achieve their biodiversity potential. Published 2015. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS Arkansas, brown-headed nuthatch, dispersal, habitat associations, habitat restoration, occupancy models, prescribed fire, range extension, *Sitta pusilla*.

Information about bird responses to habitat restoration can inform management efforts and decisions regarding potential reintroductions. Restoration planning is frequently based on the knowledge of a few focal taxa and thus may not meet the needs of the entire biotic community (Lindenmayer et al. 2002). Whether a species occurs in restored habitats may depend on spatial factors such as range margins as well as changes in habitat structure and disturbance induced by management (McRae et al. 2008).

Distinguishing the effects of spatial factors from the effects of habitat management can inform both restoration efforts and reintroduction planning (Kesler et al. 2012). For example, mismatches between the spatial scales of habitat restoration and animal dispersal behavior may lead to apparently suitable habitat remaining vacant. Vacant, apparently suitable sites can be common in range-extension zones (Gaston 2009). Understanding how restoration practices such as prescribed fire affect site occupancy, therefore, requires consideration of range-limit context. Further, sites occupied in range-extension zones may be atypical for the species for several reasons, ranging from limited dispersal to release from the density-dependent effects of conspecifics (Morris 1987, Kesler and Walters 2012). Knowing how spatial context affects which sites a species will colonize subsequent to habitat restoration can help managers identify priority locations for future restoration.

The brown-headed nuthatch (*Sitta pusilla*) is a territorial resident species restricted to fire-maintained pine (*Pinus* spp.) woodlands in the southeastern United States (Slater et al. 2013). Nuthatches are small (approx. 10 g), cavity-excavators that require well-decayed standing dead trees, i.e., snags, for nesting and use all-purpose territories throughout the year (Slater et al. 2013). Limited data indicate that brown-headed nuthatches that do not inherit a natal territory only disperse a few 100 m or occasionally 1–2 km (Cox and Slater 2007, Haas et al. 2010). Nuthatches frequently co-occur with the endangered red-cockaded woodpecker (*Picoides borealis*), a focal species for pine woodland management (James et al. 2001). Nuthatches

Received: 9 July 2014; Accepted: 21 April 2015
Published: 22 May 2015

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were extirpated from northern Arkansas and all of Missouri during the first half of the 20th century, when extensive clear cutting and fire suppression dramatically reduced the extent of pine woodlands (James and Neal 1986, Robbins and Easterla 1992). Restoration efforts in Arkansas and restoration plans for Missouri have created a need to study nuthatch habitat requirements and determine whether restored sites have been recolonized by nuthatches (Hedrick et al. 2007, Mark Twain National Forest 2011).

We studied brown-headed nuthatch patch occupancy up to the current limits of their expanding range in an area with active restoration of pine woodlands in the Ouachita and Ozark Mountains of Arkansas, USA. Our objectives were 1) to determine how stand structure, fire history, and location relative to a range boundary affected patch occupancy; and 2) to determine whether occupied sites in the range-extension zone were similar to occupied sites where the species is established. We modeled patch occupancy while accounting for spatial autocorrelation and factors affecting species detectability (MacKenzie et al. 2006, Johnson et al. 2013). We investigated stand structure, fire history, and range-limit context effects on nuthatch occupancy because climate change and habitat restoration in Arkansas and Missouri are likely expanding the amount of suitable habitat in areas formerly occupied by brown-headed nuthatches (Hedrick et al. 2007, Mark Twain National Forest 2011).

STUDY AREA

We studied brown-headed nuthatches in the Ouachita and Ozark-St. Francis National Forests (N 35° 16′, W 93° 8′) of Arkansas, USA (Fig. 1). The Ouachita National Forest is the southernmost site and has rolling mountainous terrain. The Ozark-St. Francis National Forest is to the north and has more dissected mountainous terrain (James and Neal 1986). Pine and mixed pine-deciduous woodlands occur throughout the study area. Current habitat management includes regular prescribed fire, midstory reduction, and stand thinning to restore pine woodland conditions (Fig. 1; Hedrick et al. 2007). Brown-headed nuthatches may have recently extended their range northward within the Ozark Mountains of Arkansas, USA. The number of eBird blocks with nuthatch reports increased from 0 to 17 between 1980 and 2014; 2, 6, and 13 eBird blocks had at least 1 nuthatch record as of 1990, 2000, and 2010, respectively (eBird 2014). Nuthatches were reported from 10–25% of eBird lists in most Ouachita National Forest blocks and 0–2% of lists from most occupied blocks in the Ozarks (Fig. 1; eBird 2014). We hereafter refer to the Ozarks as the range-extension zone and the Ouachitas as the established range when discussing range-limit context.

METHODS

Field Methods

Sampling design and call-response surveys.—We surveyed for brown-headed nuthatches in pine and mixed pine stands from 2 April to 23 June 2011 and 1 March to 1 June 2012. We surveyed 20 routes, 5 per National Forest per year. We identified locations with a history of prescribed fire and placed routes on traversable roads ≥5 km long (U.S. Department of Agriculture Forest Service [USDA] 2010); we acknowledge this limits inference to conditions found along roads, but given the extensive road network, we believe we sampled an adequate range of stand conditions. We

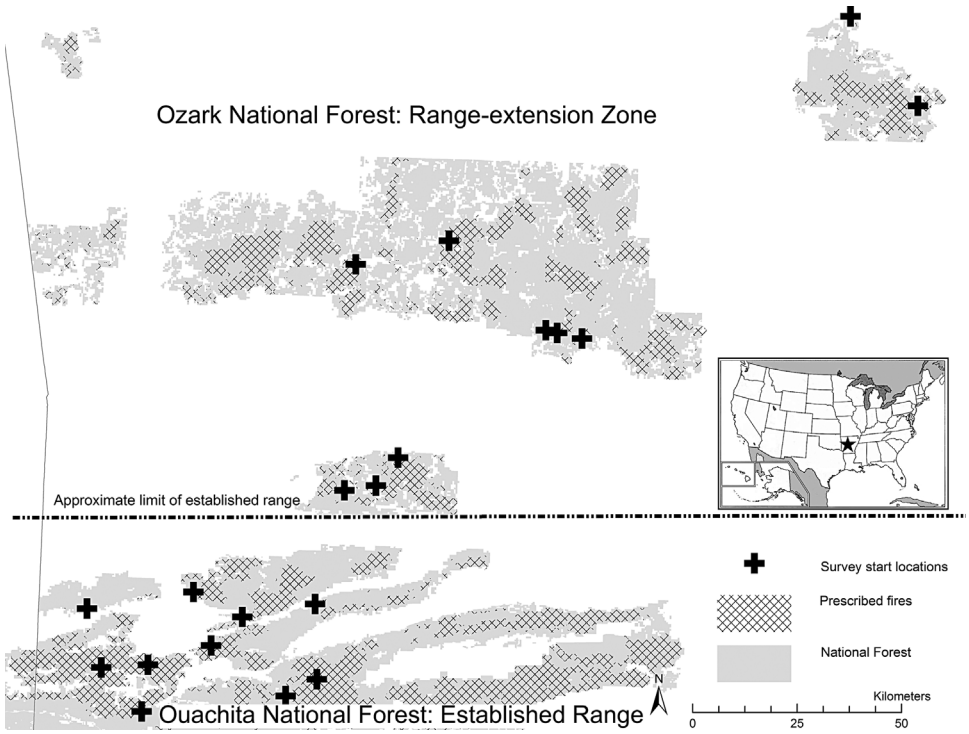

Figure 1. Locations of study areas, prescribed fires, and survey route starting positions in a study of brown-headed nuthatch site occupancy in Arkansas, USA, 2011–2012. The approximate limit of the established brown-headed nuthatch range is also shown.

randomly determined the distance from the beginning of each route to a starting point and whether to walk left or right 100 m on a bearing perpendicular to the road to a survey station (0.2–1.0 km; Fig. 1). We drove 0.5 km to each subsequent station, verified it was ≥0.3 km from neighboring points, and randomly determined which side of the road to sample. We drove >0.5 km in some cases to avoid oversampling closed canopy stands with no evidence of recent prescribed fire and under-sampling the gradient of canopy closure. We sampled most stations 4 times and all stations ≥3 times. We surveyed routes in opposite directions and with alternating observers each visit when possible. We spread surveys geographically across the study area and temporally throughout the season.

We maximized detection by broadcasting locally recorded sounds of agitated brown-headed nuthatches (derived from Spencer 2009, listen to S1 online at www.onlinelibrary.wiley.com). We played the recording at a standardized volume audible 150 m away using FOXPRO NX4 digital callers (FOXPRO, Inc., Lewiston, PA). We recorded whether we detected nuthatches and noted the observer, date, time, temperature, and wind speed during each survey (using a Brunton ADC Summit, Brunton, Inc., Riverton, WY). Each survey consisted of 2 minutes of listening, 1 minute of nuthatch vocalizations, and 3 minutes of listening. We recorded nuthatch detections if we saw or heard nuthatches during the 6-minute survey; we heard all birds that we saw. We surveyed from 15 minutes before sunrise to 5 hours after. We suspended or canceled surveys if winds exceeded 20 km/hr or if there was rain. Our field sampling protocols were approved by the Institutional Animal Care and Use Committee of the University of Missouri (reference # 7006).

Vegetation and snag sampling.—We measured tree diameters, grassy herbaceous cover, shrub cover, bare ground, and snags at each survey station. We selected trees with an English 10 factor wedge prism, measured diameter at breast height (DBH) of each tree to the nearest 5 cm with a Biltmore stick, and classified each tree as pine or hardwood (Jackson 1911, Grosenbaugh 1958). We visually estimated the proportion of grassy herbaceous cover, shrub cover, and bare ground within 12.5 m of each point so the 3 cover types totaled 100%. We defined shrubs as woody plants <2.5 m tall and DBH < 10.2 cm. We measured DBH and distance to every visible snag detected at any distance from each station using a laser rangefinder (Bushnell Yardage Pro Sport, Overland, KS). Observers visually inspected snags and classified them as fresh or punky by matching them to a series of illustrations (Maser et al. 1979). We classified recently killed, stage 4 and 5 snags as fresh and well-decayed stage 6 and 7 snags with broken crowns as punky (Maser et al. 1979). We adjusted several vegetation sampling locations by <20 m to avoid conditions that were grossly different in structure than the surrounding stand.

Derivation of vegetation and prescribed fire metrics.—We developed a set of habitat and fire management metrics from our field sampling and geospatial data. We calculated tree stocking percent using equations for mixed hardwoods (Gingrich 1967) and shortleaf pine (*Pinus echinata*; Rogers 1983). Tree stocking is a measure used by foresters to manage timber production (Johnson et al. 2009). Tree stocking of 100% is ideal for production, but stocking is lower in stands that have been mechanically thinned or repeatedly burned (Johnson et al. 2009). We estimated snag densities using distance sampling methods to correct for imperfect detection (Buckland et al. 2005, Fiske and Chandler 2011). Distance sampling models assume detectability declines as one of several functions of distance, and models are ranked using an information-theoretic approach (Burnham and Anderson 2002). We pooled snag sampling data from a concurrent study of space use within nuthatch home ranges (Stanton et al. 2014), and developed models for fresh and punky snags with DBH ≥ 10.2 cm. We fitted hazard-rate and half-normal detection models with station-level covariates for each snag class. We considered shrub cover and percent tree stocking for punky snags, which can be shorter than surrounding shrubs. We only considered percent tree stocking for fresh snags, which are taller than surrounding shrubs but may be harder to see in dense stands. We estimated snag densities for each point by using the best-supported detectability model because model averaging hazard rate and half normal functions is inappropriate (Burnham and Anderson 2002). We determined years since prescribed fire and number of fires in the last decade for each station from a geographic information system (GIS) database (USDA Forest Service 2012).

Analysis and Candidate Models

Occupancy modeling.—We related brown-headed nuthatch presence to range-limit context and patch-level measures of stand structure and fire history using single-season occupancy models (MacKenzie et al. 2006). Occupancy models use detection–nondetection data from repeat surveys to simultaneously estimate probabilities of detection (p) and occupancy (ψ; MacKenzie et al. 2006). Spatial correlation in occupancy results when points closer together have more similar occupancy than those farther apart. Approaches to occupancy modeling are increasingly accounting for spatial autocorrelation because failure to do so can result in bias and overestimated precision (Diniz-Filho et al. 2003, Johnson et al. 2013). We used the hierarchical spatial occupancy model approach of Johnson et al. (2013) because it is effective over large spatial extents, employs a probit mixture framework that resolves issues with multicollinearity and spatial confounding, and improves algorithm convergence. We followed the model-fitting process described in Broms et al. (2014) and first identified supported likelihood-based occupancy models and then used a hierarchical Bayesian approach to fit the supported models with and without spatial autocorrelation.

We fit likelihood-based logistic regression occupancy models in the R statistical package unmarked to identify supported models because it permits an information-theoretic approach to model selection and inference (Burnham and Anderson 2002, Fiske and Chandler 2011). We standardized all continuous site covariates to mean 0 and unit variance to facilitate model convergence and facilitate comparisons among covariates. We determined that

multicollinearity among candidate predictor variables was not an issue because no variance inflation factors were ≥ 4 in a global logistic regression model. We considered models with a difference in Akaike's Information Criterion adjusted for sample size (ΔAIC_c) ≤ 4 as supported and considered them in the next step.

The unmarked package cannot account for spatial autocorrelation, so we next fit spatial and nonspatial analogs of the unmarked model in R's stocc package (Johnson 2014, R Development Core Team 2014). The Bayesian spatial occupancy model included a random effect for spatial autocorrelation derived from restricted spatial regression (Hodges and Reich 2010). We ran each model with 1 chain for 60,000 iterations, discarding the first 10,000 as burn-in, and employed a thinning rate of 1/5, for a total sample of 10,000 iterations per model (after Broms et al. 2014). The Moran cut used in the spatial model was 10% of the number of sites, and the priors for the spatial component of the model were $\tau \sim \gamma$ (0.5, 0.0005; after Broms et al. 2014). We estimated median βs and 95% credible intervals from the stocc models.

Covariates and candidate models.—We identified a set of predictor variables to use in our candidate occupancy models. We formulated and selected models in a 3-step process based on factors that may affect nuthatch detectability and occupancy. We fit detectability models first, e.g., $\psi(.)p(\text{covariate})$, then range-limit context models, followed by station-scale attribute models, i.e., stand structure and fire history. We ranked models at each stage using AIC_c and considered models competitive if $\Delta AIC_c \leq 4$ (Burnham and Anderson 2002). Competitive models in each stage advanced to the next stage, ultimately constraining the number of models fit to 14 (see Appendix).

We fit models relating detectability to breeding phenology, ordinal date, observer, time, temperature (°C), wind speed (km/hr), or no sampling condition, i.e., $\psi(.)p(.)$. We did not consider more complex models because our sampling design should have minimized these nuisance effects. We assumed that detection probability did not vary spatially. Breeding phenology was a categorical variable based on data from a study of nuthatch space use during the breeding season (Stanton et al. 2014). The phenology categories and corresponding dates were: before hatch (ordinal dates: 033–120), brood rearing (ordinal dates: 121–145), or post-fledging (ordinal dates: 146–032).

We compared 3 models regarding the relationship between range-limit context and nuthatch occupancy: 1) occupancy north and south of the Ouachita Mountains differs categorically, 2) occupancy varies linearly with latitude throughout the study area, and 3) occupancy is constant throughout the region.

We developed a single model relating nuthatch occupancy to stand structure, i.e., tree stocking percent, fresh and punky snag densities, percent tree stocking in pine, and percent grassy herbaceous cover. We selected these covariates based on peer-reviewed nuthatch habitat studies, literature arguing that grassy herbaceous cover benefits red-cockaded woodpeckers, and an interest in determining whether nuthatch occupancy had different associations with fresh and punky snags (James et al. 2001, U.S. Fish and Wildlife Service 2003, Slater et al. 2013, McKellar et al. 2014). We also developed a model representing fire history that consisted of 2 covariates: years since fire and number of fires in the last decade.

We considered 4 competing models regarding relationships among nuthatch occupancy, stand structure, and fire history. First, stand structure alone might provide adequate information for understanding patch occupancy. Alternatively, fire history data might adequately predict nuthatch occupancy in the absence of data on stand structure, simplifying monitoring and management. Finally, we considered the possibility that both forest stand structure and fire history considered jointly would best predict nuthatch occupancy, and we evaluated a neither-structure-nor-fire model (i.e., $\psi(\text{range-limit context}_{\text{best}})p(\text{best})$; Appendix).

We focused on interpretation of the median $\hat{\beta}$s and 95% credible intervals for the Bayesian spatial model because the Bayesian spatial model was favored by several measures of predictive performance, detailed below. However, the magnitudes, signs, and confidence or credible interval coverages of covariates were very similar between the spatial Bayesian model and the final model-averaged likelihood-based model. We considered covariates relevant predictors of nuthatch occupancy if their 95% credible intervals in the Bayesian spatial model did not overlap 0. We calculated predicted ψ across the range of observed values for each supported site covariate from the estimated fixed effects of the Bayesian spatial model holding other continuous covariates at their respective means. We fixed breeding phenology for each site visit to before hatch for the first 2 visits and post-fledging for the last 2 visits to make these predictions because they were the modal values for those visits. We also calculated predicted ψ for fresh and punky snags combined by varying both values simultaneously from their minimum to their maximum observed values to facilitate comparisons between our results and current snag management guidelines, which do not account for the density of different classes of snags (Ouachita National Forest 2005, Tirpak et al. 2009, U.S. Fish and Wildlife Service 2013).

Model fit and predictive performance.—We used the posterior predictive loss criterion (Gelfand and Ghosh 1998) to compare the Bayesian probit regression occupancy models because AIC_c was unsuitable. The posterior predictive loss criterion is suitable only for Bayesian models and combines a goodness-of-fit term with a penalty term that can be used to select from among models. Lower values indicate better predictive performance. We then assessed the predictive performance of the model with the lowest posterior predictive loss criterion value using the area under the curve of the receiver operating characteristic, with a threshold setting of 0.5, i.e., we assumed sites with predicted $\psi \geq 0.5$ were occupied to compare predicted versus observed apparent occupancy among stations. We estimated percent classified correctly, sensitivity, and specificity of the Bayesian spatial model as well. Finally, we plotted predicted versus

observed occupancy across values of ψ using 5 binomial bins and confidence intervals derived from the F distribution for the Bayesian spatial model (Freeman and Moisen 2008).

Patch characteristics at all survey stations versus occupied stations.—We compared habitat characteristics in the established range and in the range-extension zone. We also determined how stand conditions or fire history parameters differed between occupied sites in the established range and in the range-extension zone. We calculated effect sizes, i.e., Cohen's d, plus sample sizes, sample means, and standard deviations for each covariate value by range-limit context to estimate the magnitude of any observed differences (Cohen 1998). We calculated R^2 to estimate the magnitude of any latitudinal gradients in stand conditions or fire histories that may have been present. We treated Cohen's $d > 0.3$ and $R^2 > 0.1$ as potentially important effects (Cohen 1988). We treated median Cohen's $d > 0.3$ as an indicator that average conditions differed appreciably between range-extension contexts or between sites where nuthatches were observed or not observed (Cohen 1988).

RESULTS

We surveyed 284 sites, 156 and 128 sites in the Ouachita and Ozark-St. Francis National Forests, respectively. We visited most sites 4 times (1,130 of 1,148 surveys, 98.4%) and all sites $\geq$3 times. We detected nuthatches at 76 locations, 65 and 11 locations in the Ouachita and Ozark-St. Francis National Forests, respectively.

The top detectability model was ψ (.) p (phenology) and no other models were competitive (Appendix). The top range-limit context model was ψ (latitude) p (phenology) and no other models were competitive (Appendix). Two models of stand structure and fire history were competitive (i.e., $\Delta AIC_c \leq 4$; Appendix): 1) latitude + stand structure and 2) latitude + stand structure + fire history. However, as the second-ranked model with the 2 additional fire parameters did overcome the 2-point AIC penalty for each additional parameter, we considered them uninformative and proceeded to fit the Bayesian models with only latitude + stand structure (Arnold 2010).

The Bayesian model with a spatial random effect provided the best predictive power of all models as measured by several criteria. The posterior predictive loss criteria for the Bayesian spatial and nonspatial models were 218.87 and 224.69, respectively, indicating the spatial random effect was warranted. The area under the curve values for the Bayesian spatial and nonspatial models were 0.89 and 0.84, respectively, indicating both models predicted observed occupancy better than chance. The Bayesian spatial model classified 86% of sites correctly, with a specificity of 0.92 and a sensitivity of 0.70. This means that the model correctly predicted true absences 92% of the time and true presences 70% of the time when assuming that observed occupancy was correct. The plot of predicted versus observed occupancy did not show significant departures from the fit line except in the lowest bin, suggesting the model over-predicts occupancy in sites with the lowest expected ψ (Fig. 2).

Detection probability was highest before hatch and lowest during the brood-rearing period. The 95% credible intervals overlapped one another for the brood-rearing and post-fledging periods, suggesting they were not different (Table 1). Occupancy decreased along the apparent south–north range-extension gradient and with higher tree stocking, whereas occupancy increased with fresh and punky snag density (Table 1). Predicted occupancy was 0.01 at the limits of the range-extension zone, i.e., the northernmost latitude we visited, and near 0 for stands with stocking >100%; predicted occupancy increased rapidly with increases in punky, fresh, and combined snag density (Fig. 3).

Habitat conditions between the established range and the range-extension zone were similar (median Cohen's d: 0.28, range: 0.03–0.48; Table 2), and there were no apparent latitudinal gradients in stand conditions or fire histories (R^2: 0.00–0.04). However, nuthatches in the established range occurred in different habitat conditions than those associated with nuthatches in the range-extension zone (median Cohen's d: 0.48, range: 0.11–1.29; Table 2). Nuthatch locations in the established range were typical for the species, whereas occupied sites in the range-extension zone were not (Table 2; Slater et al. 2013). Occupied sites in the established range had more snags, more grass cover, more frequent fires, and less shrub cover than occupied sites in range-extension zone (Table 2).

DISCUSSION

Range-extension context and conditions created by habitat restoration were both predictors of nuthatch occupancy. Nuthatches occurred in woodland conditions and occupancy increased with snag density, consistent with previous studies (Slater et al. 2013). This was true of both punky and fresh snags, which most researchers have treated singly (e.g., Wilson and Watts 1999). Nuthatch occupancy also declined along a south–north latitudinal gradient where no such gradients in stand structure or fire history were present.

At least 3 nonexclusive hypotheses could explain the positive relationship between fresh snags and nuthatch occupancy we found. Foraging nuthatches selected fresh snags from within individual home ranges and were observed inspecting the bark of fresh snags, suggesting fresh snags may provide a food resource (Stanton et al. 2014, R. A. Stanton, University of Missouri, personal observation). However, studies of foraging brown-headed and pygmy nuthatches (*S. pygmaea*) suggest this behavior is generally uncommon in these species (e.g., Morse 1967, Stallcup 1968). Fresh snag density may also have indirect effects on nuthatches, perhaps by altering the frequency of agonistic interactions with woodpeckers (Williams and Batzli 1979). It is also possible that nuthatches do not distinguish between fresh and punky snags because fresh snags eventually decay and become suitable for nesting and, therefore, represent a form of capital for a cooperatively breeding species. Current snag density guidelines for nuthatches range 1.2–8 snags/ha (USDA Forest Service 2005, Tirpak et al. 2009, U.S. Fish and Wildlife Service 2013); we found that 7 total snags/ha would be necessary to achieve 50% occupancy at mean stocking

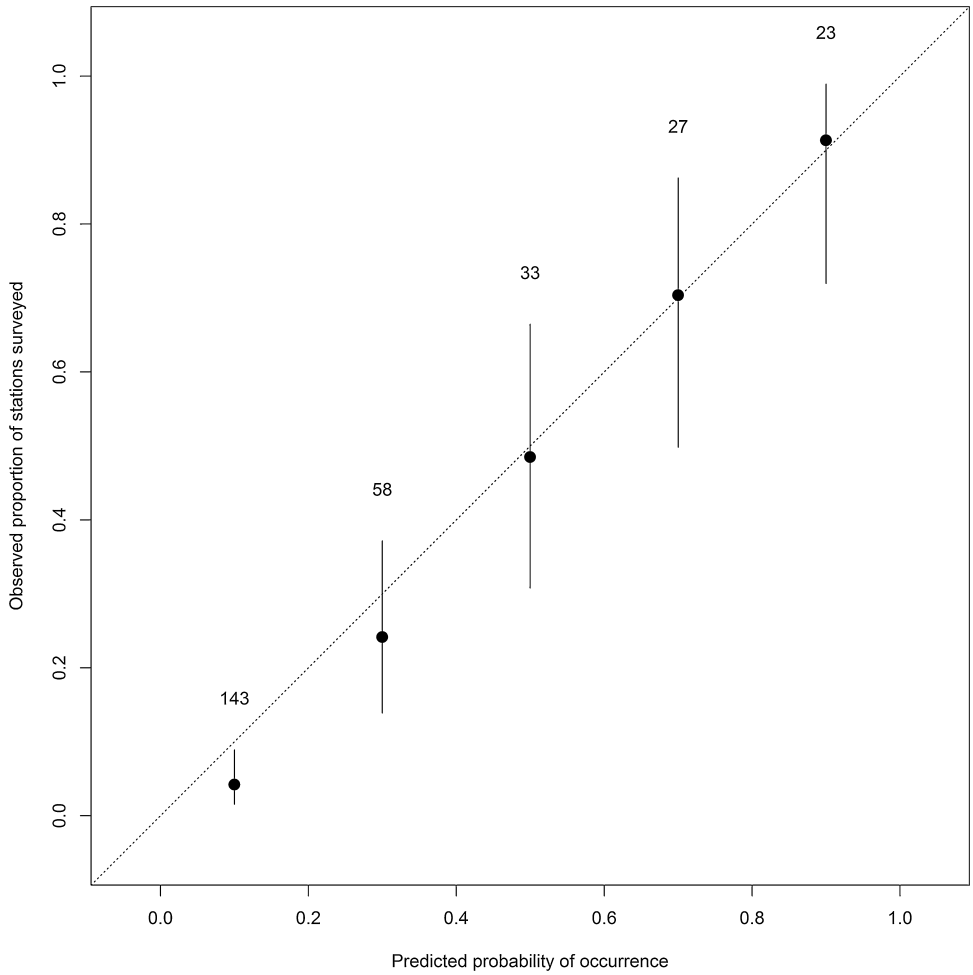

Figure 2. Observed versus predicted brown-headed nuthatch occupancy in the Ouachita and Ozark National forests of Arkansas, USA, 2011–2012, based on 5 binomial bins and confidence intervals derived from the *F* distribution. Predictions based on a Bayesian occupancy model with a spatial random effect. Bars represent the 95% confidence intervals for each binomial bin. The numbers above each bar are the number of survey stations that fall into each respective bin.

levels, and occupancy would increase with up to 15 snags/ha (Fig. 3).

Habitat management promoting grassy herbaceous cover for red-cockaded woodpeckers probably has no deleterious effects on brown-headed nuthatches. Grassy herbaceous cover had no association with nuthatch occupancy in this study and mixed associations with nuthatch space use and home-range size in the Ouachita National Forest (Stanton et al. 2014). Patterns of brown-headed nuthatch patch occupancy in Florida, USA also suggested that the habitat associations of nuthatches and red-cockaded woodpeckers differ, so this is not surprising (Cox et al. 2012).

Nuthatches in the Ozark-St. Francis National Forest (range-extension zone) were observed in stands that were atypical in structure despite the presence of stands with more typical snag densities, understory structures, and fire histories. This is important because snag densities were also relevant predictors of occupancy. We observed this pattern throughout a region where nuthatches were formerly present and restoration efforts have created apparently suitable habitat conditions (James and Neal 1986, Hedrick et al. 2007). Barriers to dispersal (e.g., Cox and Kesler 2012) and lack of propensity to disperse may have prevented colonization of apparently suitable stands in the range-extension zone. Previous work has indicated that individuals colonizing restored sites may occur at low abundance and in atypical, possibly suboptimal sites (Morris 1987). There are many possible reasons why individuals may settle in such locations ranging from Allee effects and lack of conspecific competitors to errors in our identification of

Table 1. Parameter estimates and 95% credible intervals (CRI) from a spatial occupancy model for factors related to detection (p) and occupancy (ψ) of brown-headed nuthatches in the Ouachita and Ozark National Forests of Arkansas, USA, 2011–2012.

Parameter	median $\widehat{\beta}$	95% CRI
p parameters		
Intercept	0.45	0.20, 0.70
Phenology, brood rearing	−0.98	−1.41, −0.55
Phenology, post-fledging	−0.55	−0.87, −0.23
ψ parameters		
Intercept	−0.98	−1.34, −0.68
Latitude	−1.07	−1.63, −0.67
Tree stocking percent	−0.63	−0.97, −0.35
Fresh snags/ha	0.57	0.17, 1.16
Punky snags/ha	0.36	0.05, 0.72
Percent pine	0.12	−0.10, 0.36
Percent grass	−0.19	−0.44, 0.05

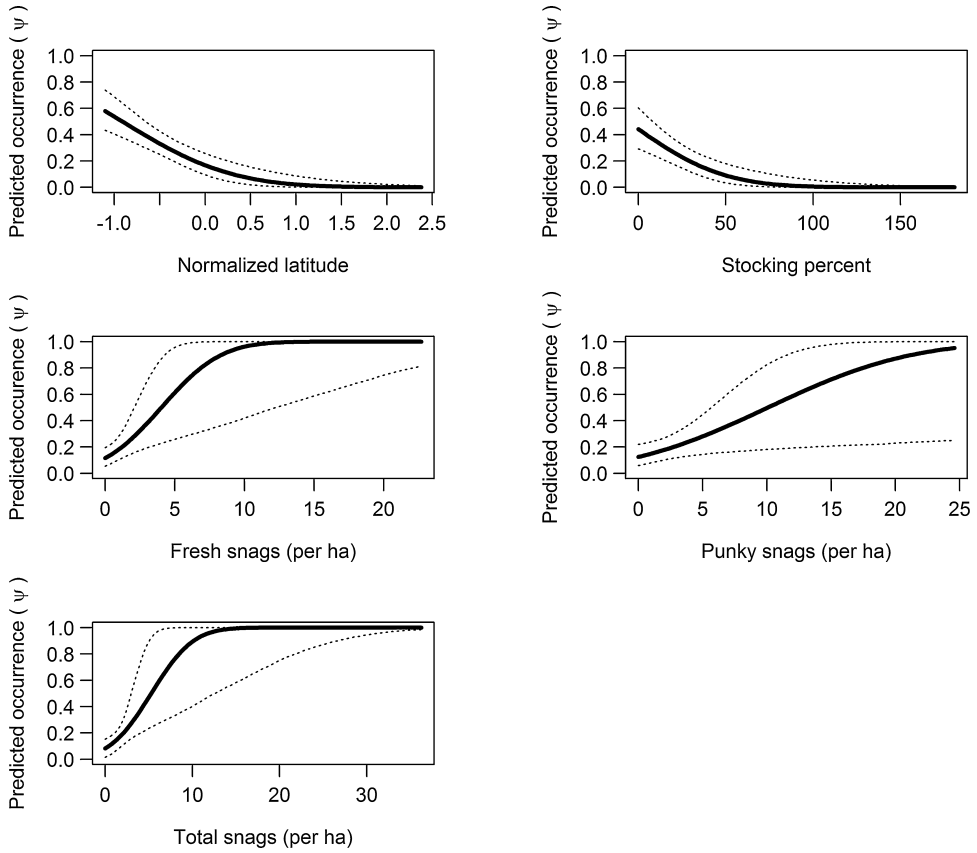

Figure 3. Predicted brown-headed nuthatch occupancy by normalized latitude (higher values are farther north), tree stocking, punky snag density, fresh snag density, and total snag density with all other stand attributes fixed at their respective mean values. Dotted lines represent bounds of 95% credible intervals. Predictions based on a Bayesian spatial occupancy model fitted to data collected in the Ouachita and Ozark National forests of Arkansas, USA, 2011–2012.

apparently suitable habitat (Morris 1987, Stevens and Sutherland 1999, Kesler and Walters 2012). For example, Cox et al. (2012) speculate that edaphic factors may lead to differences in nutrient availability or productivity that could explain patterns of nuthatch occupancy in Florida, USA. This possibility has not yet been independently evaluated. Our study was not concerned with edaphic factors, but differences in shortleaf pine growth varied little among the soils that occur in our study area (Graney 1976). Therefore, although differences in productivity that we did not measure may have affected nuthatch occupancy, we think it unlikely that such differences explain why we observed nuthatches in the range-extension

Table 2. Means, standard deviations, and effect sizes (Cohen's *d*) of stand condition metrics at stations surveyed for brown-headed nuthatches and stations where nuthatches were detected in the Ouachita and Ozark-St. Francis National Forests (NF) of Arkansas, USA, 2011–2012.

Covariate	Ouachita NF ($\bar{x}$, SD)	Ozark-St. Francis NF ($\bar{x}$, SD)	Cohen's *d*
All sampling stations	$n = 156$	$n = 128$	
Tree stocking percent	33.9, 26.2	34.8, 25.8	0.03
Fresh snags/ha	1.0, 2.5	0.5, 1.2	0.23
Punky snags/ha	1.8, 3.6	1.5, 2.4	0.11
Percent pine	58.1, 27.3	48.8, 31.3	0.32
Percent grass	28.9, 24.7	21.4, 20.2	0.33
Percent shrub cover	34.8, 26.0	40.4, 28.2	0.21
Years since fire	7.5, 7.5	11.5, 8.8	0.48
Fires in last 10 years	1.3, 1.2	0.9, 1.1	0.38
Stations with ≥1 detection	$n = 65$	$n = 11$	
Tree stocking percent	23.0, 19.1	20.9, 22.7	0.11
Fresh snags/ha	2.0, 3.6	0.5, 1.1	0.43
Punky snags/ha	3.2, 5.0	1.0, 1.3	0.47
Percent pine	63.1, 29.0	59.5, 38.4	0.12
Percent grass	35.2, 26.0	8.8, 8.8	1.08
Percent shrub cover	41.2, 25.6	73.7, 23.1	1.29
Years since fire	5.7, 6.8	9.3, 8.7	0.51
Fires in last 10 years	1.6, 1.3	1.0, 1.2	0.49

zone in sites with fewer snags and less grassy herbaceous cover. Rather, occupied sites in the range-extension zone burned less recently than occupied sites in the established range, likely explaining most of the differences in vegetation structure we observed (mean difference in time since fire: 3.6 years; Table 2).

It is also possible that the Ozark-St. Francis National Forest is not a range-extension zone but has merely been better-surveyed in recent years However, recent extensive restoration efforts render that possibility unlikely (Hedrick et al. 2007, USDA Forest Service 2012). The pattern we observed was also based on a small sample. However, such sampling issues are very difficult to avoid at range margins and similar patterns at range limits exist for other species (Oliver et al. 2009).

Habitat restoration appears to have benefitted brown-headed nuthatches by creating snags and reducing tree stocking rates. Tree stocking rates and snag densities also had effects on nuthatch space use and home-range size consistent with this conclusion (Stanton et al. 2014). Apparent cooperative breeding was common in the established range as well (Stanton et al. 2014). Habitat restoration may have also facilitated a northward range extension. However, we also found that some restored stands in the range-extension zone were vacant while stands in less-restored condition were occupied.

MANAGEMENT IMPLICATIONS

Managers should consider both habitat structure and range-limit context to improve nuthatch occupancy. Managers can set a target of >7 total snags/ha to achieve $\geq 50\%$ site occupancy. We suggest creating ≥ 3 punky snags/ha when managing snags to keep nuthatch home-range sizes at or below their median size in the established range (Stanton et al. 2014). We also suggest stand thinning to improve nuthatch occupancy by creating stocking levels of at most 50% or preferably 23% to match average occupied conditions in the Ouachita National Forest (Fig. 3, Table 2). Future habitat restoration that achieves suitable snag densities and tree stocking rates in the range-extension zone will improve nuthatch occupancy most effectively if managers prioritize more southerly sites and consider habitat connectivity. Identifying the ecological potential for restoration of pine woodland in Arkansas and Missouri can establish the practical limits of site restoration for nuthatches. Determining ecological potential for restoration will also enable potential nuthatch habitat connectivity to be estimated for the Ozark-St. Francis National Forest. Understanding restoration potential could also inform management directed at brown-headed nuthatch recolonization of Missouri and help determine if reintroductions are potentially needed to overcome dispersal limitations.

ACKNOWLEDGMENTS

We thank W. Montague for advice, direction, and logistical support. The Arkansas Game and Fish Commission provided housing in 2011. J. Foggia, H. Prelewitz, A. Henehan, and E. Underwood collected field data. J. Faaborg, A. McKellar, and several anonymous reviewers contributed valuable comments that improved this paper. G. Connette provided R code for generating predictions from the Bayesian spatial model. We thank the Ouachita National Forest for permission to work on the national forest (File code 2620/2700). Use of trade, product, or firm names does not imply endorsement by the U.S. Government.

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Associate Editor: Andrew Kroll.

SUPPORTING INFORMATION

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APPENDIX. Ranked likelihood-based logistic regression occupancy models fit in the R statistical package unmarked estimating the effects of detectability (p), range-context, and stand condition (vegetation structure and prescribed fire history) on brown-headed nuthatch occupancy (ψ) in the Ouachita and Ozark National Forests of Arkansas, USA, 2011–2012. Models were fit in the order shown, with all competitive ($\Delta AIC_c < 4$) models of a given type (e.g., detectability) carried forward to subsequent stages.

Model	K[a]	logLik[b]	ΔAIC_c[c]	w_i[d]
Detectability models				
ψ (.)p(phenology)	4	−358.33	0.00	0.99
ψ (.)p(date)	3	−363.63	8.54	0.01
ψ (.)p(temperature)	3	−367.70	16.68	0.00
ψ (.)p(time)	3	−369.29	19.85	0.00
ψ (.)p(wind)	3	−369.37	20.01	0.00
ψ (.)p(observer)	4	−368.35	20.04	0.00
ψ (.)p(.)	2	−370.71	20.65	0.00
Range-context models				
ψ (latitude)p(phenology)	5	−335.74	0.00	0.92
ψ (Ouachita)p(phenology)	5	−338.21	4.96	0.08
ψ (.)p(phenology)	4	−358.33	43.11	0.00
Stand condition models				
ψ (latitude + stand structure)p(phenology)	10	−309.87	0.00	0.85
ψ (latitude + stand structure + fire history)p(phenology)	12	−309.46	3.53	0.15
ψ (latitude + fire history)p(phenology)	7	−332.44	38.74	0.00
ψ (latitude)p(phenology)	5	−335.74	41.15	0.00

[a] Number of model parameters.
[b] Model negative log-likelihood.
[c] The difference between minimum Akaike's Information Criterion corrected for sample size (AIC_c) in a set of models and a given model. The AIC_c of the top detectability, range-extension context, and stand condition models were 724.80, 681.70, and 640.55, respectively.
[d] Akaike weight.