HABITAT SELECTION OF BROWN-HEADED NUTHATCHES AT MULTIPLE SPATIAL SCALES

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by
RICHARD A. STANTON, JR.

Dr. Dylan C. Kesler, Thesis Supervisor
Frank R. Thompson III, Ph.D., Thesis Supervisor

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The undersigned, appointed by the dean of the Graduate School, have examined the thesis entitled

HABITAT SELECTION OF BROWN-HEADED NUTHATCHES AT MULTIPLE SPATIAL SCALES

presented by Richard A. Stanton, Jr.,

a candidate for the degree of Master of Science,

and hereby certify that, in their opinion, it is worthy of acceptance.

Professor Dylan C. Kesler

Professor Frank R. Thompson III

Professor John Faaborg

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Richard A. Stanton, Jr.

Dr. Dylan C. Kesler, Thesis Supervisor
Frank R. Thompson III, Ph.D., Thesis Supervisor

ABSTRACT

Resources shape the movements and space use of birds. In turn, birds differ in their relative fitness, in part as a consequence of movement and space use decisions. The saga of each individual plays out across time and space, generating the dynamic pattern known as a species' geographic range. Then, changes in geographic range dimensions alter the selective environment encountered by individuals, potentially driving evolutionary change in movement modes. Thus, understanding resource selection requires knowledge of both individual behavior and landscape patterns of patch occupancy.

This thesis describes resource selection from both perspectives. We conducted two concurrent studies in a cooperatively breeding bird (Brown-headed Nuthatches, *Sitta pusilla*). The first study documented space use within individual home ranges while the second documented patch occupancy across a heterogeneous range extension front. The range extension front followed prescribed fire and stand thinning treatments intended to restore pine forests to savannah-woodland condition. The individuals we tracked were in sites where restoration efforts had already been deemed successful.

Together these studies enabled us estimate the relative value of several resources to nuthatches and test competing hypotheses regarding the range extension process in resident birds. These studies were also developed in order to characterize the extent of suitable habitat in Missouri where the species was extirpated, and to predict changes in the extent of habitat that may occur in response to climate change and habitat restoration efforts.

We radio-tracked 22 Brown-headed Nuthatches, and related their space use and home range size to available resources within their respective home ranges using linear mixed models and lognormal regression. Nuthatch home ranges typically had two centers of activity and areas of high use were associated with recently-killed (fresh) snags, recent prescribed fire, pine dominance, and grassy herbaceous cover in descending order of importance based upon their respective model-averaged standardized coefficients. For example, fresh snags appeared to be 1.7 times more important to Brown-headed Nuthatches than grassy herbaceous cover, based on the magnitude of their respective standardized model coefficients. Total stocking had a weak negative association with nuthatch use: 47% as important as fresh snags. These associations controlled for the influence of the nest site as a central place; thus the intensity of use associated with these resources reflected their perceived value to nesting nuthatches. Home range size was negatively related to the amount of pine, which was used for foraging, and snags, which were used for nesting. Cooperative breeding was ubiquitous (≥82%) and nest sites may have been limiting, which could explain the incidence of cooperative breeding and part of the variation in nuthatch home range size. Grassy herbaceous cover was associated with larger home ranges. This was surprising since it

has been associated with high quality foraging habitat in ecologically similar Red-cockaded Woodpeckers, and abundant high-quality resources are generally associated with smaller home range sizes. We found no evidence that resource selection differed between growing season and dormant season prescribed burns.

We also modeled patch occupancy across a range extension front created by habitat restoration. We ran repeated call-response surveys at 284 sites, and counted all nuthatches detected. Model results indicated that patch-level measures of recently-killed snags suitable for foraging and soft, "punky" snags suitable for nesting were strongly associated with probability of nuthatch occupancy (533% and 338% increase in predicted Ψ from minimum to maximum observed values of fresh and punky snag density with other covariates fixed at their respective mean values, respectively). Tree stocking percent and years since fire had a negative relationship with nuthatch occupancy (100% and 35% predicted decrease inΨ across observed values with other covariates fixed at their respective mean values). Percent pine, grassy herbaceous cover, and percent burned pine within a 2 km radius had no apparent relationship with nuthatch occupancy. These results indicate that managing for more freshly-killed snags in pine savannah-woodland sites may be warranted for increasing nuthatch occupancy, whereas grassy herbaceous cover may have little value for nuthatches. In each case, further confirmatory study is needed to establish whether these associations have verifiable, biologically significant links to nuthatch survival and reproduction.

Importantly, model results also indicated that high quality habitat near the range limit was less likely to be occupied while nuthatch detections showed that marginal habitat was occupied. This pattern is contrary to the standard model of range extension and habitat selection wherein habitats are occupied hierarchically in order of quality. However, the pattern we observed is consistent with a range extension front that has been shaped by constraints on effective dispersal. Dispersal can be highly variable within species and some range extensions might be driven by individuals at the extreme of the dispersal distance distribution. We documented a range extension front apparently driven by the behavior of average birds. This pattern may be quite common among birds given that many species are sedentary and that Allee effects are common in peripheral animal populations impeding establishment of long-distance dispersers.

We emphasize the importance of further developing and testing a theoretical model that explicitly relates individual behavior to species distributions. Improvement and resolution of this model will be a critical component of achieving “predictive ecology,” a desperately-needed means of managing global change.

THESIS FORMAT

The chapters of this thesis were written as independent manuscripts prepared for submission to peer-reviewed journals. As a result, some essential introductory and methodological materials are repeated, and a separate literature cited section follows each chapter. In addition, I use the plural noun "we" rather than "I" throughout each chapter**.**

CHAPTER 1

COST-SENSITIVE RESOURCE SELECTION IN A COOPERATIVELY-BREEDING RESIDENT BIRD

ABSTRACT

Activities associated with acquiring and maintaining access to critical resources drive movement and space use in birds. Theory indicates that the spatial configuration of resources within home ranges should influence bird movements, and that resource values are relative to their locations. We radio-tracked 22 Brown-headed Nuthatches and related their space use and home range sizes to available resources within their home ranges while taking nest site locations into account. We developed utilization distributions (UDs) from nuthatch relocations, treating the area of each 95% isopleth as home range size and the height of the UD as relative probability of use. We fit models relating home range size to mean resource measures within home ranges using lognormal regression and related intensity of use to resource metrics at random points by ranking linear mixed models. Nuthatch home ranges typically had two centers of activity and areas of high use were associated with density of recently-killed snags (a likely foraging resource), recent prescribed fire, pine dominance, low tree stocking rates, and grassy herbaceous cover. Home ranges were generally large (median 7.1 ha, range 0.3-47.6 ha) and smaller home range sizes were associated with pine dominance and nest snag density. Predicted home range size decreased by 77% and 69% respectively when percent pine and nest snag density in home ranges were maximized with other covariates held constant. Nest sites may have been limiting given extensive cooperative breeding (≥82%) and a linkage between potential nest sites and home range size. Our results illustrate that territory-scale

movement decisions are driven by both the availability and spatial distribution of resources while indicating that ongoing savannah-woodland management for Brown-headed Nuthatches is necessary.

INTRODUCTION

Foraging substrates and nest sites are among the critical resources needed by all birds in order to survive and reproduce (Newton 1998). Acquiring and maintaining access to these critical resources drives movements and space use in birds. The relationship between resources and space use is especially important in resident species. Many such species remain on all-purpose territories throughout the year and choice of home range after natal dispersal is often permanent (Nice 1937, Jackson 1994, Golabek et al. 2012). Several studies have also documented extensive prospecting movements in resident and cooperatively breeding birds, reinforcing the importance of optimizing home range selection in sedentary species (Hooge 1995, Kesler and Haig 2007, Kesler et al. 2010, Cox and Kesler 2012).

The spatial arrangement of resources should influence bird movement within home ranges most during the nesting season. Central place foraging influences movements because individuals return to a focal location after each foraging bout (Orians and Peterson 1979). Thus, all birds that incubate or raise young in the nest are central place foragers during that time. Central place foraging theory posits that distance from the focal area will impact the relative value of a resource (Kacelnik 1984). The value of a resource is influenced by the cost to access that resource (Morris 1987, Rhodes et al. 2005); a unit of a given resource should be used less when the cost of access is increased (Collier et al. 1990). For the same reason, treating a territory or home range as an assemblage of uniformly-valued resources may be inappropriate during nesting because some resources are more distant from the nest, and thus more costly. Similarly, territorial boundaries can render some resources effectively unavailable, and classifying resources outside of the home range as available can be problematic for resource selection studies (Fretwell 1972, Jones 2001, Marzluff et al. 2004).

Few researchers have evaluated how territorial animal movements are influenced by the distribution of resources and the associated costs of accessing those resources from a central place (Carrete and Donázar 2005, Rainho and Palmeirim 2011). Further, no studies have examined movement within the home range of a resident cooperatively breeding bird in this manner (e.g. 3rd order selection, sensu Johnson 1980, corrected for the influence of a central place). Third order habitat selection, in which animals select habitat components within home ranges, is generally not evaluated in areas perceived by researchers to be uniform (Levin 1992, Rhodes et al. 2005).

Similarly, animal home range sizes are often smaller when available resources are abundant and larger when resources are scarce (Haskell et al. 2002, Mitchell and Powell 2004). Thus, describing the relationship between resources and home range size can identify possible limiting factors. We studied resource selection in a population of Brown-headed Nuthatches (*Sitta pusilla*). We related available resources to relative probability of use within individual home ranges and to home range size. We accounted for the distance between available resources and nest sites to develop cost-sensitive resource utilization functions (Rosenberg and McKelvey 1999, Manly et al. 2010).

METHODS

Focal species

The Brown-headed Nuthatch is a resident species restricted to pine (*Pinus* spp.) and mixed-pine forests in the fire-maintained savannah-woodlands of the southeastern United States (Withgott and Smith 1998). The species co-occurs with the federally-endangered Red-cockaded Woodpecker (*Picoides borealis*), and is widely presumed to benefit from habitat management for that species (Wilson et al. 1995, Withgott and Smith 1998). Nuthatches are small (10g) primary cavity nesters, requiring well-decayed snags for nesting (Withgott and Smith 1998). Limited nest site availability may drive cooperative breeding in nuthatches as it does in Red-cockaded Woodpeckers (Brawn and Balda 1988, Walters et al. 1992, Withgott and Smith 1998).

Study site

We studied Brown-headed Nuthatches in the Pine-Bluestem Ecosystem Management Area of the Ouachita National Forest in Arkansas, USA (34.823°N -94.208°E) where Brown-headed Nuthatches are common (James and Neal 1986, Hedrick et al. 2007). Current forest management includes regular prescribed fire, midstory reduction, and stand thinning, all of which are aimed at restoring pine savannah-woodland conditions (Wilson and Watts 1999, Hedrick et al. 2007). The Pine-Bluestem Ecosystem Management Area is ~101,000 ha; ≥57% has been treated with prescribed fire on ≥1 occasions and ≥7.5% is in "substantially restored" condition (Hedrick et al. 2007).

Field methods

Capture, marking, and radio tracking

We captured, marked, and radio tracked nuthatches from 21 March to 20 May in 2011 and from 12 Mar to 23 May in 2012. We captured nuthatches by targeted mist netting using calls modified from Spencer (2009a, 2009b) in program Audacity (Audacity Development Team 2011). Each bird was banded with a unique combination consisting of one aluminum size 0 United States Geological Survey butt-end metal band and two Darvic™ color bands (Pyle 1997). We collected 4-6 ventral feathers from each bird for molecular sexing (Avian Biotech International, Tallahassee, FL; Kin Han, Department of Biology, University of Florida, Gainesville, FL). We also used brood patches, cloacal protuberances, and behavioral clues to estimate sex (Figs. 20-22 in Pyle 1997).

We attached radio transmitters to the 2 central rectrices using gel-type ethyl cyanoacrylate glue and an accelerant applied to the feathers using a cotton swab (Instacure^{+TM} and Instaset^{TM}, BSI Inc., Atascadero, CA; Mong and Sandercock 2007, Kesler et al. 2010). Transmitters weighed ~0.27 g, with battery lives of roughly 17 days in 2011 (Holohil model LB-2X, Carp, ON) and 45 days in 2012 (Advanced Telemetry Systems model A2414, Asanti, MN). If a transmitter fell off before the bird had been relocated ≥30 times, we attempted to recapture it and replace the transmitter by attachment to the two innermost remaining rectrices.

We located birds using the homing method with a handheld receiver and Yagi-Uda antenna (R-1000 receiver, RA-165 Antenna, Communications Specialists Inc., Orange, CA; Uda 1927, Yagi 1928, White and Garrott 1990). We attempted to locate each bird 1-3 times each day, beginning 1 day post-capture, and continuing until the transmitter failed, reached the end of its predicted battery life, or was jettisoned by a bird with ≥30 relocations. Successive relocations were separated by > 1 h to ensure behaviorally independent samples and reduce temporal autocorrelation (Seaman et al. 1999) and we relocated birds in a different sequence each tracking bout to ensure sampling throughout the day. We recorded bird locations with a handheld global positioning system (GPS; Garmin eTrex Vista HCX, Garmin Ltd., Olathe KS). We only located birds in low winds (<15 km/hr) and no precipitation in order to control for the effects of weather on detectability and bird behavior. We did not sample birds attending the nest and only one bird from each group was included in analyses. We classified a bird as breeding if we observed it carrying food, attending a nest, provisioning fledglings, or excavating a cavity. We classified a bird as part of a cooperative group if we observed ≥3 adults simultaneously at any point during the study, territorial disputes excluded. Lastly, we visited the home ranges of all birds radio-tracked in 2011 on ≥ 1 occasion to verify that those sites were occupied in 2012. We counted those sites as occupied if we saw ≥1 color-banded bird in a 2011 home range at any point in 2012.

We searched exhaustively for birds that were not located immediately by homing. We walked in concentric circles up to 450 m beyond any prior location, and drove all roads within 2 km of prior locations to locate such birds using an omnidirectional tracking antenna. We spent 30 mins at both the capture location and nest sites attempting to re-sight missing birds. Two birds were not located despite these efforts, but had live transmitters during a roost check that evening. Missing observations can result in serious bias so we did not include either bird in any analyses (Rodgers 2001). One bird made a substantial directed movement (~ 1 km), after which it appeared to have settled on a new home range, so we excluded those initial observations and only analyzed its post-movement space use (per Burt 1943, pp. 350-351).

Developing utilization distributions

We developed a fixed-kernel utilization distribution for each bird (UD; Marzluff et al. 2004). The UD is a probability density function developed from relocation coordinates using kernel smoothing methods (Worton 1989, Millspaugh et al. 2006). Each UD was bounded by the 95% isopleth to avoid misclassification of neighboring territories as available (Worton 1989, Rittenhouse et al. 2008). Bandwidth selection was calculated using the plug-in method (Wand and Jones 2002, Gitzen et al. 2006, Duong 2012). We determined that birds with ≥17 locations per animal were adequately sampled for analysis (median: 42, range: 17-63). We inspected each UD and found no apparent relationship between UD topographies or home range sizes for birds with ≥17 locations and the number of observations used for UD generation. There was also no significant correlation between sampling intensity and minimum convex polygon home range size ($r = -0.11$, $n = 22$, $P = 0.30$; Marzluff et al. 2004).

Vegetation and snag sampling

We randomly selected 20-59 points ≥25 m apart within each home range and measured vegetation at those locations. We measured live trees and ground cover at each vegetation sampling location in 2011 and 2012. In 2012, we also measured snags at the vegetation points, but we had to revisit locations where we tracked birds in 2011 to measure snags and measured snags at a different set of random locations than those used to collect the other vegetation data. Because we needed snag densities for each vegetation point for our analyses, we assigned a snag density to each 2011 vegetation point by using an inverse distance weighting algorithm implemented in ArgGIS 9.3 (Environmental Systems Research Institute). We used the area-weighted mean snag density from up to 5 random locations within 150 m of a vegetation point with a distance weighting power function of 2.

We measured tree diameters, grassy herbaceous cover, shrub cover, and snags at vegetation points. We measured the diameter at breast height (DBH) of all trees to the nearest 5 cm class with a Biltmore stick (Grosenbaugh 1958, Jackson 1911) selected with a 10 factor wedge prism and classified them as pine or hardwood (i.e. *Pinus* spp. or other). We visually estimated the proportion of grassy herbaceous cover and shrub cover within 12.5 m of each point. We measured DBH and distance to every snag detected at each point using a laser rangefinder (Bushnell Yardage Pro Sport, Overland Kansas, USA) and classified them as fresh or punky. Fresh snags were freshly-killed or class 2 snags as classified by Maser et al. (1979) and punky snags were crumbly, well-decayed snags (conditions 3 and 4; Maser et al. 1979).

Derivation of vegetation and prescribed fire metrics

We developed a set of habitat and fire management metrics from our field measurements and geospatial data. The habitat structure metrics included percent tree stocking and snag density. We calculated percent stocking from our tree diameters using equations for mixed hardwoods (Gingrich 1967 *in* Johnson et al. 2010) and shortleaf pine (*Pinus echinata*; Rogers 1983*in* Johnson et al. 2010). We treated total stocking as the sum of these figures and percent stocking in pine as the quotient of pine stocking/total stocking. We estimated snag density by applying distance sampling methods that correct for imperfect detection (Buckland et al. 2004, Fiske and Chandler 2011). We pooled data from a concurrent study of occupancy and abundance from the same area, and developed separate models for fresh (class 2) and punky snags (classes 3 and 4 combined) with DBH ≥ 10.2 cm. We fitted hazard rate and half normal detection models with appropriate site level covariates for each snag class. We considered local shrub cover and percent tree stocking for punky snags, and percent tree stocking only for fresh snags. We calculated snag density estimates for each point by correcting our observed values based on the best-supported detectability models.

We extracted years since prescribed fire and fire season for each point from a GIS database (growing: May-October, or dormant; Sparks et al. 1998, USDA Forest Service 2012). We classified a home range as impacted by a growing season burn if ≥1 vegetation sampling points had a growing season burn. Similarly, if a home range spanned multiple burn boundaries, the most recent burn to impact that home range was considered the most recent fire for the home range as a whole.

Analyses

Home range size and resource availability

We fit lognormal linear models relating home range size to mean resources available to each bird (Table 1.1; Barton 2012). We fit all linear combinations of models with covariates that might be associated with home range size for a total of 32 models.

Resource selection within home ranges

We fit population-level resource utilization functions (RUFs; Marzluff et al. 2004, Manly et al. 2010) relating nuthatch space use to fine-scale resources. These were random intercept linear mixed models treating the standardized height of the UD at each randomly selected point as the response variable and individual identity as a random effect (Bates et al. 2012). We used mixed models because they are suitable for correlated data such as telemetry relocations (Bolker et al. 2009). We fit a priori models that included all linear combinations of habitat and fire management covariates, with log-transformed distance to nest in all models, for a total of 64 models (Table 1.1.; Burnham and Anderson 2002). We calculated standardized and unstandardized model coefficients with unconditional standard errors because we were interested in evaluating the relative value of resources and predicting habitat suitability (Marzluff et al. 2004). We inspected each UD and counted centers of activity, e.g. distinct peaks in the topography of the UD. Peaks were counted if they appeared to be >60% as tall as the primary peak in the same UD.

Analytical methods

We ranked models for all analyses using Akaike's Information Criterion adjusted for small sample sizes (AIC$_c$; Burnham and Anderson 2002). We considered models competitive for inference if ΔAIC$_c$ ≤4 and they did not contain uninformative parameters (Arnold 2010). We also did not consider models with ΔAIC$_c$ ≤that of the null model to be competitive. Competitive models were model-averaged (Burnham and Anderson 2002, Barton 2012). We present model-averaged coefficients and unconditional 95% confidence intervals (i.e. ±1.96 SE) for all competitive models. Confidence intervals for the mixed model analysis and associated predictions were based upon model-averaged fixed effects only. We considered the inclusion of a covariate in our competitive model set as evidence that it had an influence on nuthatch space use because ~85% confidence intervals of those covariates should not include 0 (Arnold 2010). We refer to these covariates as "less supported" if their 95% confidence intervals overlapped 0. We considered 95% confidence intervals that did not overlap 0 as additional evidence that a given covariate influenced nuthatch space use (hereafter “more supported”).

We present predicted standardized UD heights and home range sizes for all supported covariates. All predictions were limited to the range of observed values for each plotted covariate with all other covariates fixed at their respective mean values. We assessed adequate model fit for the global general linear mixed model relative to a cost-distance null model by ANOVA test (sensu Rosenberg and McKelvey 1999). Model fit for the global lognormal regression model was assessed by ANOVA test and the $\hat{c}$ statistic. All analyses were done in R version 2.15.2 (R Core Team 2012).

RESULTS

We captured 40 nuthatches and 22 were outfitted with transmitters and relocated 17-63 times (mean: 42.2); all 22 were from different groups. All groups were territorial and attempted to breed. All groups tracked in 2011 remained on the same territories in 2012. Eighteen of 22 groups were composed of ≥3 members. Our sample was strongly biased in favor of males (15 male, 3 female, 4 unknown). We noted brood patch development in 6 of 15 males.

Nuthatch home ranges were in stands with 11-40% stocking and 41-91% pine (Table 1.2). Both fresh and punky snags averaged <2.5/ha across home ranges (Table 1.2). Resources such as snags were more variable among sampling points within home ranges than among averages across home ranges (i.e. fresh snags ranged from 0-73/ha; Table 1.3, *n* = 965).

Home ranges were large and ranged from 0.3-47.6 ha (median = 7.1 ha, *n*=22). Fourteen of 22 (64%) nuthatch utilization distributions had 2 centers of activity (Fig. 1.1) indicating birds were foraging primarily in two distinct locations. There was no evidence of lack of fit of the global model predicting home rang size; the global model was an improvement over the null model and did not exhibit evidence of overdispersion (**Δ** in residual deviances = 8.03; $\hat{c}$ = 0.65). Four of the 32 models were competitive for inference (Appendix 1.1). Home range size was related to percent pine, punky snag density, and percent grassy herbaceous cover (top 3 models, w_i= 0.85; Table 1.4). There was also support for the null model (**Δ**AIC$_c$ = 2.01, w_i= 0.15; Table 1.4). Model-averaged predicted home range sizes declined 71% and 77% across the range of punky snag density and percent pine, respectively (Fig. 1.2). Grassy herbaceous cover was associated with larger predicted home range sizes, which increased by 113% when grassy herbaceous cover was maximized (Fig. 1.2). Model-averaged coefficient ± standard error and 95% confidence intervals for pine, punky snags, and grass were: pine (-0.039±0.015 [-0.068, -0.010]); punky snags (-0.303±0.129 [-0.556, -0.050]); grass (0.028±0.015 [-0.001, 0.057]).

Nuthatches selected particular resources within home ranges. We found no evidence of lack of fit for the global resource selection model; it was an improvement over the cost-distance null model that incorporated distance to the nest and the random effect of individual identity but no habitat covariates (χ^2 = 38.68, p<0.001). We fitted 64 third-order resource selection models and 3 were competitive for inference (App. 1.2). Fresh snags, years since last fire, percent pine, total stocking, and grassy herbaceous cover were all associated with nuthatch use (Table 1.5). Fresh snag density, percent pine, and grassy herbaceous cover were positively associated with relative probability of use (Fig. 1.4), whereas use declined with increasing total stocking and years since prescribed fire (Fig. 1.4). Resources differed in their apparent importance to nuthatches. For example, the standardized model-averaged coefficient for fresh snags was 2.4 times larger than the same coefficient for total stocking (Table 1.6).

DISCUSSION

Home range size was related to punky snags suitable for nesting, pine trees needed for foraging, and grassy herbaceous cover that might influence nuthatch invertebrate prey (Withgott and Smith 1998, James et al. 2001). Space use within home ranges was heavily dominated by the influence of a central place, yet several resource metrics were also associated with nuthatch use. Nuthatches avoided areas within home ranges where fire exclusion and heavy tree stocking predominated, while favoring recently-killed snags and grassy herbaceous cover. Most nuthatches had two centers of activity within their home ranges. We believe these activity centers are indicative of centers of foraging activity because we relocated nuthatches that were not attending the nest site and nuthatches were nearly always actively foraging when relocated.

The distribution of suitable nest sites may limit the carrying capacity of managed pine-bluestem habitats for Brown-headed Nuthatches. In many species habitat quality can be inferred when there is an apparent relationship between home range size and available resources (Gompper and Gittleman 1991). The resource we suspected to be limiting, punky snags, had a strong relationship with nuthatch home range size.

A relationship between home range size and percent pine was also present; home ranges with maximum pine representation and other resources at mean values were predicted to be 77% smaller. A post-hoc analysis indicated that high punky snag density only co-occurred with low percent pine values (Fig. 1.3). This suggests that some of the predicted home range sizes reflect conditions that did not exist in our sample and might not be achievable in managed landscapes. While home range size increased 113% across the range of grassy herbaceous; the relationship was in the opposite direction hypothesized and the 95% CI overlapped 0. Grassy herbaceous cover had a less-supported, weak positive association with nuthatch space use within home ranges (Fig. 1.6) and no apparent relationship with nuthatch site occupancy (Stanton, this volume). Overall, the evidence suggests that grassy herbaceous cover may be unimportant to Brown-headed Nuthatches, in contrast to Red-cockaded Woodpeckers (James et al. 2001).

Resource selection within Brown-headed Nuthatch home ranges was primarily driven by the influence of the nest site, as indicated by the relatively large model-averaged standardized coefficient of log distance to nest that did not overlap 0 (Table 1.6). However, fine-scale variation in resources also influenced space use in nuthatches as shown by overall model selection results and model-averaged confidence intervals for several covariates that did not overlap 0 (Table 1.6). Pine savannahs and woodlands can look very homogenous to the casual observer. If the configuration of resources in such an environment has a measurable influence, it should be even more important to animals using visibly patchy environments. Likewise, each species has evolved to perceive its environment in a particular way: its *Umwelt* (von Uexküll 1957). This study is thoroughly primitive as an approximation of how Brown-headed Nuthatches see their world. As voracious predators of many insect species, nuthatches and small birds generally must be able to perceive the world quite finely indeed. Thus, our results likely underestimate how much resource configuration influences nuthatch movement behavior.

We measured several structural vegetation characteristics associated with both nuthatch use and prescribed fire (Wright and Bailey 1982, Wilson and Watts 1999). Prescribed fire influences vegetation structure and stand dynamics; that it was supported in addition to these factors is consistent with speculation that prescribed fire may have beneficial effects on the invertebrate prey base. We also found an association between fresh snags and relative probability of nuthatch use. Fresh snags may represent a valuable foraging resource since they host a variety of beetle larvae and other suitable prey (Nesbitt and Hetrick 1976, Ulyshen and Hanula 2009). Further confirmatory study will be needed to determine whether this association has a verifiable, biologically significant link to nuthatch survival and reproduction.

The invertebrate prey of nuthatches may also explain why they typically have two centers of activity in their home ranges. All nuthatch utilization distributions had either one or two centers of activity; 64% had two (Fig.1.1). To our knowledge, this reflects the first documentation of bimodal foraging for a nesting passerine, although the phenomenon is probably common (per Welcker 2009). When birds select prey that vary substantially in size or handling time, it may be most efficient to gather them from different locations, focusing on a particular prey type during a given trip (Ydenberg and Davies 2010). Major nuthatch food items include scale insects and wood roaches, which are substantially different in size and likely handling time (Coccoidea, 1-6 mm; Blattaria, 19-25 mm; Nesbitt and Hetrick 1976).

Brown-headed Nuthatches have been declining in abundance, with the greatest declines at the southern limits of their range (Slater 1997, Sauer et al. 2008). The species has simultaneously extended its range northward, perhaps in response to climate change and habitat restoration (Haney 1981, Whitehurst 1986, Renfrow 2003). While climate projections are both mixed and uncertain, the extent of suitable habitat for nuthatches may increase in the future (Iverson and Prasad 2002, Murphy et al. 2004, Karl et al. 2009). However, nuthatches appear to have poor dispersal ability, and there is reason to doubt that re-colonization of suitable habitat will occur in places like the Missouri Ozarks (~400 km northeast of our study area) without human assistance (Slater 1997, Haas et al. 2010, Stanton, this volume). The findings from this study can be used to identify the extent of suitable habitat in Missouri, informing reasoned discussion on whether translocations should be attempted. Pine woodland and savannah management requires ongoing active management (Wright and Bailey 1982). The relationships we found support the value of active prescribed fire and other pine restoration efforts to Brown-headed Nuthatches during the breeding season.

LITERATURE CITED

Arkansas Audubon Society.2013. [Web application]. http://www.arbirds.org/searchspecies.asp (Accessed: 15 February 2013).

Arnold, T. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74:1175-1178.

Audacity, version 2.0. 2011. [Software program, online]. Available at: http://audacity.sourceforge.net/download/windows.

Barton, K. 2012. MuMIn: Multi-model inference. R package version 1.8.0. http://CRAN.R-project.org/package=MuMIn.

Bates, D., M. Maechler, and B. Bolker. 2012. lme4: Linear mixed-effects models using S4 classes. package version 0.999999-0. http://CRAN.R-project.org/package=lme4.

Beyer, H. L. 2004.Hawth's Analysis Tools for ArcGIS. Available at http:// www.spatialecology.com/htools.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, & J. S. S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution, 24: 127-135.

Brawn, J.D. and R.P. Balda. 1988. Population biology of cavity nesters in northern Arizona: Do nest sites limit breeding densities? Condor 90:61-71.

Buckland, S.T., Anderson, D.R., Burnham, K.P. and Laake, J.L. 1993. Distance Sampling: Estimating Abundance of Biological Populations. Chapman and Hall, London, reprinted 1999 by RUWPA, University of St. Andrews, Scotland.

Burnham, K.P., and D.R. Anderson.2002. Model Selection and Multimodel Inference: a Practical Information-theoretic Approach. 2nd edition. Springer-Verlag. New York.

Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. Journal of Mammalogy24:346-352.

Carrete, M., and J.A. Donázar. 2005. Application of central-place foraging theory shows the importance of Mediterranean dehesas for the conservation of the cinereous vulture, *Aegypius monachus*. Biological Conservation 126:582-590.

Collier, G.H., D.F. Johnson, K.A. CyBulski, and C.A. McHale. 1990. Activity patterns in rats (*Rattus norvegicus*) as a function of the cost of access to four resources. Journal of Comparative Psychology 104:53-65.

Cox, S.A., and D.C. Kesler. 2012. Prospecting behavior and the influence of forest cover on natal dispersal in a resident bird. Behavioral Ecology 23:1068-1077.

Dornak, L.L., D.B. Burt, D.W. Coble, and R.N. Conner.2004. Relationships between habitat and snag characteristics and the reproductive success of the Brown-headed Nuthatch in eastern Texas. Southeastern Naturalist 3:683-694.

Duong, T. 2012. ks: Kernel smoothing. R package version 1.8.10.http://CRAN.R-project.org/package=ks.

eBird. 2013. eBird: An online database of bird distribution and abundance [web application]. Version 2.eBird, Ithaca, New York. Available: http://www.ebird.org. (Accessed: 22 April 2013).

Environmental Systems Research Institute. ArcGIS: Release 3.3 [software]. Redlands, California: Environmental Systems Research Institute.

Environmental Systems Research Institute. ArcGIS: Release 9.3 [software]. Redlands, California: Environmental Systems Research Institute.

Fiske, I. and R. Chandler. 2011. unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software 43:1-23. [online]. http://www.jstatsoft.org/v43/i10/.

Fretwell, S.D. 1972. Populations in a Seasonal Environment. Princeton University Press. Princeton, New Jersey, USA.

Gingrich, S.F., 1967. Measuring and evaluating stocking and stand density in upland hardwood forests in the Central States. Forest Science 13:38-53.

Gitzen, R.A., J.J. Millspaugh, and B.J. Kernohan.2006. Bandwidth selection for fixed-kernel analysis of animal utilization distributions. Journal of Wildlife Management 70:1334-1344.

Gompper, M.E., and J.L. Gittleman 1991. Home range scaling: intraspecific and comparative trends. *Oecologia*87:343-348.

Golabek, K.A., A.R. Ridley, and A.N. Radford. 2012. Food availability affects strength of seasonal territorial behavior in a cooperatively breeding bird. Animal Behaviour 83:613-619.

Grosenbaugh, L.R. 1958. Point-sampling and line sampling: probability theory, geometric implications, synthesis. USDA Forest Service Southern Forestry Experiment Station Occasional Papers. 160. 34 p.

Haas, S.E., J.A. Cox, J.V. Smith, and R.T. Kimball. 2010. Fine-scale spatial genetic structure in the cooperatively breeding Brown-headed Nuthatch (*Sitta pusilla*). Southeastern Naturalist, 9:743-756.

Haney, J.C. 1981. The distribution and life history of the Brown-headed Nuthatch (*Sitta pusilla*) in Tennessee. Migrant 52:77-86.

Haskell, J.P., M.E. Ritchie, & H. Off. 2002. Fractal geometry predicts varying body size scaling relationships for mammal and bird home ranges. Nature 418:527-530.

Hedrick, L.D., G.A. Bukenhofer, W.G. Montague, W.F. Pell, and J.M. Guldin.2007. Shortleaf pine-bluestem restoration in the Ouachita National Forest *in*: Kabrick, J.M., D.C. Dey, and D. Gwaze, eds. Shortleaf pine restoration and ecology in the Ozarks: Proceedings of a symposium; 2006 November 7-9; Springfield, MO. General Technical Report NRS-P-15. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station: 206-213.

Hooge, P. N. (1995). Dispersal dynamics of the cooperatively breeding acorn woodpecker. Doctoral dissertation, University of California, Berkeley.

Iverson, L.R. and A.M. Prasad.2002. Potential redistribution of tree species habitat under five climate change scenarios in the eastern US. Forest Ecology and Management 155:205-222.

Jackson, A.G. 1911. The Biltmore stick and its use on national forests. Journal of Forestry, 9: 406-411.

Jackson, J.A. 1994. Red-cockaded Woodpecker (*Picoides borealis*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/085doi:10.2173/bna.85.

James, D. A. and J. C. Neal.1986. Arkansas birds. University of Arkansas Press, Fayetteville.

Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65-71.

Jones, J. 2001. Habitat selection studies in avian ecology: a critical review. Auk 118:557-562.

Kacelnik, A. 1984.Central place foraging in Starlings (*Sturnis vulgaris*). I. Patch residence time. Journal of Animal Ecology 53:283-299.

Karl, T.R., J.M. Melillo, and T.C. Peterson, eds. 2009.Global Climate Change Impacts in the United States. Cambridge University Press, New York, New York.

Kesler, D. C. and S.M. Haig. 2007. Territoriality, prospecting, and dispersal in cooperatively breeding Micronesian Kingfishers. Auk 124:381-395.

Kesler, D. C., J.R. Walters, and J.J. Kappes.2010. Social influences on dispersal and the fat-tailed dispersal distribution in red-cockaded woodpeckers. Behavioral Ecology21:1337-1343.

Kernohan, B. J., R.A. Gitzen, and J.J. Millspaugh.2001. Analysis of animal space use and movements *in* (eds. J.J. Millspaugh and J.M. Marzluff) Radio tracking and animal populations. Academic Press, San Diego, California, USA, 125-166.

Levin, S.A. 1992. The problem of pattern and scale in ecology: The Robert H. MacArthur Award Lecture. Ecology 73:1943-1967.

Manly, B.F.J., L.L. McDonald, D.L. Thomas, T.L. McDonald, and W.P. Erickson.2010. Resource Selection by Animals: Statistical Design and Analysis for Field Studies. *2nd*edition.Kluwer Academic Publishers. Boston, Massachusetts, USA.

Marzluff, J.M., J.J. Millspaugh, P. Hurvitz, and M.S. Handcock.2004. Relating resources to a probabilistic measure of space use: Forest fragments and Steller’s Jays. Ecology 85:1411-1427.

Maser, C., R.G. Anderson, K.Cromack Jr., J.T. Williams, and R. E. Martin. 1979. Dead and down woody material. Wildlife habitats in managed forests--the Blue Mountains of Oregon and Washington. USDA Agricultural Handbook553: 78-95.

Millspaugh, J.J., R.M. Nielsen, L. McDonald, J.M. Marzluff, R.A. Gitzen, C.D. Rittenhouse, M.W. Hubbard, and S.L. Sheriff. 2006. Analysis of resource selection using utilization distributions. Journal of Wildlife Management 70:384-395.

Mitchell, M.S. and R.A. Powell. 2004. A mechanistic home range model for optimal use of spatially distributed resources. Ecological Modelling 177:209-232.

Mong, T.W. and B.K. Sandercock.2007. Optimizing radio retention and minimizing radio impacts in a field study of upland sandpipers. Journal of Wildlife Management 71:971-980.

Morris, D.W. 1987. Spatial scale and the cost of density-dependent habitat selection. Evolutionary Ecology 1:379-388.

Murphy, J.M., D.M.H. Sexton, D.N. Barnett, G.S. Jones, M.J. Webb, M. Collins, and D.A. Stainforth.2004. Quantification of modeling uncertainties in a large ensemble of climate change scenarios. Nature 430:768-772.

Nesbitt, S.A. and W.M. Hetrick. 1976. Foods of the pine warbler and brown-headed nuthatch. Florida Field Naturalist 4:28-32.

Newton. I. 1998. Population Limitation in Birds. Academic Press. Boston, Massachusetts, USA.

Nice, M.M. 1937. Studies in the Life History of the Song Sparrow. Linnaean Society of New York. New York, New York.

Orians, G. H., and N.E. Pearson.1979. On the theory of central place foraging *in* Analysis of Ecological Systems. Ohio State University Press, Columbus, 155-177.

Pyle P. 1997. Identification guide to North American birds. Slate Creek Press, Bolinas, California, USA.

R Core Team.2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0 [Online].http://www/R-project.org.

Rainho, A., and J.M. Palmeirim, 2011.The importance of distance to resources in the spatial modelling of bat foraging habitat. PLoS ONE 6: e19227. doi:10.1371/journal.pone.0019227.

Renfrow, F. 2003. Notes on vagrancy in Brown-headed Nuthatch, with attention to recent range expansion and long-term habitat changes. North American Birds 57:422-428.

Rhodes, J.R, C.A. McAlpine, D. Lunney, and H.P. Possingham. 2005. A spatially explicit habitat selection model incorporating home range behavior. Ecology 86:1199-1205.

Rogers, R. 1983.Guides for thinning shortleaf pine. USDA Forest Service Technical Report SE-24. USDA Forest Service, Southeastern Forest Experiment Station, Asheville, North Carolina, pp. 217-225.

Robbins, M. B. and D. A. Easterla.1992. Birds of Missouri. University of Missouri Press, Columbia.

Rodgers, A. R. 2001. Recent telemetry technology. Pages 79-121 *in* J.J. Millspaugh and J.M. Marzluff, eds. Radio Tracking and Animal Populations. Academic Press, San Diego, California, USA, 79-121.

Rosenberg, D. K., and K.S. McKelvey. 1999. Estimation of habitat selection for central-place foraging animals. Journal of Wildlife Management 63:1028-1038.

Rotenberry, J.T. and J.A. Wiens. 1998. Foraging patch selection by shrubsteppe sparrows. Ecology 79:1160-1173.

Sauer, J. R., J. E. Hines, and J. Fallon.2008.The North American Breeding Bird Survey, Results and Analysis 1966 - 2007. Version 5.15.2008.USGS Patuxent Wildlife Research Center, Laurel, MD [Online].

Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63:739-747.

Slater, G. 1997. Brown-headed Nuthatches and Eastern Bluebirds in southern Florida pinelands: breeding biology, nest-site selection, and the influence of habitat on nesting success. Master's Thesis. University of Florida, Gainesville.

Sparks, J.C., R.E. Masters, D.M. Engle, M.W. Palmer, and G.A. Bukenhofer.1998. Effects of late growing-season and late dormant-season prescribed fire on herbaceous vegetation in restored pine-grassland communities. Journal of Vegetation Science 9:133-142.

Spencer, A. 2009a. [Web resource] XC33526. Accessible at www.xeno-canto.org/33526.

Spencer, A. 2009b. [Web resource] XC33523. Accessible at www.xeno-canto.org/33523.

Uda, S. 1927. Wireless beam of short electric waves. Journal of the IEE (Japan). March 1927:1209-1219.

USDA Forest Service. 2012. Ouachita National Forest Prescribed Burn History [Online]. Accessed 15 January 2013 at: http://www.fs.usda.gov/main/ouachita /landmanagement/gis.

Von Uexküll, J.J. 1957.A Stroll through the Worlds of Animals and Men: A Picture Book of Invisible Worlds *in* Instinctive Behavior: The Development of a Modern Concept, ed. and trans. Claire H. Schiller (New York: International Universities Press, Inc.), pp. 5–80.

Wand, M. P., and M.C. Jones. 2002. Kernel smoothing (Vol. 60). Chapman and Hall/CRC.

Welcker, J., A. Harding, N. Karnovsky, J. Steen, H. Strøm, and G.W. Gabrielsen. 2009. Flexibility in the bimodal foraging strategy of a high Arctic alcid, the little auk *Alle alle*. Journal of Avian Biology 40:388-399.

White, G., and R. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego.

Whitehurst, G. 1986. Range extension of the Brown-headed Nuthatch in western North Carolina. Chat 50:19.

Wilson, M.D., and B.D. Watts.1999. Response of Brown-headed Nuthatches to thinning of pine plantations. Wilson Bulletin 111:56-60.

Wilson, C. W., R. E. Masters, and G. A. Bukenhofer.1995. Breeding bird response to pine-grassland community restoration for red-cockaded woodpeckers. Journal of Wildlife Management 59:56-67.

Withgott, J.H. and K.G. Smith.1998. Brown-headed Nuthatch (*Sitta pusilla*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/349.

Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in home range studies. Ecology 70:164-168.

Wright, H. A. and A.W. Bailey.1982. Fire ecology. John Wiley & Sons, New York.

Yagi, H. 1928.Beam transmission of ultra-shortwaves. Proceedings of the IRE16:715–740.

Ydenberg, R. C., and W.E. Davies. 2010. Resource geometry and provisioning routines. Behavioral Ecology21:1170-1178.

FIGURES

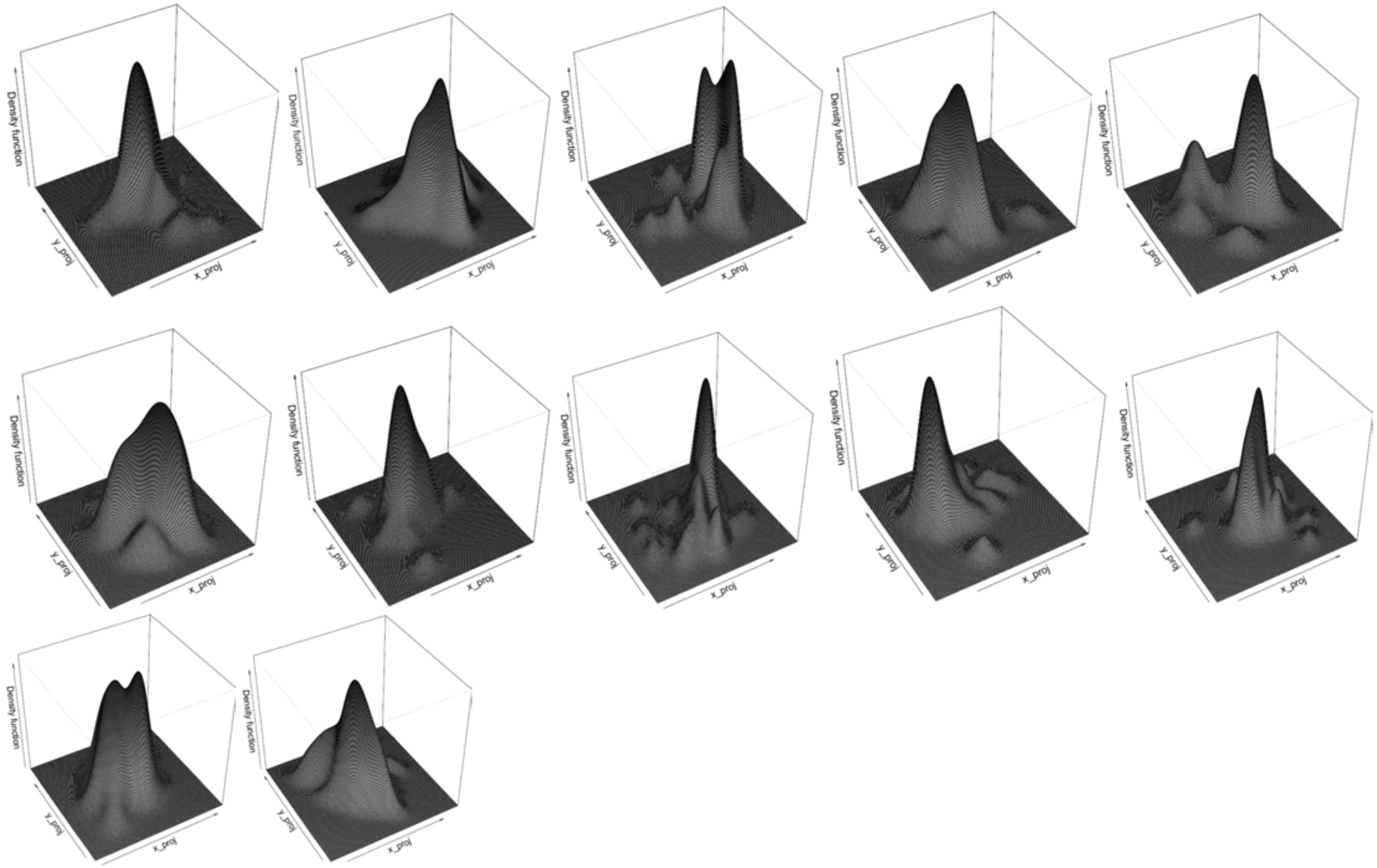


Figure 1.1. Utilization distributions for 22 Brown-headed Nuthatches, in Arkansas, USA, 2011-2012, demonstrating local maxima in intensity of space use. Axes' scale varies among individuals. Page 1 of 2.

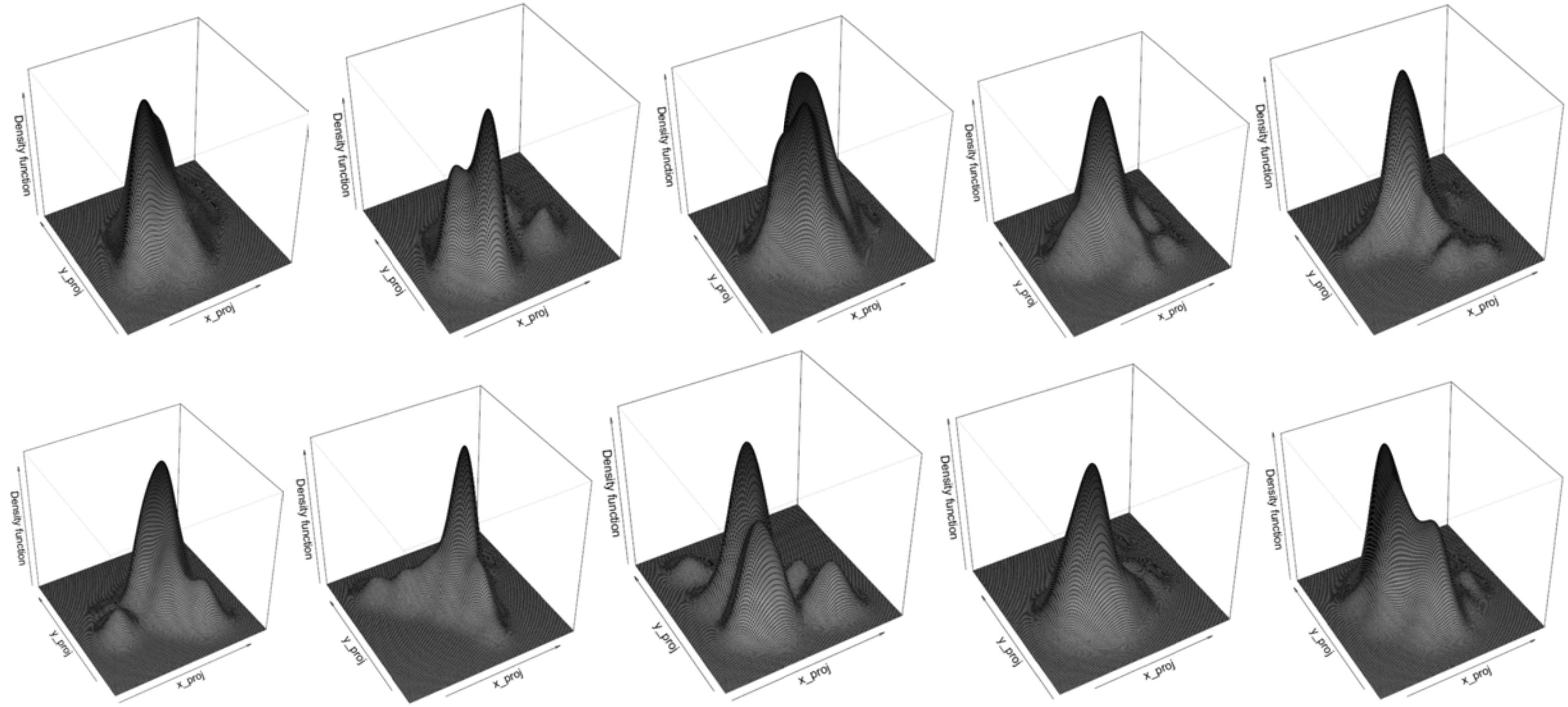


Figure 1.1. (Continued). Utilization distributions for 22 Brown-headed Nuthatches, in Arkansas, USA, 2011-2012, demonstrating local maxima in intensity of space use. Axes' scale varies among individuals. Page 2 of 2.

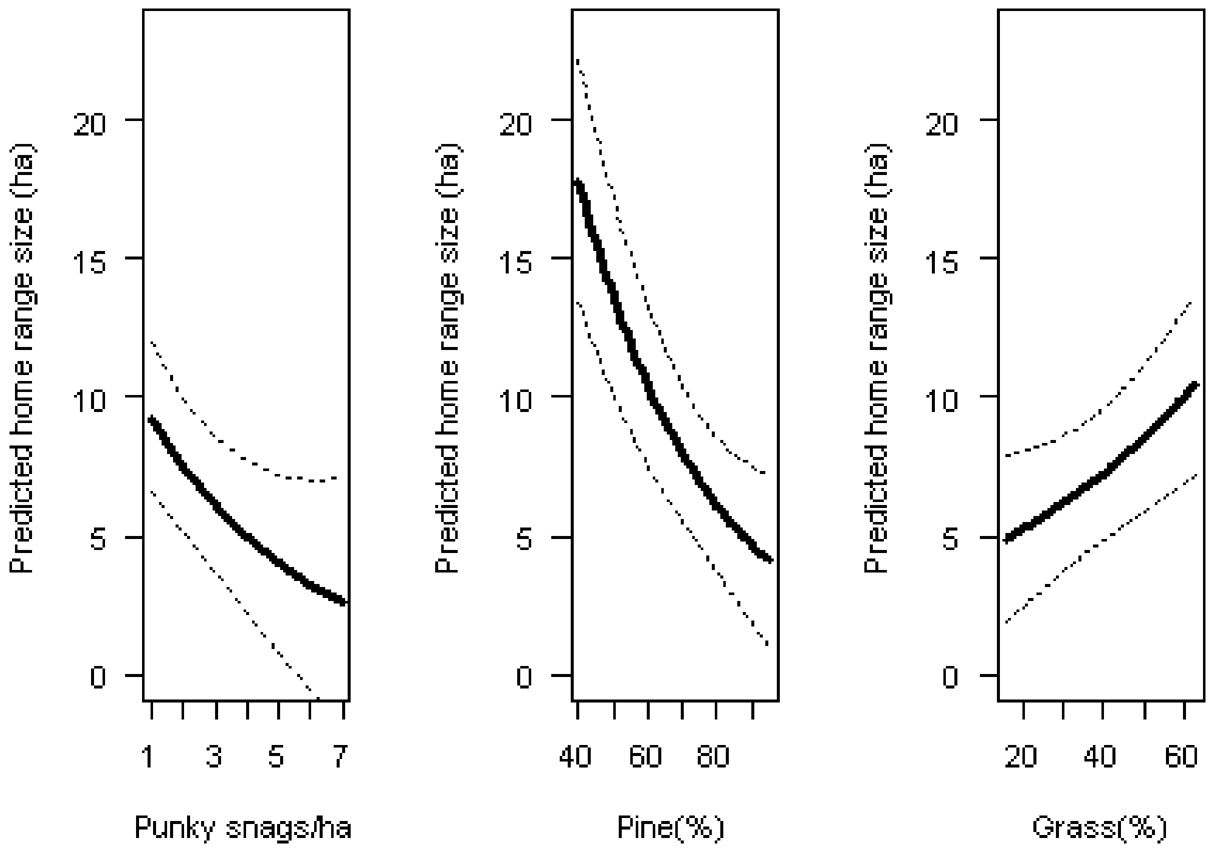


Figure 1.2. Model-averaged predicted home range size at different levels of punky snag density, pine percent, and percent grassy herbaceous cover in Brown-headed Nuthatch home ranges in Arkansas, USA, 2011-2012. Dotted lines are 95% confidence intervals.

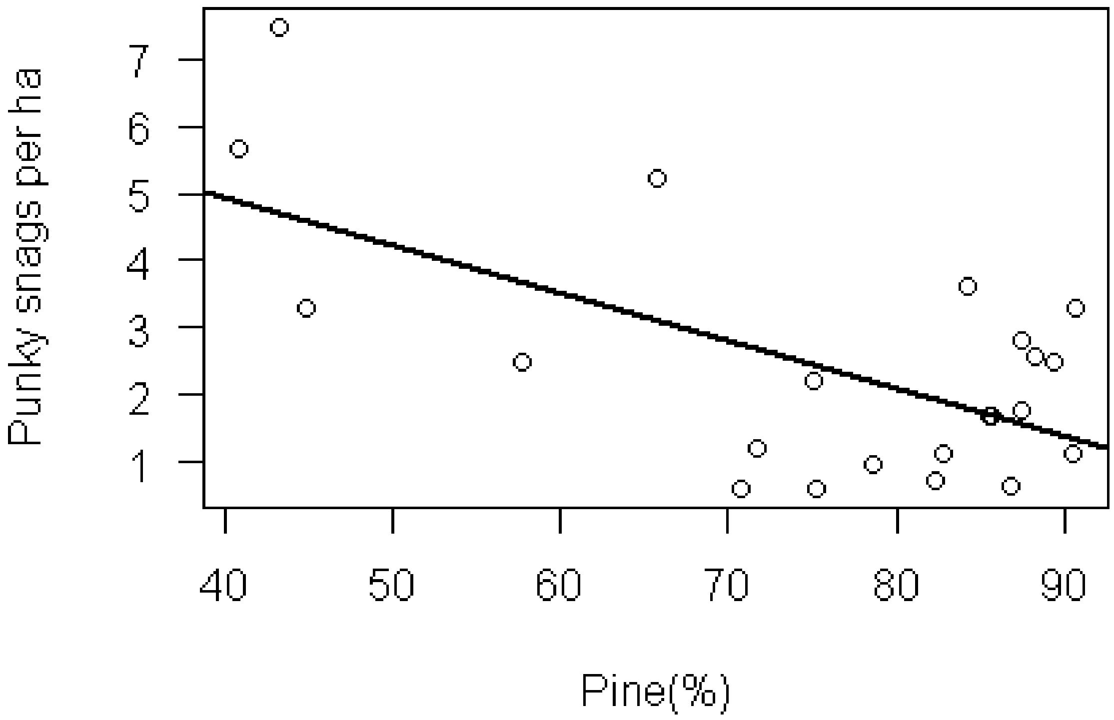


Figure 1.3. Observed mean percent pine within 22 Brown-headed Nuthatch home ranges in Arkansas, USA, 2011-2012, plotted against mean observed snag density. Best fit line and r^2 values are from a linear regression ($r^2 = 0.39$, 20 df, SE = 0.02, $p<0.01$).

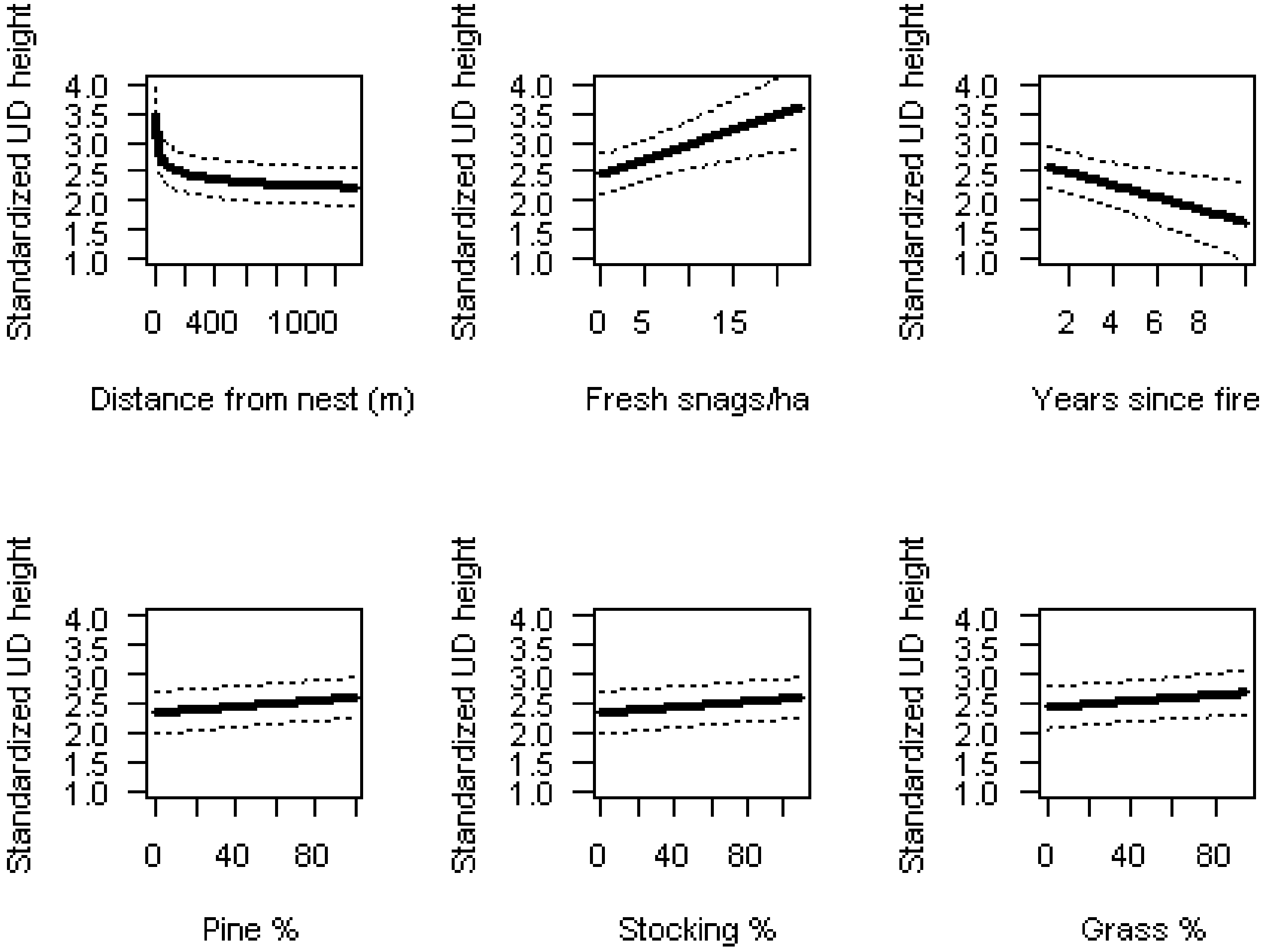


Figure 1.4. Predicted utilization distribution (UD) heights at different levels of habitat and fire management covariate values within Brown-headed Nuthatch home ranges in Arkansas, USA, 2011-2012. Dotted lines are 95% confidence intervals.

TABLES

Table 1.1. Habitat and prescribed fire covariates evaluated in analyses of space use within Brown-headed Nuthatch home ranges and nuthatch home range size in Arkansas, USA, 2011-2012. We used lognormal regression models to relate resources within home ranges to home range sizes. We investigated intensity of use by using linear mixed models to relate the standardized height of utilization distributions at points within home ranges to resources at those points.

Covariate(description)	**Intensity of use**	**Home range size**
Distance (log distance from nest, m)	✓	
Grass (Grassy herbaceous cover, %)	✓	✓
Pine (percent of total stocking in pine)	✓	✓
Stocking (total stocking percent)	✓	✓†
Punky snags(punky snag density, stems/ha)		✓
Fresh snags(fresh snag density, stems/ha)	✓	
Fire season (growing/dormant)	✓†	✓†
Years since fire (most recent fire, 0-10 yrs)	✓	

†Uninformative parameter removed from consideration during analysis.

Table 1.2. Summary of vegetation and snag characteristics of 22 Brown-headed Nuthatch home ranges in Arkansas USA, 2011-2012, based upon mean values for each bird.

	%Shrub	**Grass**	**%Litter**	**Pine**	**Stocking**	**Fresh snags**	**Punky snags**
Mean	35.68	36.94	27.38	75.64	26.87	1.68	2.42
σ	11.43	12.01	13.86	15.81	7.33	1.69	1.80
Min.	17.52	16.45	9.48	40.74	11.18	0.34	0.61
Max.	57.23	62.67	65.40	90.64	40.67	8.00	7.47

Table 1.3. Summary of vegetation and snag characteristics sampled from 965 plots on 22 Brown-headed Nuthatch home ranges in Arkansas, USA, 2011-2012.

	%Shrub	**Grass**	**%Litter**	**Pine**	**Stocking**	**Fresh snags**	**Punky snags**
Mean	35.46	38.45	26.09	75.14	26.68	1.56	2.40
σ	24.01	22.76	25.60	33.41	16.13	2.26	4.38
Min.	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Max.	100.00	95.00	100.00	100.00	109.20	22.60	73.49

Table 1.4. Model rankings relating home range size of Brown-headed Nuthatches in Arkansas, USA, 2011-2012, to mean resource metrics and recent prescribed fire impacts. Covariate names are described in Table 1.1. *K* is the number of parameters in each model, Loglik is the negative log-likelihood, and ΔAIC_c represents the difference in corrected Akaike's Information Criterion values among models, with 0.00 being the top-ranking model. The Akaike weight for each model is denoted by w_i.

Model	***K***	**Loglik**	**ΔAICc**	w_i
Pine+punkysnags+grass	5	-24.35	0.00	0.41
Pine+punky snags	4	-26.42	0.73	0.28
Grass	3	-28.48	1.85	0.16
Null	2	-29.92	2.01	0.15

Table 1.5. Model rankings relating standardized utilization distribution height at a point (a measure of relative probability of use) to available resources based on 22 Brown-headed Nuthatches in Arkansas, USA, 2011-2012. Covariate names are described in Table 1.1. *K* is the number of parameters in each model, Loglik is the negative log-likelihood, and ΔAIC_c represents the difference in corrected Akaike's Information Criterion values among models, with 0.00 being the top-ranking model. The Akaike weight for each model is denoted by w_i.

Model	***K***	**Loglik**	**ΔAICc**	w_i
Distance+fresh snags +stocking+pine+grass+years since fire	9	-1221.23	0.00	0.63
Distance+fresh snags + pine+grass+years since fire	8	-1223.25	2.00	0.23
Distance+fresh snags +stocking+pine+years since fire	8	-1223.82	3.14	0.13
Distance	4	-1212.75	29.58	0.00
Null	3	-918.40	617.64	0.00

Table 1.6. Model-averaged standardized and unstandardized parameter estimates and unstandardized standard errors for covariates relating intensity of space use in 22 Brown-headed Nuthatches from Arkansas, USA, 2011-2012, to resource and fire management metrics.

Parameter	**β(stand.)**	**β(unstand.)**	**SE**	**95% CI**
Intercept	NA	3.658	0.276	3.118 - 4.198
Distance	-0.622	-0.794	0.044	-0.785 - -0.629
Fresh snags	0.115	0.051	0.016	0.020 - 0.082
Pine	0.100	0.003	0.001	0.001 - 0.004
Years since fire	-0.096	-0.106	0.037	-0.178 - -0.034
Grass	0.068	0.003	0.001	0.000 - 0.006
Stocking	-0.048	-0.004	0.002	-0.007 - 0.000

APPENDICES

Appendix 1.1. Complete ranked candidate model set relating home range size of Brown-headed Nuthatches in Arkansas, USA, 2011-2012, to mean resource metrics and recent prescribed fire impacts. Covariate names are described in table 1.1. *K* is the number of parameters in each model, Loglik is the negative log-likelihood, and ΔAIC_c represents the difference in corrected Akaike's Information Criterion scores among models, with 0.00 being the top-ranking model. The Akaike weight for each model is denoted by w_i.

Model	***K***	**Loglik**	**ΔAIC_c**	**w_i**
Pine+punky snags+grass	5	-24.35	0.00	0.19
Pine+punky snags	4	-26.42	0.73	0.13
Grass	3	-28.48	1.85	0.07
Null	2	-29.92	2.01	0.07
Pine+grass	4	-27.36	2.61	0.05
Stocking	3	-29.10	3.08	0.04
Pine	3	-29.13	3.13	0.04
Pine+punky snags+grass+fire season	6	-24.10	3.34	0.04
Pine+punky snags+fire season	5	-26.03	3.35	0.04
Grass+stocking	4	-27.94	3.78	0.03
Pine+punky snags+grass+stocking	6	-24.35	3.84	0.03
Fire season	3	-29.48	3.84	0.03
Pine+punky snags+stocking	5	-26.30	3.89	0.03
Punky snags+stocking	4	-28.00	3.90	0.03
Punky snags	3	-29.52	3.92	0.03
Punky snags+grass	4	-28.16	4.22	0.02

Model	K	Loglik	ΔAIC_c	w_i
Grass+fire season	4	-28.20	4.30	0.02
Pine+fire season	4	-28.35	4.59	0.02
Pine+grass+fire season	5	-26.75	4.79	0.02
Stocking+fire season	4	-28.48	4.85	0.02
Punky snags+grass+stocking	5	-27.07	5.43	0.01
Pine+stocking	4	-28.93	5.75	0.01
Pine+grass+stocking	5	-27.35	6.00	0.01
Grass+stocking+fire season	5	-27.51	6.32	0.01
Punky snags+fire season	4	-29.26	6.42	0.01
Punky snags+stocking+fire season	5	-27.69	6.68	0.01
Pine+punky snags+stocking+fire season	6	-25.91	6.96	0.01
Punky snags+grass+fire season	5	-28.00	7.30	0
Pine+stocking+fire season	5	-28.15	7.60	0
Pine+punky snags+grass+stocking+fire season	7	-24.09	7.73	0
Pine+grass+stocking+fire season	6	-26.74	8.63	0
Punky snags+grass+stocking+fire season	6	-26.86	8.87	0

Appendix 1.2. Complete ranked candidate models relating standardized utilization distribution height at a point (a measure of relative probability of use) to available resources in Arkansas, USA, 2011-2012. Covariate names are described in Figure 2.2. *K* is the number of parameters in each model, Loglik is the negative log-likelihood, and ΔAIC_c represents the difference in corrected Akaike's Information Criterion scores among models, with 0.00 being the top-ranking model. The Akaike weight for each model is denoted by w_i.

Model	***K***	**Loglik**	**ΔAIC_c**	**w_i**
Distance+fresh snags+stocking+pine+grass+years since fire	9	-1221.23	0.00	0.38
Distance+fresh snags+stocking+pine+grass+years since fire+fire season	10	-1221.13	1.83	0.15
Distance+fresh snags+pine+grass+years since fire	8	-1223.25	2.00	0.14
Distance+fresh snags+stocking+pine+years since fire	8	-1223.82	3.14	0.08
Distance+fresh snags+pine+grass+years since fire+fire season	9	-1223.18	3.90	0.05
Distance+fresh snags+pine+years since fire	7	-1225.62	4.70	0.04
Distance+fresh snags+stocking+pine+years since fire+fire season	9	-1223.65	4.84	0.03
Distance+fresh snags+stocking+pine+grass	8	-1225.36	6.21	0.02
Distance+fresh snags+stocking+grass+years since fire	8	-1225.43	6.36	0.02
Distance+fresh snags+pine+years since fire+fire season	8	-1225.49	6.48	0.02
Distance+fresh snags+grass+years since fire	7	-1226.75	6.95	0.01
Distance+fresh snags+stocking+pine+grass+fire season	9	-1224.94	7.41	0.01
Distance+fresh snags+pine+grass	7	-1227.23	7.92	0.01
Distance+stocking+pine+grass+years since fire	8	-1226.32	8.13	0.01
Distance+fresh snags+stocking+grass+years since fire+fire season	9	-1225.32	8.18	0.01
Distance+fresh snags+grass+years since fire+fire season	8	-1226.67	8.83	0.00
Distance+fresh snags+pine+grass+fire season	8	-1226.88	9.26	0.00
Distance+stocking+pine+grass+years since fire+fire season	9	-1226.28	10.09	0.00

Model	***K***	**Loglik**	**ΔAIC_c**	**w_i**
Distance+fresh snags+stocking+years since fire	7	-1228.40	10.26	0.00
Distance+fresh snags+years since fire	6	-1229.49	10.42	0.00
Distance+fresh snags+stocking+pine	7	-1228.81	11.08	0.00
Distance+stocking+pine+years since fire	7	-1229.12	11.69	0.00
Distance+pine+grass+years since fire	7	-1229.19	11.85	0.00
Distance+fresh snags+stocking+pine+fire season	8	-1228.20	11.90	0.00
Distance+fresh snags+stocking+years since fire+fire season	8	-1228.22	11.94	0.00
Distance+fresh snags+years since fire+fire season	7	-1229.35	12.16	0.00
Distance+fresh snags+pine	6	-1230.42	12.27	0.00
Distance+fresh snags+stocking+grass	7	-1229.68	12.82	0.00
Distance+fresh snags+grass	6	-1230.87	13.17	0.00
Distance+fresh snags+pine+fire season	7	-1229.90	13.26	0.00
Distance+stocking+grass+years since fire	7	-1229.96	13.38	0.00
Distance+stocking+pine+years since fire+fire season	8	-1229.04	13.57	0.00
Distance+pine+grass+years since fire+fire season	8	-1229.18	13.86	0.00
Distance+fresh snags+stocking+grass+fire season	8	-1229.25	13.99	0.00
Distance+fresh snags+grass+fire season	7	-1230.49	14.45	0.00
Distance+pine+years since fire	6	-1231.73	14.90	0.00
Distance+stocking+grass+years since fire+fire season	8	-1229.92	15.33	0.00
Distance+stocking+pine+grass	7	-1230.94	15.35	0.00
Distance+grass+years since fire	6	-1232.00	15.43	0.00
Distance+stocking+pine+grass+fire season	8	-1230.66	16.81	0.00
Distance+pine+years since fire+fire season	7	-1231.69	16.84	0.00
Distance+grass+years since fire+fire season	7	-1231.98	17.42	0.00
Distance+stocking+years since fire	6	-1233.11	17.66	0.00

Model	***K***	**Loglik**	**ΔAIC_c**	**w_i**
Distance+fresh snags	5	-1234.53	18.48	0.00
Distance+fresh snags+stocking	6	-1233.60	18.63	0.00
Distance+pine+grass	6	-1233.68	18.79	0.00
Distance+years since fire	5	-1234.88	19.17	0.00
Distance+fresh snags+fire season	6	-1233.97	19.37	0.00
Distance+fresh snags+stocking+fire season	7	-1232.96	19.39	0.00
Distance+stocking+years since fire+fire season	7	-1233.03	19.52	0.00
Distance+pine+grass+fire season	7	-1233.47	20.41	0.00
Distance+stocking+grass	6	-1234.68	20.79	0.00
Distance+stocking+pine	6	-1234.71	20.85	0.00
Distance+years since fire+fire season	6	-1234.83	21.10	0.00
Distance+stocking+pine+fire season	7	-1234.26	21.99	0.00
Distance+stocking+grass+fire season	7	-1234.38	22.22	0.00
Distance+grass	5	-1236.59	22.58	0.00
Distance+pine	5	-1237.13	23.67	0.00
Distance+grass+fire season	6	-1236.36	24.15	0.00
Distance+pine+fire season	6	-1236.79	25.00	0.00
Distance+stocking	5	-1238.88	27.16	0.00
Distance+stocking+fire season	6	-1238.40	28.24	0.00
Distance	4	-1240.47	28.33	0.00
Distance+fire season	5	-1240.09	29.58	0.00

CHAPTER 2
INVISIBLE TAILS: RANGE EXTENSION IN BROWN-HEADED NUTHATCHES

ABSTRACT

Range extension processes are widely presumed to be hierarchical. High quality patches are expected to be occupied first and subsequent patches should be occupied in descending order according to quality. Such range extension processes may be driven by individuals at the long-distance tail of the natal dispersal distance distribution that locate isolated patches of high quality habitat and occupy them before lower quality patches. This course of events is most likely when dispersal behavior is a good predictor of effective dispersal, i.e. establishment by successful breeding. However, many bird species are remarkably sedentary or have life-history traits that may inhibit establishment in new locations. Those species might display a dramatically different pattern of range extension shaped by the behavior of average individuals either because long-distance dispersers do not exist or because long-distance dispersers consistently fail to reproduce. We studied Brown-headed Nuthatch (*Sitta pusilla*) occupancy at the limits of its expanding range based upon repeated call-response occupancy surveys. We expected both local site quality and range extension context to explain nuthatch occupancy across the range-extension zone. Range extension context strongly influenced nuthatch presence. We found nuthatches along the range extension front in lower quality habitats than in the core of range even though high quality habitats were present. Occupancy was also related to patch-level stand structural characteristics and fire history. Nuthatch presence was positively associated with nest snag density and freshly-killed snag density

(338% and 533% increase in predicted Ψ, respectively), but negatively associated with tree stocking percent and years since prescribed fire (100% and 35% decrease in predicted Ψ, respectively). Our results indicated that poorer quality habitats can be occupied first during range extensions, perhaps because dispersal limitation or Allee effects prevent organisms from occupying high-quality vacant sites. Thus, these findings locate a void in current theory regarding range extensions that limits our ability to predict how species will respond to global climate and land use changes.

INTRODUCTION

Range extension processes are often presumed to be hierarchical (Hildén 1965, Hengeveld 1989). A species extending its range should occupy high quality patches first and subsequent patches should be occupied in descending order according to quality (Hildén 1965). Such range extensions may be driven by individuals at the long-distance tail of the natal dispersal distance distribution, who locate isolated patches of high quality habitat and occupy them before lower quality patches (Hildén 1965). This course of events is most likely when dispersal behavior is a good predictor of effective dispersal, i.e. establishment by successful breeding (Angert et al. 2011).

This model of range extension may seem well-suited to birds, which are capable of dispersing incredible distances (Diamond 1974). Migratory birds in particular can survey the landscape efficiently and discover the best vacant sites first, initially bypassing marginal sites (Hildén 1965, Hengeveld 1989). Successively lower-quality habitats should then be occupied as range filling proceeds (Hildén 1965, Fretwell and Lucas 1972).

However, range extensions might proceed quite differently for some species. Most of the world's bird species are resident and many are remarkably sedentary (Berthold 1988, Terborgh et al. 1990). Such species might display a dramatically different pattern of range extension because constraints to effective dispersal exist. Either resident species may disperse only short distances or long-distance dispersers may exist but fail to become established. However, short distance dispersal is typical of resident birds in general and cooperatively-breeding species in particular (Terborgh et al. 1990, James et al. 2001, Hass et al. 2010). Thus, most individuals of species with these life history traits never survey the landscape as extensively as individuals of more mobile species.

Dispersal distance can vary widely among individuals (Van Houtan et al. 2007). Many species, including several cooperatively-breeding birds, exhibit "fat-tailed" or leptokurtic dispersal distributions in which a handful of individuals disperse much further than typical individuals (Kesler et al. 2010). Dispersal distributions may also be approximately normal in some cases, with no apparent outliers (Haas et al. 2010). The limited spatial extent of many studies hinders determinations regarding which dispersal distribution predominates in a given setting (Kesler et al. 2010). We cannot distinguish whether long-distance dispersal is absent or merely unsuccessful without incredibly hard to obtain data; hence the tail of the dispersal distribution is effectively invisible for most species.

In either event, range extensions shaped by constrained effective dispersal will appear to be driven by the dispersal behavior of normal individuals. Thus, range extensions conforming to the "invisible tails" model we propose will have three patch occupancy characteristics that distinguish them from range extensions conforming to the conceptual model developed by Hildén (1965). First, there will be high quality habitats in the zone of range extension, many of which are vacant. Second, animals in zones of range extension will be present in a narrow range of lower-quality habitats instead. Finally, we need to be reasonably confident that the observed pattern of patch occupancy was generated by constraints to effective dispersal and not other broadly limiting factors. Thus, the sites considered in an empirical evaluation of invisible tails range extension should be fairly proximal to one another. We can also be reasonably assured that constrained dispersal is shaping a range extension when the species in question is recolonizing its former range in response to habitat restoration efforts, suggesting that abiotic factors are unlikely to be limiting range extension.

We studied range extension and habitat selection in Brown-headed Nuthatches (*Sitta pusilla*) along a heterogeneous range extension front created by pine savannah-woodland restoration efforts in the Ouachita and Ozark Mountains of Arkansas, USA. We assessed whether the range extension process was compatible with Hildén's (1965) model or with the invisible tails model. We measured habitat quality using occupancy models with covariates developed from the literature, assessing site quality and patch occupancy simultaneously (Withgott and Smith 1998). We determined the relationship between patch-level habitat characteristics and location relative to an expanding range front with nuthatch site occupancy in order to better understand factors affecting resource selection and habitat suitability. These factors are of particular interest for this species in this region because climate warming and habitat restoration in Arkansas and Missouri are likely expanding the amount of potential habitat to the north of the current Brown-headed Nuthatch range into areas formerly occupied by Brown-headed Nuthatches.

METHODS

Focal Species

The Brown-headed Nuthatch is a resident species restricted to pine (*Pinus* spp.) and mixed-pine fire-maintained savannah-woodland, and is endemic to the southeastern United States (Withgott and Smith 1998). Nuthatches are small (10g) primary cavity nesters that require well-decayed snags for nesting (Withgott and Smith 1998, MacKenzie et al. 2006). Brown-headed Nuthatches are poor dispersers and typically settle about 300 m from the natal territory (Cox and Slater 2007). A genetic study suggested maximum dispersal distance in one nuthatch population was only 1-2 km (Haas et al. 2010). However, a handful of extralimital records exist, so long-distance movements are known to occur but may be rare (Renfrow 2003, eBird 2013). The species has been extirpated from Missouri and was likely once common in northern Arkansas before extensive clear cutting and fire suppression dramatically reduced the extent of pine savannah-woodlands (Robbins and Easterla 1987, Neal 2009).

Study Sites

This study occurred in the Ouachita and Ozark-St. Francis National Forests (N 35° 16', W 93° 8') in Arkansas, USA. Brown-headed Nuthatches have been extending their range northward into the Ozark Mountains in recent years (Fig. 2.1; eBird 2013). However, site descriptions associated with new Brown-headed Nuthatch records have often indicated that the birds are in less than ideal habitats (Arkansas Audubon Society 2013). Current habitat management in both National Forests includes regular prescribed fire, midstory reduction, and stand thinning to restore pine savannah-woodland conditions (Fig. 2.2; Hedrick et al. 2007).

Our study area encompassed the Ouachita Mountains, Mount Magazine, and the Ozark Mountains (Fig 2.1). The Ouachita Mountains are the most southerly of the three and are characterized by east-west ridge alignment and rolling terrain. Mount Magazine is the highest point in the state and has rugged terrain with sheer cliff faces, although we worked well below the summit on Ozark-St. Francis National Forest lands (Baerg 1927). The Ozark Mountains are the most northerly of the three ranges and are more rugged than the Ouachita Mountains but less so than Mount Magazine (James and Neal 1986). We worked primarily in a region of the Ozark Mountains where a deeply dissected plateau predominates (James and Neal 1986, Sauer 1920). All ranges included significant pine and pine-deciduous mixed stands. Nuthatches are common in the Ouachita Mountains (hereafter "established range"), uncommon around adjacent Mount Magazine (<10 km to the north; hereafter " edge of range"), and uncommon to rare in the Ozarks (hereafter "current range limit"), which is peripheral to the Ouachitas (~75 km to the north; Fig. 2.2; L. Anderson, pers. comm., 07 February 2012). We refer to the edge of range (Mount Magazine) and the current range limit (Ozark Mountains) collectively as the "range extension zone." We refer to these categories generically as range extension context or simply "context."

Field methods

Sampling design and call-response surveys

We conducted surveys for Brown-headed Nuthatches in managed pine and mixed pine savannah-woodlands from 2 April - 23 June 2011 and 1 March -1 June 2012. We surveyed 20 routes, 5 per National Forest per year. We placed routes on roads traversable by a passenger truck and ≥5 kilometers in length. We then rolled a six-sided die and used the number rolled to indicate how many tenths of a mile to drive to a starting point from the beginning of the route and flipped a coin to determine which direction to proceed 100 paces into the forest to a survey station (heads=left, tails=right, perpendicular to the road, using a compass bearing). We drove 0.5 km to each subsequent station, verified it was ≥0.3 km from neighboring points, and determined the side of the road to sample by a coin toss. We made minor adjustments to survey station locations to capture variation in stand composition. We marked each survey station using flagging tape and recorded the location in a global positioning system (GPS; Garmin eTrex Vista HCx, Garmin Ltd., Olathe KS). We sampled most stations 4 times (~ 98%) and all stations ≥3 times. All visually observed birds were also detected aurally. We ran routes in alternating directions each visit and with alternating observers whenever possible. We spread surveys throughout the season at sites in the established range and the range extension zone.

We maximized detection probability by broadcasting locally-recorded Brown-headed Nuthatch sounds (“rubber ducky” vocalizations; Withgott and Smith 1998, Spencer 2009, Audacity Development Team 2011). We played the recording at a standardized volume with an estimated detection radius of 150 m using FOXPRO NX4 digital callers (FOXPRO Inc., Lewiston, PA). We recorded if nuthatches were detected and noted the observer, date, time, temperature, and wind speed during each survey (using a hand-held anemometer). Each survey consisted of a 2 minute listening period, 1 minute of nuthatch vocalizations, and 3 minutes of listening (Bibby2000). We surveyed from 15 mins before sunrise to 5 hrs after. We suspended or canceled surveys if winds exceeded 20 km/hr or if it was raining.

Vegetation and snag sampling

We measured tree diameters, grassy herbaceous cover, shrub cover, and snags at each survey station. We measured the diameter at breast height (DBH) of all trees to the nearest 5 cm class with a Biltmore stick (Grosenbaugh 1958, Jackson 1911) selected with a 10 factor wedge prism and classified them as pine or hardwood (i.e. *Pinus* spp. or other). We visually estimated the proportion of grassy herbaceous cover and shrub cover within 12.5 m of each point. We measured DBH and distance to every snag detected at each point using a laser rangefinder (Bushnell Yardage Pro Sport, Overland Kansas, USA) and classified them as fresh or punky. Fresh snags were freshly-killed or condition 2 snags as classified by Maser et al. (1979) and punky snags were crumbly, well-decayed snags (conditions 3-4; Maser et al. 1979).

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 *in* Johnson et al. 2010) and shortleaf pine (*Pinus echinata*; Rogers 1983*in* Johnson et al. 2010). We estimated snag density using distance sampling methods to correct for imperfect detection (Buckland et al. 2004, Fiske and Chandler

2011). Distance sampling entails modeling detectability as one of several functions of distance, which are then ranked using an information-theoretic approach (Burnham and Anderson 2002). The parameters used to describe the distance-detection function can in turn be modified by covariates representing site conditions (Buckland et al. 2004, Fiske and Chandler 2011). We pooled data from a concurrent radio telemetry study in the Ouachita Mountains (Stanton, this volume), and developed separate 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, and percent tree stocking for fresh snags. We estimated snag density for each point by using the best-supported detectability models. We extracted years since prescribed fire for each station from a GIS database (USDA Forest Service 2012). We calculated the percentage of burned pine within a 2 km radius of each station using FRAGSTATS (McGarigal et al. 2002, USDA Forest Service 2011). We report box plots representing the mean and range of each covariate by landscape context to demonstrate the distribution of habitat characteristics in each context and the range of conditions modeled.

Analysis and candidate models

Occupancy modeling

We related Brown-headed Nuthatch presence in landscapes managed with prescribed fire to range extension context and patch-level resource measures using single-season occupancy models (Mackenzie et al. 2006). Occupancy models use detection-nondetection data from repeat surveys to simultaneously estimate both detection (*p*) and occupancy (Ψ) probabilities (Mackenzie et al. 2006). We followed a 2-stage model selection approach (Hansen et al. 2011). We fitted and ranked models for detection probability by considering all linear combinations of ≤2 covariates for a total of 15 models while holding occupancy constant (e.g.Ψ [.], *p* [covariate]). We then held the top detectability model constant and evaluated models concerned with occupancy.

Candidate models

We developed a set of a priori models relating nuthatch occupancy to landscape context and patch level forest metrics. Field observation and expert opinion suggested that habitat conditions in Mount Magazine were fair to marginal for nuthatches and that a number of high quality Ozark sites might be vacant (L. Hedrick, 25 January 2011 pers. comm.). Thus, we expected occupancy to vary among range extension contexts independent of habitat conditions. We considered all linear combinations of range extension context, several patch-level stand condition metrics, and prescribed fire measures that might be associated with nuthatch occurrence as a suitable candidate set (256 models; Table 2.1; Withgott and Smith 1988). We modeled detection probability in relation to sampling conditions and Brown-headed Nuthatch breeding phenology. We based phenology categories on observations from a concurrent study in the established range (before hatch [ordinal dates: 033-120], brood rearing [ordinal dates: 121-145], or post-fledging [ordinal dates: 146-032]; Stanton, this volume).

Habitat quality at all survey stations vs. occupied stations

We wanted to determine habitat quality in the established range and the range extension zone, comparing it to habitat quality where Brown-headed Nuthatches were found in the established range and in the range extension zone. We treated predicted patch level site quality (Ψ) as a suitable estimate of site quality because occupancy models resemble resource selection functions (Manly et al. 1993 *in* Hansen 2011). We generated predictions of patch-level habitat quality for each survey station from our final (model-averaged) occupancy model by holding the effect of range extension context constant, and plotted those values for the established range and the range extension zone. We generated and plotted the same predictions for sites where we detected nuthatches on ≥1 occasion.

We also wanted to determine which habitat conditions differed between occupied sites in the established range and in the range extension zone. We tested whether the patch-level site covariate values in our candidate set differed between the sites where we detected nuthatches in the established range and the range extension zone using Welch's t-tests. We also tested whether the percentage of shrub cover (associated with fire exclusion) where we detected nuthatches differed between the established range and the range extension zone. We calculated Cohen's *d* (a measure of effect size), sample sizes, sample means and standard errors for each covariate value by landscape context to estimate the magnitude of any observed differences.

Analytical methods

We ranked occupancy models using Akaike's Information Criterion adjusted for small sample sizes (AIC_c; Burnham and Anderson 2002). We considered models competitive for inference if $\Delta AIC_c \leq 4$ and they did not contain uninformative parameters (Arnold 2010) and if more than one model was competitive we model-averaged parameter estimates and predictions (Burnham and Anderson 2002, Barton 2012, Fiske and Chandler 2012). We calculated model-averaged coefficients, odds ratios and unconditional 95% odds ratio confidence intervals (i.e. ±1.96 SE). We considered the inclusion of a covariate in our competitive model set as evidence that it had an influence on nuthatch space use because ~85% odds ratio confidence intervals of those covariates should not overlap1 (Arnold 2010). We refer to these covariates as "less supported" if their 95% odds ratio confidence intervals overlapped 1. We considered 95% odds ratio confidence intervals that did not overlap 1 as additional evidence that a given covariate influenced nuthatch space use (hereafter "more supported").

We calculated predicted detection (p) and occupancy (Ψ) probabilities for all supported site covariates. We limited predictions to the range of observed values for each plotted covariate while holding other continuous covariates at their mean. We fixed breeding phenology for each site visit to "early" for the first two visits and "late" for the last two visits, which were the modal values for those visits. We fixed landscape context so that each context was weighted relative to its representation in our sample. We assessed goodness-of-fit for the global occupancy model by computing Pearson-Tukey chi-squared tests with 10,000 bootstrap replicates (Fiske and Chandler 2012). We assessed overdispersion by calculating $\hat{c}$ as an estimate of model fit to data (Burnham and Anderson2002, Fig. 2.8 in Mackenzie and Bailey 2004). We calculated area under the curve (AUC), sensitivity, and specificity of the receiver operating characteristic (ROC) for the final (model-averaged) occupancy model as an estimate of predictive performance (Freeman and Moisen 2008). We selected a threshold for calculating AUC, sensitivity and specificity by maximizing the sum of sensitivity and specificity (Freeman and Moisen 2008). We fit a single season occupancy model because we visited different locations each year and did not expect factors influencing nuthatch occupancy to change between years. All models were fit in R version 2.15.2 using the package unmarked (Fiske and Chandler 2011, R Core Team 2012).

RESULTS

We surveyed 284 sites; 156, 50, and 78 sites in the established range, edge of range, and current range limit, respectively. We visited most sites 4 times (1130 of 1148 surveys, 98.4%) and all sites $\geq$3 times. We detected nuthatches at 76 locations; 65 in the established range, 8 in the edge of range, and 3 in the region of the current range limit.

The top detectability model was Ψ (.) *p* (phenology) and no other models were competitive (App. 2.1). Predicted detection probability ±SE was 0.56±0.05, 0.43±0.04, and 0.62±0.06 for the before-hatch, brood-rearing and post-fledgling periods, respectively. Thus, the probability of detecting nuthatches at a station on ≥1 occasion provided they were present was ~0.97. Model selection indicated five models were competitive for the best approximating occupancy model ($\Delta AIC_c \leq 4$; Table 2.2; App. 2.2). Range extension context had the most support and all supported models contained range extension context as a covariate. Other supported covariates were stocking, fresh snags, punky snags, and years from fire (Table 2.2). Model-averaged parameter estimates and their associated odds ratio confidence intervals did not overlap 1 for range extension context or percent tree stocking (Table 2.3). Odds ratio confidence intervals for fresh snags, punky snags, and years since fire overlapped 1, but to differing degrees (Table 2.3). There was no evidence of lack of fit for the global occupancy model (mean Freeman-Tukey $\chi^2 = 151$, $P = 0.70$, $\hat{c} = 1.00$). The AUC of the ROC for the final (model-averaged) occupancy model was 0.85 given a threshold of 0.33, indicating that the model predicted observed nuthatch patch occupancy better than chance (i.e. AUC >0.50).

Sensitivity and specificity for the same model and threshold were 0.76 and 0.79, respectively. This means that predicted patch occupancy matched observed patch occupancy 76% of the time and predicted patch vacancy matched observed patch vacancy 79% of the time when assuming sites with predicted $\Psi>0.33$ were occupied.

Estimated occupancy was markedly different among range extension contexts; predicted nuthatch occupancy probability ±SE was0.41± 0.05, 0.15±0.06, and 0.03±0.02 for sites in the established range, edge of range, and current range limit contexts, respectively. Predicted occupancy decreased 100% from 0.40 at 0% tree stocking to 0.00 at 181% stocking (Fig. 2.3). Predicted occupancy probability was 0.95 at maximum fresh snag density, but was only 0.15 at minimum density, an increase of 533% (Fig. 2.3). A similar relationship with punky snags existed; predicted occupancy was 16% at minimum density and 70% at maximum density, an increase of 338% (Fig. 2.3). Occupancy probability decreased with increasing years since fire, but only by 35%, from 0.23 to 0.15 across the range of observed values (Fig 2.3). The percentages of burned pine within 2 km, patch-level pine, and patch-level grassy herbaceous cover had no apparent relationship with predicted occupancy (App. 2.2).

We found that high quality habitats were present in both the established range and the range extension zone (Fig. 2.4). We also found Brown-headed Nuthatches in the range extension zone in a narrow range of habitats that were of lower quality than those in the established range where we found nuthatches (Fig. 2.4). Habitat conditions where we found nuthatches where significantly different in the established range than along the range extension front in several ways. Fresh snags, punky snags, grassy herbaceous cover, shrubs at each station, and burned pine within 2 km of each station were all different (all $P \leq 0.01$; Table 2.4). Nuthatch locations in the established range had conditions more associated with nuthatch occupancy or pine savannah-woodland restoration objectives in each case (Table 2.4; Hedrick et al. 2007).

DISCUSSION

We found that Brown-headed Nuthatch occupancy was very sensitive to range extension context, and declined as we sampled closer to the limits of the range extension front. Our observation that occupancy declined near the limits of the range extension front is not necessarily surprising. However, we did not find nuthatches in isolated patches of the highest quality habitat along the range extension front as predicted by Hildén's conceptual model. Rather, nuthatches on the range-extension front were found mainly in poorer habitats along the edge of range. Nuthatches found in the range extension zone were in sites with significantly fewer snags, more shrub cover, less grassy herbaceous cover, more years since prescribed fire and less burned pine within 2 km than occupied sites in the established range. We observed this pattern across a region <300 km in diameter in areas where nuthatches were formerly present and habitat conditions were formerly more favorable and uniform. This pattern is entirely contrary to the one predicted by Hildén (1965) and meets the patch occupancy criteria we established. Thus, we believe we have documented an invisible tails range extension in the Brown-headed Nuthatch. Our findings confirm earlier anecdotal reports while facilitating applied conservation for nuthatches (Arkansas Audubon Society 2013).

We regard the invisible tails model as a conceptually straightforward extension of Hildén's model of range extension processes. We assume that range extensions are indeed hierarchical in birds but often at finer scales than has been assumed. We can take the best available knowledge of dispersal behavior and context-specific demography into account, resulting in spatially explicit models of range extensions. We risk grave errors in predicting how species will shift their ranges in response to a changing environment if we do not. One possible measure to extend Hildén's principle would be to develop models of range extension by life-history traits or by species that include estimates of expected effective dispersal. These estimates will necessarily be quite coarse at first, but additional empirical data and theoretical developments in dispersal ecology will allow further refinements over time.

We also found that nuthatch occupancy was related to fire-mediated savannah-woodland conditions (percent tree stocking and years since fire), and available nest sites ("punky snags"). This is consistent with what is known about nuthatch biology (Withgott and Smith 1998). Importantly, fresh snags were also associated with nuthatch occupancy. These trees are often targeted by beetles and other invertebrates preyed upon by nuthatches (Ulyshen and Hanula 2009, Nesbitt and Hetrick 1976). They likely represent a valuable foraging resource for Brown-headed Nuthatches since they were also selected within individual nuthatch home ranges (Stanton, this volume). Previous studies have either not explicitly distinguished between fresh and punky snags or looked at only one snag type (Wilson and Watts 1999, Dornak et al. 2004, Cox et al. 2012). Thus, this study is among the first to establish that each snag type may have separate functions and values for nuthatches (Stanton, this volume). Further confirmatory study is recommended to establish whether higher fresh snag densities have verifiable and significant impacts on nuthatch survival and reproduction.

We found no evidence that grassy herbaceous cover was associated with Brown-headed Nuthatch occupancy. It was associated with larger nuthatch home range sizes but nuthatch space use within home ranges was slightly higher (Stanton, this volume). Thus, the available evidence remains equivocal regarding whether habitat management for Brown-headed Nuthatches should include promoting grassy herbaceous cover as recommended for Red-cockaded Woodpeckers (James et al. 2001). Brown-headed Nuthatches forage predominantly in tree canopies while Red-cockaded Woodpecker forage principally on tree trunks (Thompson 2000,Jackson 1994); invertebrates moving from ground cover to tree trunks may be a less important part of their diet. The sites we surveyed also had several species of conservation interest that require some shrubby cover (Stanton et al., unpublished data; e.g. Yellow-breasted Chat, *Icteria virens*, and Prairie Warbler, *Setophaga discolor*; Tirpak et al. 2009).

An occupancy modeling study of Brown-headed Nuthatches in Florida, USA also found evidence that Brown-headed Nuthatches and Red-cockaded Woodpecker habitat requirements may differ (Cox et al. 2012). Estimated occupancy was 0.56 in mature Florida sandhill forest managed for Red-cockaded Woodpeckers and 0.96 in flatwood forests were Red-cockaded Woodpeckers were absent (Cox et al. 2012). They speculate that differences in food availability or limiting nutrients may account for the difference (Cox et al. 2012). We estimated lower occupancy in the shortleaf pine savannah-woodlands of the Ouachita Mountains (0.41). The sites we surveyed in the Ouachita Mountains are managed in part for Red-cockaded Woodpeckers (Hedrick et al. 2007). However, we found evidence of extensive cooperative breeding with possible nest site limitation, and nuthatches in the region appear to be increasing (Sauer et al. 2008, Stanton, this volume). Nuthatch home ranges in the established range (Ouachita Mountains) were also remarkably large, particularly in stands with more hardwood than pine (median 7.1 ha; Stanton, this volume). Thus, we speculate that the Ouachita Mountains are relatively good habitat for Brown-headed Nuthatches, and that either nest site availability or hardwood dominance can be limiting depending on the setting.

We surveyed sites in the range extension zone that were often patchier, with longer fire return intervals and less burned pine within 2 km. Many of these sites may lack connectivity with other suitable sites, as rugged terrain or incomplete restoration efforts result in increased interspersion of pine and hardwood stands. We speculate that this lack of functional connectivity may be limiting the rate of range extension and resulting in the "inefficient" process of range-filling we observed wherein low-quality sites are occupied while high quality sites only tens of kilometers away are vacant.

The distribution of dispersal distances in Brown-headed Nuthatches may not have a "fat-tail" to facilitate range extension into new areas (Fig. 4 in Haas et al. 2010). If Brown-headed Nuthatch dispersal is indeed fat-tailed, long-distance dispersers may fail to reproduce as a result of Allee effects such as lack of mates or possibly winter roosting partners (Stevens 1999). We cannot distinguish which is the case with the data at hand. Regardless, nuthatches are filling in vacant habitat not "in order of superiority" as postulated by Hildén (1965), but piecemeal as demographic vagaries or limited dispersal propensities permit. Nuthatches are populating the vacant landscape in a manner that may be common to many species. Indeed, the pattern they are displaying may be the norm even among birds, the quintessential mobile organism. Species that are unable to respond to a changing climate are at risk (Møller et al. 2008). Predicting the manner in which species will shift their ranges in response to habitat management and climate change requires that we shine more light on the currently invisible tails of animal dispersal distributions.

Our findings provide evidence that ongoing prescribed fire and other pine savannah-woodland restoration efforts have facilitated range extension in the Brown-headed Nuthatch. However, we also found evidence that some restored habitats remain vacant while marginal habitats are occupied. Thus, efforts to evaluate potential habitat connectivity are warranted if full community representation is one of the conservation goals of pine savannah-woodland restoration. We recommend that the ecological potential for restoration to pine savannah-woodland be evaluated for the Ozark-St. Francis National Forest, encompassing the range extension zone and extensive forests in Missouri to the north. This will allow us to distinguish current habitat connectivity from potential connectivity, informing discussions about how to allocate restoration efforts and whether conservation translocations of Brown-headed Nuthatches or other dispersal-limited species should take place.

LITERATURE CITED

Angert, A.L., L.G. Crozier, L.J. Rissler, S.E. Gilman, J.J. Tewskbury, and A.J. Chunco. 2011. Do species' traits predict recent shifts at expanding range edges? Ecology Letters 14: 677-689.

Arkansas Audubon Society.2013. [Web application]. http://www.arbirds.org/searchspecies.asp (Accessed: 22 April 2013).

Arnold, T. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74:1175-1178.

Audacity Development Team. 2010. Audacity (Version 1.3.4-beta) [Computer program]. http://audacity.sourceforge.net (Accessed: 5 November 2010).

Baerg, W.J. 1927. Summer birds on Mount Magazine, Logan County, Arkansas. Auk 44:545-548.

Berthold, P. 1998. Bird migration: genetic programs with high adaptability. Zoology 101: 235-245.

Bibby, C.J. 2000.Bird Census Techniques. Academic Press. San Diego.

Buckland, S.T., Anderson, D.R., Burnham, K.P. and Laake, J.L. 1993. Distance Sampling: Estimating Abundance of Biological Populations. Chapman and Hall, London, reprinted 1999 by RUWPA, University of St. Andrews, Scotland.

Burnham, K.P., and D.R. Anderson. 2002. Model Selection and Multimodel Inference: a Practical Information-theoretic Approach. 2nd edition. Springer-Verlag. New York.

Cox, A.S., and D.C. Kesler. 2012. Prospecting behavior and the influence of forest cover on natal dispersal in a resident bird. Behavioral Ecology 23:1068-1077.

Cox, J.A., and G.L. Slater. 2007. Cooperative breeding in the Brown-headed Nuthatch. Wilson Journal of Ornithology 119:1-8.

Cox, J.A., L.C. Scopel, and M.R. Klostermann. 2012. Brown-headed Nuthatch occupancy in central Florida and its relationship to forest type, forest structure, and the presence of Red-cockaded Woodpeckers. Condor 114:622-628.

Diamond, J. M. 1974. Colonization of exploded volcanic islands by birds: the supertramp strategy. Science184: 803-806.

Ducey, M.J. 2000. Prism cruising with diameter classes: theoretical considerations and practical recommendations. Northern Journal of Applied Forestry 17:110-115.

eBird. 2013. eBird: An online database of bird distribution and abundance [web application]. Version 2. eBird, Ithaca, New York. Available: http://www.ebird.org. (Accessed: 22 April 2013).

Freeman, E. A. and Moisen, G. (2008).PresenceAbsence: An R package for presence-absence model analysis. Journal of Statistical Software 23:1-31. http://www.jstatsoft.org/v23/i11.

Fiske, I. and R. Chandler. 2011). unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software 43:1-23. [online]. http://www.jstatsoft.org/v43/i10/.

Gammon, D.E. and B.A. Maurer. 2002. Evidence for non-uniform dispersal in the biological invasions of two naturalized North American bird species. Global Ecology and Biogeography 11:155-161.

Golabek, K.A., A.R. Ridley, and A.N. Radford. 2012. Food availability affects strength of seasonal territorial behavior in a cooperatively breeding bird. Animal Behaviour 83:613-619.

Grosenbaugh, L.R. 1958. Point-sampling and line sampling: probability theory, geometric implications, synthesis. USDA Forest Service Southern Forestry Experiment Station Occasional Papers. 160. 34 p.

Haas, S.E., J.A. Cox, J.V. Smith, and R.T. Kimball. 2010. Fine-scale spatial genetic structure in the cooperatively breeding Brown-headed Nuthatch (*Sitta pusilla*). Southeastern Naturalist, 9:743-756.

Hansen, C.P., J.J. Millspaugh and M.A. Rumble. 2011. Occupancy modeling of ruffed grouse in the Black Hills National Forest. The Journal of Wildlife Management, 75:71-77.

Hedrick, L.D., G.A. Bukenhofer, W.G. Montague, W.F. Pell, and J.M. Guldin. 2007. Shortleaf pine-bluestem restoration in the Ouachita National Forest. *In*: Kabrick, J.M., D.C. Dey, and D. Gwaze, eds. Shortleaf pine restoration and ecology in the Ozarks: Proceedings of a symposium; 2006 November 7-9; Springfield, MO. General Technical Report NRS-P-15. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station: 206-213.

Hengeveld, R. 1989. Dynamics of Biological Invasions. Kluwer Academic Publishers. Boston, Massachusetts, USA.

Hildén, O. 1965. Habitat selection in birds: A review. *Annales Zoologici Fennici* 2:53-75.

Jackson, A.G. 1911. The Biltmore stick and its use on national forests. Forestry Quarterly 9:406–411.

Jackson, J.A. 1994. Red-cockaded Woodpecker (*Picoides borealis*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/085doi:10.2173/bna.85.

James, C.F., C.A. Hess, B.C. Kicklighter, and R.A. Thum. 2001. Ecosystem management and the niche gestalt of the red-cockaded woodpecker in longleaf pine forests. Ecological Applications 11:854-870.

James, D.A. and J.C. Neal.1986. Arkansas birds. University of Arkansas Press, Fayetteville.

Johnson, P.S., S.R. Shifley, and R. Rogers. 2009. The Ecology and Silviculture of Oaks, 2nd Edition. CAB International, Cambridge, Massachusetts.

MacKenzie, D.I., J.D. Nichols, J.A. Royle, K.H. Pollock, L.L. Bailey, and J.E. Hines. 2006. Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence. Academic Press, Burlington, Massachusetts, USA.

Maser, C, Anderson, R. G., Cromack, Jr., K., Williams, J. T. and Martin, R. E. 1979.Dead and down woody material. - In: Thomas, J. W., ed., Wildlife habitats in managed forests, the Blue Mountains of Oregon and Washington. Agricultural Handbook 553. USDA Forest Service Portland, pp. 79-85.

McGarigal, K., S. A. Cushman, M.C. Neel, and E. Ene. 2002. FRAGSTATS: Spatial pattern analysis program for categorical maps. Computer software program produced by the authors at the University of Massachusetts, Amherst.

Møller, A.P., D. Rubolini, and E. Lehikoinen. 2008. Populations of migratory bird species that did not show a phenological response to climate change are declining. Proceedings of the National Academy of Sciences 105:16195-16200.

Neal, J.C. 2009. Birds in Northwestern Arkansas: An Ecological Perspective. Northwest Arkansas Audubon Society. Fayetteville, AR, USA.

Nesbitt, S. A., and Hetrick, W. M. 1976.Foods of the pine warbler and brown-headed nuthatch. Florida Field Naturalist4:28-32.

R Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0 [Online]. http://www/R-project.org

Renfrow, F. 2003. Notes on vagrancy in Brown-headed Nuthatch, with attention to recent range expansion and long-term habitat changes. North American Birds 57:422-428.

Robbins, M. B. and D. A. Easterla.1992. Birds of Missouri. University of Missouri Press, Columbia, Missouri.

Sauer, C.O. 1920. The Geography of the Ozark Highland of Missouri. The University of Chicago Press. Chicago, Illinois.

Sauer, J. R., J. E. Hines, and J. Fallon.2008.The North American Breeding Bird Survey, Results and Analysis 1966 - 2007. Version 5.15.2008.USGS Patuxent Wildlife Research Center, Laurel, MD [Online].

Spencer, A. 2009. [Online] http://www.xeno-canto.org/33526 (Accessed 3 November 2010).

Stevens, P.A., and W.J. Sutherland. 1999. Consequences of the Allee effect for behavior, ecology and conservation. Trends in Ecology and Evolution 14:401-405.

Terborgh, J., S.K. Robinson, T.A. Parker III, C.A. Munn, and N. Pierpont. 1990. Structure and organization of an Amazonian forest bird community. Ecological Monographs 60:213-238.

Tirpak, J.M, D.T. Jones-Farrand, F.R. Thompson, D.W. Twedt, C.K. Baxter, J.A. Fitzgerald, and W.B. Uihleinn. 2009. Multiscale habitat suitability index models for priority landbirds in the Central Hardwoods and West Gulf Coastal Plain/Ouachitas Bird Conservation Regions. United States Department of Agriculture Forest Service General Technical Report NRS-49.

Ulyshen, M.D., and J.L. Hanula. 2009. Habitat associations of saproxylic beetles in the southeastern United States: A comparison of forest types, tree species and wood postures. Forest Ecology and Management 357:653-664.

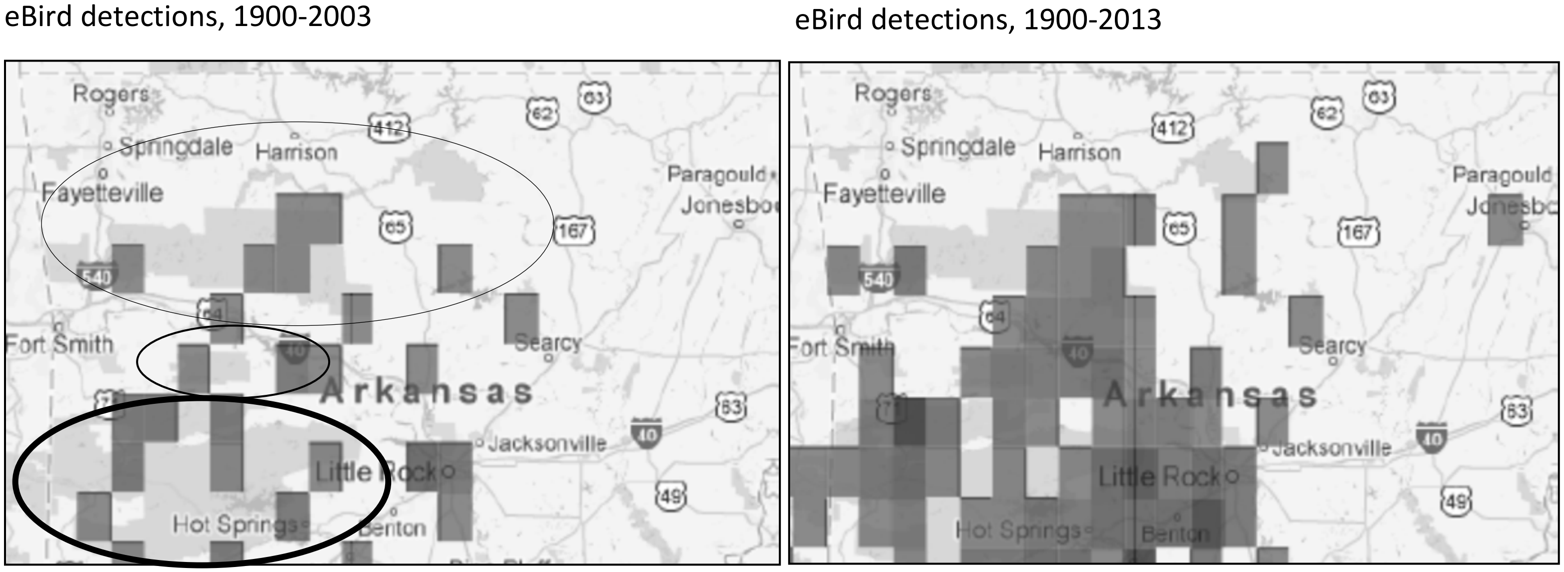
USDA Forest Service. 2011. Ouachita National Forest Prescribed Burn History [Online]. Accessed 8 August 2012 at: http://www.fs.usda.gov/main/ouachita/landmanagement/gis.

USDA Forest Service. 2012. Ouachita National Forest Prescribed Burn History [Online]. Accessed 15 January 2013 at: http://www.fs.usda.gov/main/ouachita/landmanagement/gis.

Van Houtan, K.S., S.L. Pimm, J.M. Halley, R.O. Bierregaard, Jr., and T.O. Lovejoy. 2007. Dispersal of Amazonian birds in continuous and fragmented forest. Ecology Letters 9:1–11.

Withgott, J. H. and K.G. Smith. 1998. Brown-headed Nuthatch (*Sitta pusilla*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/349.

FIGURES


eBird detections, 1900-2003

eBird detections, 1900-2013

Figure 2.1. Maps of eBird Brown-headed Nuthatch detections (dark gray rectangles) in northwest Arkansas, USA to 2003(left) and 2013 (right), respectively, indicating possible range extension. Nuthatches are common and established in the Ouachita Mountains (thick lower ellipse), uncommon around Mount Magazine (“edge of range”; small center ellipse), and uncommon to rare in the Ozark Mountains (“current range limit”; large upper ellipse), where they are absent from many apparently suitable sites. National Forests are shown in medium gray. Map data: Google, MapLink.

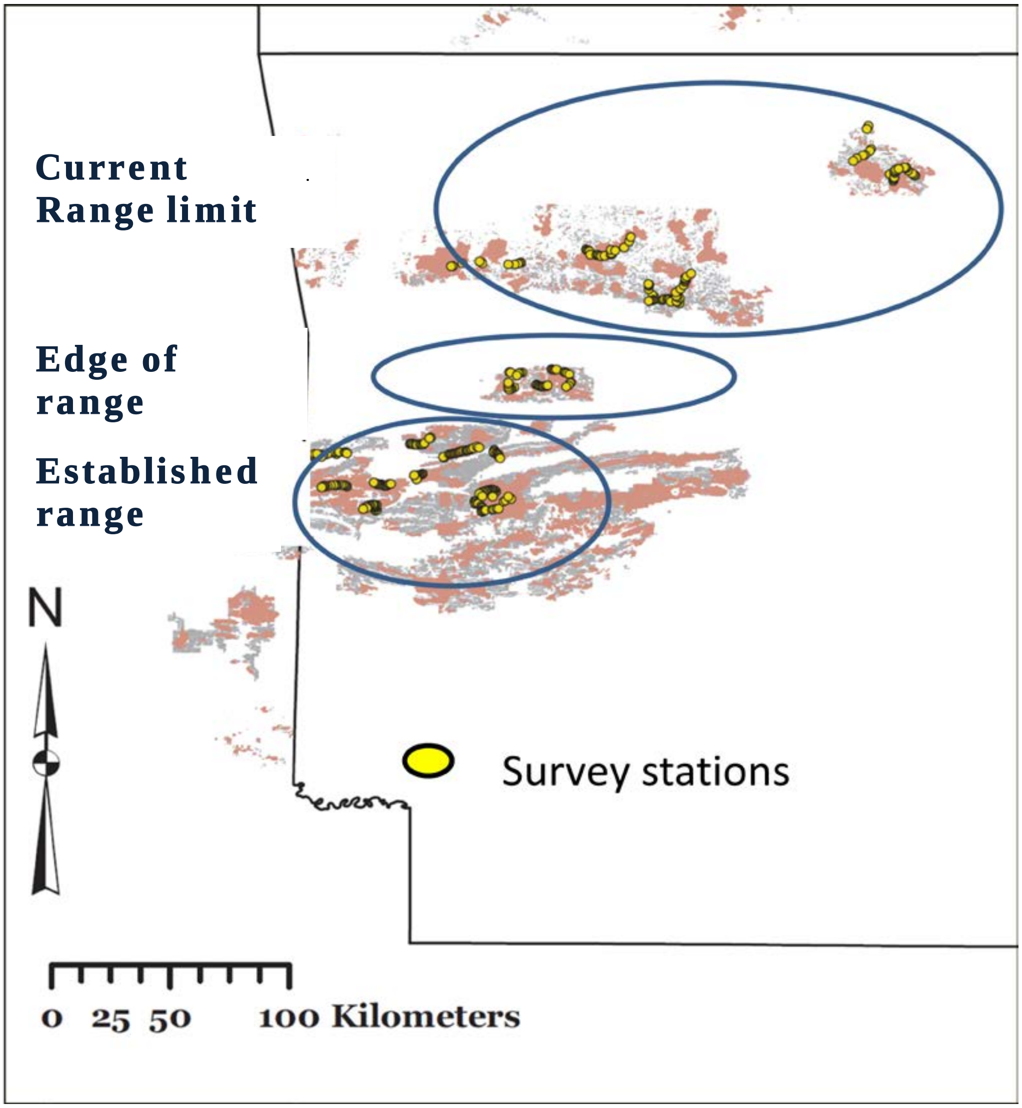


Figure 2.2. Map of landcover types and Brown-headed Nuthatch survey stations in the National Forests of Arkansas, USA. The locations we surveyed are marked with yellow circles. Grey indicates pine and mixed pine stands with no history of prescribed fire while red indicates that ≥1 prescribed fires have occurred.

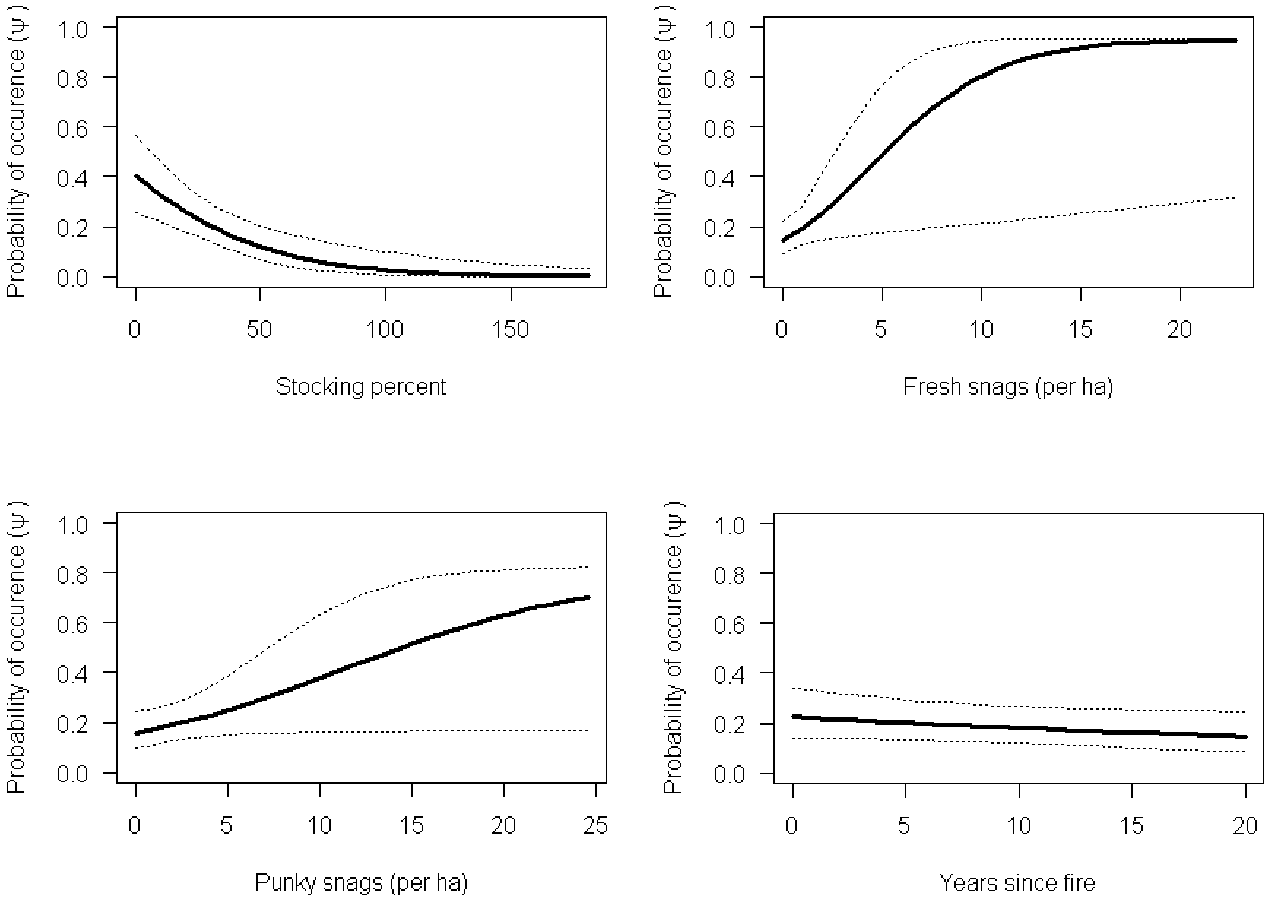


Figure 2.3. Model-averaged predictions of occupancy probability for percent tree stocking, fresh snag density, punky snag density and years since fire with all other covariates fixed at their respective mean values. Dashed lines are upper and lower 95% confidence intervals.

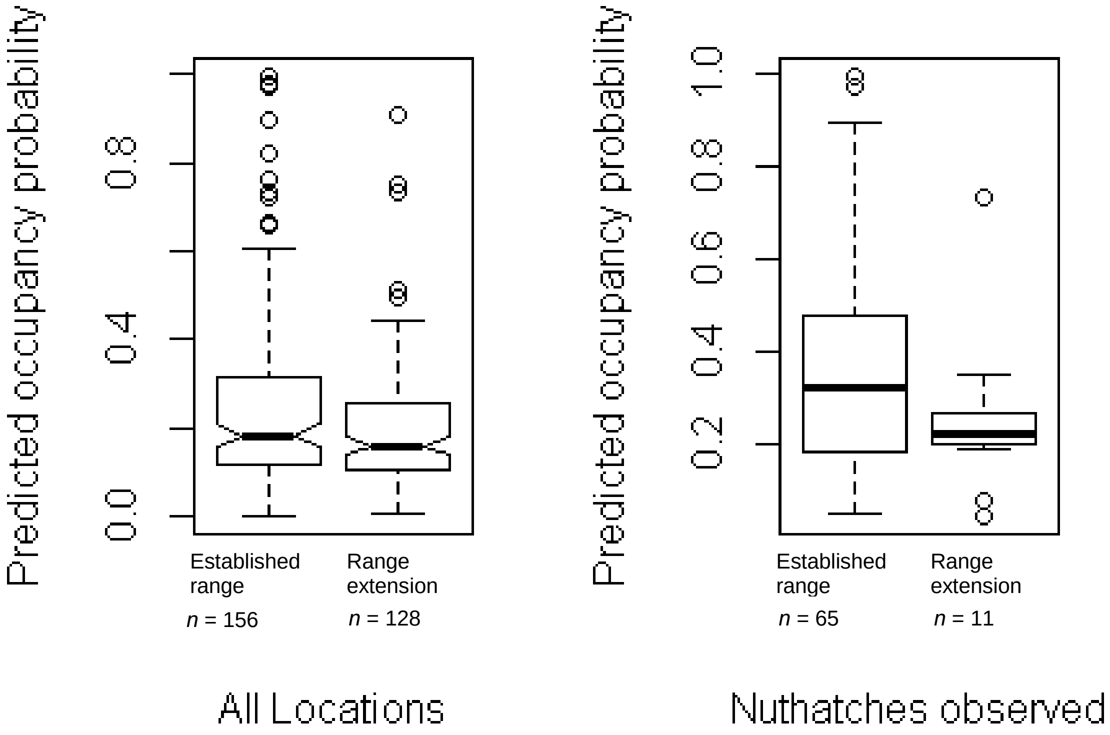


Figure 2.4. Box plots of predicted probability of Brown-headed Nuthatch occupancy among sites in the Ouachita Mountains and a range extension front (encompassing Mount Magazine and the Ozark Mountains) in Arkansas, USA, 2011-2012, based on patch-level habitat covariates while holding the effect of range extension context constant. “All Locations” includes all survey stations; “Observed Locations” includes only stations where nuthatches were observed on ≥1 occasion.

TABLES

Table 2.1. Covariates considered in candidate models of Brown-headed Nuthatch occupancy and detection in the Ouachita and Ozark-St. Francis National Forests of Arkansas, USA, 2011-2012.

Covariate (description)
Ψ~**Landscape context** (established range, edge of range, current range limit)
Ψ~**Stocking** (total stocking %)
Ψ~**Fresh snags** (fresh snag density, stems/ha)
Ψ~**Punky snags** (punky snag density, stems/ha)
Ψ~**Yrs from fire** (years since last prescribed fire)
Ψ~**Pine** (percent of total stocking in pine)†
Ψ~**Grass** (grassy herbaceous cover, %) †
Ψ~**BP2k** (percent of burned pine forest within 2 k)†
p~**Phen** (population breeding phenology: before hatch, brood rearing, or post-fledging)
p~**Obs** (observer)†
p~**Time** (time of day)†
p~**Temp** (temperature, °C)†
p~**Wind** (wind speed, km/h)†

†Uninformative parameter removed from consideration during analysis.

Table 2.2. AIC_c table showing relative support for several models relating the probability of Brown-headed Nuthatch occupancy (Ψ) to landscape context (Ouachita Mountains-core population, Mount Magazine-adjacent population, Ozark Mountains- peripheral population; Fig. 2.1) and patch-level forest stand characteristics. Covariate names are further described in Table 2.1. *K* is the number of parameters in each model, logLik is the negative log-likelihood, and $\Delta\mathrm{AIC}_c$ represents differences in Akaike's Information Criterion scores among models, with 0.00 being the top-ranking model. The Akaike weight for each model is denoted by w_i.

Model	***K***	**logLik**	**$\Delta\mathrm{AIC}_c$**	**w_i**
Ψ(context+stocking+fresh snags+punky snags+years from fire) *p*(phen)	10	-317.12	0.00	0.37
Ψ(context+stocking+fresh snags+punky snags) *p*(phen)	9	-318.58	0.77	0.25
Ψ(context+stocking+fresh snags+years from fire) *p*(phen)	9	-318.85	1.31	0.19
Ψ(context+stocking+fresh snags) *p*(phen)	8	-320.52	2.53	0.11
Ψ(context+stocking+punky snags+years from fire) *p*(phen)	9	-320.16	3.93	0.05
Ψ(.)*p* (phen)	4	-365.15	83.40	<0.01

Table 2.3. Model averaged coefficients (β), standard errors (SE), odds ratios, and 95% odds ratio confidence intervals (CI) for covariates related to Brown-headed Nuthatch detection (*p*) and occupancy (Ψ) in Arkansas, USA, 2011-2012.

Parameter	β	SE	Odds ratio	95% CI
***p* parameters**				
Intercept	0.240	0.208		
Phenology (Late)	–0.530	0.259	0.52	0.35-0.98
Phenology (Middle)	0.254	0.336	0.94	0.67-2.49
Ψ parameters				
Intercept	–0.889	0.556		
Established range	1.368	0.499	3.93	1.48-10.44
Current range limit	–1.724	0.848	0.18	0.03-0.94
Stocking	–0.032	0.009	0.97	0.95-0.99
Fresh snags	0.417	0.238	1.52	0.95-2.42
Punky snags	0.146	0.076	1.16	1.00-1.34
Years since fire	-0.042	0.024	0.96	0.92-1.01

Table 2.4. Summary of vegetation, snag, and prescribed fire metrics at survey stations where Brown-headed Nuthatches were detected in two National Forests in Arkansas, USA, 2011-2012. Covariate descriptions and units are in Fig. 2.1. Differences were assessed using Welch's 2-sample t-test.

Covariate	**Ouachita, established range** mean±SE, *n*=65	**Ozark-St. Francis, range extension zone** mean±SE, *n*=11	**Cohen's *d* (effect size)**	**p-value**	**df**
Stocking	23.0±2.4	20.9±6.8	0.11	0.778	12.5
Fresh snags	2.0±0.3	0.5±0.1	0.43	0.012	49.8
Punky snags	3.2±0.6	1.0±0.4	0.47	0.004	63.0
Years since fire	5.7±1.1	9.3±2.6	0.51	0.216	12.1
Grass	35.2±3.2	8.8±2.6	1.08	<0.001	45.9
Shrub cover	41.2±3.2	73.7±7.0	1.29	<0.001	14.5
BP.2k	51.6±4.6	25.5±1.0	1.03	<0.001	21.8
Pine	63.2±3.6	59.5±11.6	0.12	0.765	12.0

APPENDICES

Appendix 2.1. Complete ranked candidate model set relating Brown-headed Nuthatch call response survey detection probability to breeding phenology and sampling conditions in Arkansas, USA. Covariate names are described in Table 2.1. *K* is the number of parameters in each model, Loglik is the negative log-likelihood, and ΔAIC_c represents the difference in corrected Akaike's Information Criterion scores among models, with 0.00 being the top-ranking model. The Akaike weight for each model is denoted by w_i.

Model	***K***	**logLik**	**ΔAIC_c**	**w_i**
Ψ(.), *p* (phen)	4	-365.15	0.00	0.30
Ψ(.), *p* (phen+temp)	5	-364.87	1.51	0.14
Ψ(.), *p* (phen+wind)	5	-364.91	1.60	0.14
Ψ(.), *p* (phen+time)	5	-364.98	1.73	0.13
Ψ(.), *p* (phen+observer)	6	-364.72	3.30	0.06
Ψ(.), *p* (temp)	3	-367.83	3.31	0.06
Ψ(.), *p* (observer+temp)	5	-366.20	4.17	0.04
Ψ(.), *p* (temp+time)	4	-367.40	4.51	0.03
Ψ(.), *p* (temp+wind)	4	-367.82	5.35	0.02
Ψ(.), *p* (observer)	4	-367.93	5.56	0.02
Ψ(.), *p* (time)	3	-369.00	5.65	0.02
Ψ(.), *p* (wind)	3	-369.05	5.75	0.02
Ψ(.), *p* (.)	2	-370.71	7.02	0.01
Ψ(.), *p* (observer+time)	5	-367.67	7.12	0.01
Ψ(.), *p* (observer+wind)	5	-367.69	7.16	0.01
Ψ(.), *p* (time+wind)	4	-369.01	7.72	0.01

Appendix 2.2. Complete ranked candidate model set relating Brown-headed Nuthatch occupancy probability to landscape context and site conditions in Arkansas, USA. Covariate names are described in Table 2.1. *K* is the number of parameters in each model, Loglik is the negative log-likelihood, and ΔAIC_c represents the difference in corrected Akaike's Information Criterion scores among models, with 0.00 being the top-ranking model. The Akaike weight for each model is denoted by w_i.

Model	***K***	**logLik**	ΔAIC_c	w_i
Ψ (context+stock+fresh snags+punky snags+years from fire) *p* (phen)	10	-317.12	0.00	0.10
Ψ (context+stock+fresh snags+punky snags+years from fire+BP2k) *p* (phen)	11	-316.30	0.53	0.08
Ψ (context+stock+fresh snags+punky snags+years from fire+pine) *p* (phen)	11	-316.39	0.71	0.07
Ψ (context+stock+fresh snags+punky snags) *p* (phen)	9	-318.58	0.77	0.07
Ψ (context+stock+fresh snags+punky snags+pine) *p* (phen)	10	-317.77	1.30	0.05
Ψ (context+stock+fresh snags+years from fire) *p* (phen)	9	-318.85	1.31	0.05
Ψ (context+stock+fresh snags+punky snags+years from fire+BP2k+pine) *p* (phen)	12	-315.61	1.32	0.05
Ψ (context+stock+fresh snags+punky snags+years from fire+grass) *p* (phen)	11	-316.90	1.72	0.04
Ψ (context+stock+fresh snags+years from fire+BP2k) *p* (phen)	10	-318.04	1.85	0.04
Ψ (context+stock+fresh snags+years from fire+pine) *p* (phen)	10	-318.19	2.14	0.03
Ψ (context+stock+fresh snags+punky snags+years from fire+pine+grass) *p* (phen)	12	-316.16	2.44	0.03
Ψ (context+stock+fresh snags) *p* (phen)	8	-320.52	2.53	0.03
Ψ (context+stock+fresh snags+punky snags+years from fire+BP2kgrass) *p* (phen)	12	-316.21	2.53	0.03
Ψ (context+stock+fresh snags+years from fire+BP2k+pine) *p* (phen)	11	-317.40	2.73	0.03
Ψ (context+stock+fresh snags+punky snags+grass) *p* (phen)	10	-318.54	2.85	0.02
Ψ (context+stock+fresh snags+punky snags+BP2k) *p* (phen)	10	-318.56	2.88	0.02
Ψ (context+stock+fresh snags+pine) *p* (phen)	9	-319.78	3.18	0.02
Ψ (context+stock+fresh snags+years from fire+grass) *p* (phen)	10	-318.72	3.21	0.02
Ψ (context+stock+fresh snags+punky snags+years from fire+BP2k+pine+grass) *p* (phen)	13	-315.52	3.34	0.02
Ψ (context+stock+fresh snags+punky snags+pine+grass) *p* (phen)	11	-317.73	3.39	0.02
Ψ (context+stock+fresh snags+punky snags+BP2k+pine) *p* (phen)	11	-317.75	3.43	0.02

Model	***K***	**logLik**	**ΔAIC_c**	**w_i**
Ψ (context+stock+fresh snags+years from fire+BP2k+grass) *p* (phen)	11	-318.00	3.92	0.01
Ψ (context+stock+punky snags+years from fire) *p* (phen)	9	-320.16	3.93	0.01
Ψ (context+stock+fresh snags+years from fire+pine+grass) *p* (phen)	11	-318.06	4.04	0.01
Ψ (context+stock+punky snags+years from fire+pine) *p* (phen)	10	-319.19	4.14	0.01
Ψ (context+stock+fresh snags+BP2k) *p* (phen)	9	-320.52	4.65	0.01
Ψ (context+stock+fresh snags+grass) *p* (phen)	9	-320.52	4.66	0.01
Ψ (context+stock+fresh snags+years from fire+BP2k+pine+grass) *p* (phen)	12	-317.36	4.82	0.01
Ψ (context+stock+fresh snags+punky snags+BP2k+grass) *p* (phen)	11	-318.53	5.00	0.01
Ψ (context+stock+punky snags+years from fire+BP2k) *p* (phen)	10	-319.63	5.02	0.01
Ψ (context+stock+punky snags+years from fire+BP2k+pine) *p* (phen)	11	-318.68	5.29	0.01
Ψ (context+stock+fresh snags+BP2k+pine) *p* (phen)	10	-319.77	5.31	0.01
Ψ (context+stock+fresh snags+pine+grass) *p* (phen)	10	-319.78	5.32	0.01
Ψ (context+stock+fresh snags+punky snags+BP2k+pine+grass) *p* (phen)	12	-317.72	5.55	0.01
Ψ (context+stock+punky snags+years from fire+grass) *p* (phen)	10	-320.07	5.91	0.01
Ψ (context+stock+punky snags+years from fire+pine+grass) *p* (phen)	11	-319.09	6.11	4.68E-03
Ψ (context+stock+punky snags+pine) *p* (phen)	9	-321.28	6.18	4.51E-03
Ψ (context+stock+punky snags) *p* (phen)	8	-322.40	6.28	4.28E-03
Ψ (context+stock+fresh snags+BP2k+grass) *p* (phen)	10	-320.51	6.79	3.32E-03
Ψ (context+stock+punky snags+years from fire+BP2k+grass) *p* (phen)	11	-319.61	7.15	2.78E-03
Ψ (context+stock+punky snags+years from fire+BP2k+pine+grass) *p* (phen)	12	-318.66	7.42	2.43E-03
Ψ (context+stock+fresh snags+BP2k+pine+grass) *p* (phen)	11	-319.77	7.47	2.37E-03
Ψ (context+stock+punky snags+BP2k+pine) *p* (phen)	10	-321.25	8.27	1.58E-03
Ψ (context+stock+punky snags+pine+grass) *p* (phen)	10	-321.28	8.33	1.54E-03
Ψ (context+stock+punky snags+BP2k) *p* (phen)	9	-322.37	8.35	1.52E-03
Ψ (context+stock+punky snags+grass) *p* (phen)	9	-322.39	8.40	1.48E-03
Ψ (context+stock+punky snags+BP2k+pine+grass) *p* (phen)	11	-321.25	10.44	5.37E-04
Ψ (context+stock+punky snags+BP2k+grass) *p* (phen)	10	-322.37	10.50	5.21E-04
Ψ (context+stock+years from fire) *p* (phen)	8	-324.61	10.69	4.72E-04

Model	***K***	**logLik**	**ΔAIC_c**	**w_i**
Ψ (context+stock+years from fire+pine) *p* (phen)	9	-323.70	11.02	4.00E-04
Ψ (context+fresh snags+punky snags+years from fire+pine) *p* (phen)	10	-323.02	11.80	2.71E-04
Ψ (context+stock+years from fire+BP2k) *p* (phen)	9	-324.41	12.43	1.98E-04
Ψ (context+fresh snags+punky snags+years from fire) *p* (phen)	9	-324.46	12.53	1.89E-04
Ψ (context+stock+years from fire+grass) *p* (phen)	9	-324.57	12.76	1.68E-04
Ψ (context+stock+years from fire+BP2k+pine) *p* (phen)	10	-323.52	12.81	1.64E-04
Ψ (context+fresh snags+punky snags+years from fire+BP2k+pine) *p* (phen)	11	-322.58	13.08	1.43E-04
Ψ (context+stock+years from fire+pine+grass) *p* (phen)	10	-323.68	13.12	1.41E-04
Ψ (context+fresh snags+punky snags+pine) *p* (phen)	9	-325.00	13.61	1.10E-04
Ψ (context+fresh snags+punky snags+years from fire+BP2k) *p* (phen)	10	-324.02	13.81	9.94E-05
Ψ (context+fresh snags+punky snags+years from fire+pinegrass) *p* (phen)	11	-322.95	13.83	9.85E-05
Ψ (context+fresh snags+years from fire+pine) *p* (phen)	9	-325.29	14.20	8.20E-05
Ψ (context+stock+years from fire+BP2k+grass) *p* (phen)	10	-324.32	14.40	7.39E-05
Ψ (context+fresh snags+punky snags+years from fire+grass) *p* (phen)	10	-324.40	14.57	6.79E-05
Ψ (context+fresh snags+years from fire) *p* (phen)	8	-326.62	14.72	6.30E-05
Ψ (context+fresh snags+punky snags) *p* (phen)	8	-326.64	14.76	6.19E-05
Ψ (context+stock+years from fire+BP2k+pine+grass) *p* (phen)	11	-323.44	14.81	6.02E-05
Ψ (context+fresh snags+punky snags+years from fire+BP2k+pine+grass) *p* (phen)	12	-322.57	15.24	4.86E-05
Ψ (context+fresh snags+years from fire+BP2k+pine) *p* (phen)	10	-324.89	15.54	4.19E-05
Ψ (context+stock+pine) *p* (phen)	8	-327.04	15.57	4.13E-05
Ψ (context+stock) *p* (phen)	7	-328.11	15.58	4.10E-05
Ψ (context+fresh snags+punky snags+BP2k+pine) *p* (phen)	10	-324.96	15.69	3.88E-05
Ψ (context+fresh snags+punky snags+pine+grass) *p* (phen)	10	-324.98	15.72	3.82E-05
Ψ (context+fresh snags+punky snags+years from fire+BP2k+grass) *p* (phen)	11	-324.02	15.97	3.38E-05
Ψ (context+fresh snags+years from fire+BP2k) *p* (phen)	9	-326.23	16.08	3.20E-05
Ψ (context+fresh snags+years from fire+pine+grass) *p* (phen)	10	-325.28	16.33	2.83E-05
Ψ (context+fresh snags+pine) *p* (phen)	8	-327.53	16.54	2.54E-05
Ψ (context+stock+grass) *p* (phen)	8	-327.64	16.76	2.27E-05

Model	***K***	**logLik**	**ΔAIC$_c$**	**w_i**
Ψ (context+fresh snags+punky snags+BP2k) *p* (phen)	9	-326.59	16.80	2.23E-05
Ψ (context+fresh snags+punky snags+grass) *p* (phen)	9	-326.60	16.82	2.20E-05
Ψ (context+fresh snags+years from fire+grass) *p* (phen)	9	-326.62	16.85	2.17E-05
Ψ (context+stock+pine+grass) *p* (phen)	9	-326.62	16.86	2.16E-05
Ψ (context+stock+BP2k) *p* (phen)	8	-327.70	16.88	2.15E-05
Ψ (context+stock+BP2k+pine) *p* (phen)	9	-326.65	16.91	2.11E-05
Ψ (context+punky snags+years from fire+pine) *p* (phen)	9	-326.82	17.25	1.78E-05
Ψ (context+fresh snags+punky snags) *p* (phen)	7	-329.06	17.48	1.59E-05
Ψ (context+fresh snags+years from fire+BP2k+pine+grass) *p* (phen)	11	-324.88	17.70	1.42E-05
Ψ (context+fresh snags+punky snags+BP2k+pine+grass) *p* (phen)	11	-324.96	17.85	1.32E-05
Ψ (context+fresh snags+punky snags+years from fire+BP2k+grass) *p* (phen)	10	-326.22	18.21	1.10E-05
Ψ (context+fresh snags+pine+grass) *p* (phen)	9	-327.42	18.46	9.75E-06
Ψ (context+stock+BP2k+grass) *p* (phen)	9	-327.45	18.52	9.42E-06
Ψ (context+fresh snags+BP2k+pine) *p* (phen)	9	-327.46	18.54	9.34E-06
Ψ (context+stock+BP2k+pine+grass) *p* (phen)	10	-326.43	18.63	8.91E-06
Ψ (context+fresh snags+punky snags+BP2k+grass) *p* (phen)	10	-326.58	18.92	7.71E-06
Ψ (context+punky snags+years from fire+BP2k+pine) *p* (phen)	10	-326.60	18.97	7.54E-06
Ψ (context+punky snags+years from fire) *p* (phen)	8	-328.81	19.11	7.03E-06
Ψ (context+fresh snags+grass) *p* (phen)	8	-328.91	19.30	6.38E-06
Ψ (context+punky snags+years from fire+pine+grass) *p* (phen)	10	-326.81	19.38	6.13E-06
Ψ (context+fresh snags+BP2k) *p* (phen)	8	-328.98	19.44	5.96E-06
Ψ (context+fresh snags+BP2k+pine+grass) *p* (phen)	10	-327.40	20.56	3.41E-06
Ψ (context+punky snags+years from fire+BP2k) *p* (phen)	9	-328.63	20.87	2.91E-06
Ψ (context+punky snags+years from fire+BP2k+pine+grass) *p* (phen)	11	-326.60	21.13	2.56E-06
Ψ (context+punky snags+years from fire+grass) *p* (phen)	9	-328.81	21.24	2.42E-06
Ψ (context+punky snags+pine) *p* (phen)	8	-329.91	21.30	2.35E-06
Ψ (context+fresh snags+BP2k+grass) *p* (phen)	9	-328.88	21.38	2.25E-06
Ψ (context+punky snags+BP2k+pine+) *p* (phen)	9	-329.59	22.79	1.11E-06

Model	***K***	**logLik**	**ΔAIC_c**	**w_i**
Ψ (context+punky snags+years from fire+BP2k+grass) *p* (phen)	10	-328.61	22.99	1.01E-06
Ψ (context+punky snags+pine+grass) *p* (phen)	9	-329.71	23.04	9.83E-07
Ψ (context+punky snags) *p* (phen)	7	-332.34	24.05	5.94E-07
Ψ (context+punky snags+BP2k+pine+grass) *p* (phen)	10	-329.53	24.83	4.03E-07
Ψ (context+punky snags+BP2k) *p* (phen)	8	-331.93	25.35	3.11E-07
Ψ (context+punky snags+grass) *p* (phen)	8	-332.04	25.56	2.79E-07
Ψ (context+punky snags+BP2k+grass) *p* (phen)	9	-331.82	27.26	1.19E-07
Ψ (context+years from fire+pine) *p* (phen)	8	-333.27	28.02	8.14E-08
Ψ (context+years from fire) *p* (phen)	7	-335.17	29.71	3.51E-08
Ψ (context+years from fire+pine+grass) *p* (phen)	9	-333.06	29.73	3.48E-08
Ψ (context+years from fire+BP2k+pine) *p* (phen)	9	-333.26	30.13	2.84E-08
Ψ (stock+fresh snags+years from fire+BP2k+pine) *p* (phen)	9	-333.69	30.99	1.85E-08
Ψ (stock+fresh snags+years from fire+BP2k) *p* (phen)	8	-334.78	31.05	1.79E-08
Ψ (context+years from fire+grass) *p* (phen)	8	-334.89	31.26	1.62E-08
Ψ (stock+fresh snags+BP2k+pine) *p* (phen)	8	-334.97	31.42	1.49E-08
Ψ (stock+fresh snags+BP2k) *p* (phen)	7	-336.13	31.62	1.35E-08
Ψ (stock+fresh snags+years from fire+pine) *p* (phen)	8	-335.07	31.63	1.34E-08
Ψ (context+years from fire+BP2k+pine+grass) *p* (phen)	10	-332.99	31.74	1.27E-08
Ψ (context+years from fire+BP2k) *p* (phen)	8	-335.16	31.81	1.23E-08
Ψ (stock+fresh snags+years from fire+) *p* (phen)	7	-336.34	32.04	1.09E-08
Ψ (stock+fresh snags+punky snags+BP2k+pine) *p* (phen)	9	-334.47	32.55	8.47E-09
Ψ (stock+fresh snags+punky snags+years from fire+BP2k+pine) *p* (phen)	10	-333.41	32.59	8.33E-09
Ψ (stock+fresh snags+punky snags+years from fire+BP2k) *p* (phen)	9	-334.56	32.73	7.74E-09
Ψ (stock+fresh snags+years from fire+BP2k+pine+grass) *p* (phen)	10	-333.50	32.76	7.62E-09
Ψ (stock+fresh snags+years from fire+BP2k+grass) *p* (phen)	9	-334.62	32.85	7.31E-09
Ψ (stock+fresh snags+punky snags+BP2k) *p* (phen)	8	-335.69	32.86	7.27E-09
Ψ (context+years from fire+BP2k+grass) *p* (phen)	9	-334.82	33.26	5.93E-09
Ψ (stock+fresh snags+punky snags+years from fire+pine) *p* (phen)	9	-334.87	33.35	5.68E-09

Model	***K***	**logLik**	**ΔAIC_c**	**w_i**
Ψ (stock+fresh snags+BP2k+pine+grass) *p* (phen)	9	-334.88	33.37	5.61E-09
Ψ (stock+fresh snags+BP2k+grass) *p* (phen)	8	-336.06	33.60	5.02E-09
Ψ (stock+fresh snags+years from fire+pine+grass) *p* (phen)	9	-335.01	33.63	4.95E-09
Ψ (stock+fresh snags+punky snags+years from fire) *p* (phen)	8	-336.19	33.87	4.38E-09
Ψ (stock+fresh snags+years from fire+grass) *p* (phen)	8	-336.29	34.06	3.99E-09
Ψ (stock+fresh snags+punky snags+years from fire+BP2k+pine+grass) *p* (phen)	11	-333.10	34.12	3.87E-09
Ψ (stock+fresh snags+punky snags+BP2k+pine+grass) *p* (phen)	10	-334.25	34.26	3.61E-09
Ψ (stock+fresh snags+punky snags+years from fire+BP2k+grass) *p* (phen)	10	-334.29	34.34	3.46E-09
Ψ (stock+fresh snags+punky snags+BP2k+grass) *p* (phen)	9	-335.51	34.64	2.99E-09
Ψ (stock+fresh snags+punky snags+years from fire+pine+grass) *p* (phen)	10	-334.74	35.24	2.21E-09
Ψ (context+pine+grass) *p* (phen)	8	-337.02	35.51	1.93E-09
Ψ (context+BP2k+pine) *p* (phen)	8	-337.09	35.67	1.78E-09
Ψ (stock+fresh snags+punky snags+years from fire+grass) *p* (phen)	9	-336.10	35.81	1.66E-09
Ψ (context+pine) *p* (phen)	7	-338.42	36.21	1.36E-09
Ψ (context+BP2k+pine+grass) *p* (phen)	9	-336.46	36.54	1.15E-09
Ψ (stock+fresh snags+pine) *p* (phen)	7	-338.96	37.29	7.91E-10
Ψ (context+grass) *p* (phen)	7	-339.19	37.74	6.34E-10
Ψ (stock+fresh snags) *p* (phen)	6	-340.38	38.02	5.49E-10
Ψ (context+BP2k) *p* (phen)	7	-339.37	38.10	5.28E-10
Ψ (stock+punky snags+years from fire+BP2k+pine) *p* (phen)	9	-337.29	38.19	5.06E-10
Ψ (stock+fresh snags+punky snags+pine) *p* (phen)	8	-338.38	38.24	4.93E-10
Ψ (stock+punky snags+BP2k+pine) *p* (phen)	8	-338.44	38.37	4.62E-10
Ψ (context+BP2k+grass) *p* (phen)	8	-338.59	38.66	4.00E-10
Ψ (stock+punky snags+years from fire+BP2k) *p* (phen)	8	-338.67	38.83	3.67E-10
Ψ (context+) *p* (phen)	6	-340.89	39.05	3.29E-10
Ψ (stock+fresh snags+punky snags) *p* (phen)	7	-339.89	39.15	3.13E-10
Ψ (stock+punky snags+BP2k) *p* (phen)	7	-339.92	39.19	3.06E-10
Ψ (stock+fresh snags+pine+grass) *p* (phen)	8	-338.93	39.35	2.83E-10

Model	K	logLik	$\Delta \mathrm{AIC_c}$	w_i
Ψ (stock+fresh snags+grass) *p* (phen)	7	-340.34	40.04	2.00E-10
Ψ (stock+punky snags+years from fire+BP2k+pine+grass) *p* (phen)	10	-337.17	40.10	1.94E-10
Ψ (stock+fresh snags+punky snags+pine+grass) *p* (phen)	9	-338.38	40.37	1.70E-10
Ψ (stock+punky snags+BP2k+pine+grass) *p* (phen)	9	-338.39	40.39	1.68E-10
Ψ (stock+punky snags+years from fire+BP2k+grass) *p* (phen)	9	-338.60	40.82	1.36E-10
Ψ (stock+punky snags+BP2k+grass) *p* (phen)	8	-339.89	41.26	1.09E-10
Ψ (stock+fresh snags+punky snags+grass) *p* (phen)	8	-339.89	41.26	1.09E-10
Ψ (fresh snags+BP2k+pine) *p* (phen)	7	-341.07	41.50	9.63E-11
Ψ (stock+years from fire+BP2k+pine) *p* (phen)	8	-340.10	41.68	8.83E-11
Ψ (fresh snags+years from fire+BP2k+pine) *p* (phen)	8	-340.14	41.77	8.45E-11
Ψ (stock+punky snags+years from fire+pine) *p* (phen)	8	-340.20	41.88	7.99E-11
Ψ (stock+years from fire+BP2k) *p* (phen)	7	-341.48	42.33	6.38E-11
Ψ (fresh snags+punky snags+BP2k+pine) *p* (phen)	8	-340.44	42.36	6.29E-11
Ψ (fresh snags+punky snags+years from fire+BP2k+pine) *p* (phen)	9	-339.72	43.06	4.42E-11
Ψ (stock+punky snags+years from fire) *p* (phen)	7	-341.97	43.31	3.90E-11
Ψ (fresh snags+years from fire+pine) *p* (phen)	7	-342.04	43.45	3.64E-11
Ψ (stock+BP2k+pine) *p* (phen)	7	-342.05	43.47	3.60E-11
Ψ (fresh snags+BP2k+pine+grass) *p* (phen)	8	-341.07	43.61	3.36E-11
Ψ (stock+years from fire+BP2k+pine+grass) *p* (phen)	9	-340.09	43.79	3.08E-11
Ψ (fresh snags+years from fire+BP2k+pine+grass) *p* (phen)	9	-340.10	43.82	3.03E-11
Ψ (stock+punky snags+years from fire+pine+grass) *p* (phen)	9	-340.20	44.01	2.75E-11
Ψ (fresh snags+BP2k) *p* (phen)	6	-343.38	44.03	2.73E-11
Ψ (fresh snags+years from fire+BP2k) *p* (phen)	7	-342.41	44.19	2.52E-11
Ψ (stock+BP2k) *p* (phen)	6	-343.54	44.35	2.32E-11
Ψ (fresh snags+punky snags+BP2k+pine+grass) *p* (phen)	9	-340.37	44.36	2.31E-11
Ψ (stock+years from fire+BP2k+grass) *p* (phen)	8	-341.46	44.39	2.27E-11
Ψ (fresh snags+punky snags+years from fire+pine) *p* (phen)	8	-341.73	44.93	1.73E-11
Ψ (fresh snags+punky snags+years from fire+BP2k+pine+grass) *p* (phen)	10	-339.60	44.97	1.70E-11

Model	***K***	**logLik**	**ΔAIC$_c$**	**w_i**
Ψ (fresh snags+punky snags+BP2k) *p* (phen)	7	-342.82	45.01	1.67E-11
Ψ (stock+punky snags+years from fire+grass) *p* (phen)	8	-341.96	45.41	1.37E-11
Ψ (stock+BP2k+pine+grass) *p* (phen)	8	-341.97	45.42	1.36E-11
Ψ (stock+years from fire+pine) *p* (phen)	7	-343.06	45.49	1.32E-11
Ψ (fresh snags+years from fire+pine+grass) *p* (phen)	8	-342.04	45.56	1.27E-11
Ψ (fresh snags+punky snags+years from fire+BP2k) *p* (phen)	8	-342.06	45.61	1.24E-11
Ψ (fresh snags+BP2k+grass) *p* (phen)	7	-343.38	46.13	9.55E-12
Ψ (stock+BP2k+grass) *p* (phen)	7	-343.42	46.21	9.18E-12
Ψ (fresh snags+years from fire+BP2k+grass) *p* (phen)	8	-342.40	46.28	8.83E-12
Ψ (fresh snags+years from fire) *p* (phen)	6	-344.79	46.85	6.66E-12
Ψ (stock+years from fire) *p* (phen)	6	-344.80	46.86	6.62E-12
Ψ (fresh snags+punky snags+years from fire+pinegrass) *p* (phen)	9	-341.72	47.06	5.98E-12
Ψ (fresh snags+punky snags+BP2k+grass) *p* (phen)	8	-342.81	47.09	5.89E-12
Ψ (stock+years from fire+pine+grass) *p* (phen)	8	-342.85	47.18	5.65E-12
Ψ (fresh snags+punky snags+years from fire+BP2k+grass) *p* (phen)	9	-342.01	47.64	4.48E-12
Ψ (fresh snags+pine) *p* (phen)	6	-345.41	48.08	3.60E-12
Ψ (stock+years from fire+grass) *p* (phen)	7	-344.51	48.39	3.08E-12
Ψ (fresh snags+punky snags+years from fire) *p* (phen)	7	-344.57	48.51	2.90E-12
Ψ (fresh snags+punky snags+pine) *p* (phen)	7	-344.69	48.75	2.57E-12
Ψ (fresh snags+years from fire+grass) *p* (phen)	7	-344.75	48.86	2.43E-12
Ψ (stock+punky snags+pine) *p* (phen)	7	-345.07	49.50	1.77E-12
Ψ (fresh snags+pine+grass) *p* (phen)	7	-345.14	49.65	1.64E-12
Ψ (fresh snags+punky snags+years from fire+grass) *p* (phen)	8	-344.56	50.60	1.02E-12
Ψ (fresh snags+punky snags+pine+grass) *p* (phen)	8	-344.59	50.65	9.94E-13
Ψ (stock+punky snags+pine+grass) *p* (phen)	8	-344.86	51.21	7.52E-13
Ψ (punky snags+BP2k+pine) *p* (phen)	7	-346.08	51.52	6.43E-13
Ψ (stock+punky snags) *p* (phen)	6	-347.15	51.56	6.30E-13
Ψ (punky snags+years from fire+BP2k+pine) *p* (phen)	8	-345.18	51.85	5.47E-13

Model	***K***	**logLik**	**ΔAIC_c**	**w_i**
Ψ (fresh snags) *p* (phen)	5	-348.34	51.86	5.43E-13
Ψ (fresh snags+punky snags) *p* (phen)	6	-347.75	52.77	3.45E-13
Ψ (stock+punky snags+grass) *p* (phen)	7	-346.84	53.04	3.01E-13
Ψ (fresh snags+grass) *p* (phen)	6	-347.90	53.06	2.98E-13
Ψ (punky snags+BP2k+pine+grass) *p* (phen)	8	-346.08	53.64	2.23E-13
Ψ (punky snags+years from fire+BP2k+pine+grass) *p* (phen)	9	-345.16	53.94	1.93E-13
Ψ (fresh snags+punky snags+grass) *p* (phen)	7	-347.50	54.35	1.56E-13
Ψ (punky snags+BP2k) *p* (phen)	6	-349.14	55.54	8.64E-14
Ψ (punky snags+years from fire+BP2k) *p* (phen)	7	-348.16	55.68	8.06E-14
Ψ (stock+pine+grass) *p* (phen)	7	-348.91	57.19	3.78E-14
Ψ (punky snags+years from fire+pine) *p* (phen)	7	-349.07	57.50	3.24E-14
Ψ (punky snags+BP2k+grass) *p* (phen)	7	-349.11	57.59	3.09E-14
Ψ (stock+ pine) *p* (phen)	6	-350.19	57.64	3.02E-14
Ψ (punky snags+years from fire+BP2k+grass) *p* (phen)	8	-348.16	57.79	2.80E-14
Ψ (years from fire+BP2k+pine) *p* (phen)	7	-349.42	58.20	2.28E-14
Ψ (stock+grass) *p* (phen)	6	-350.80	58.86	1.64E-14
Ψ (punky snags+years from fire+pine+grass) *p* (phen)	8	-348.98	59.45	1.22E-14
Ψ (BP2k+pine) *p* (phen)	6	-351.19	59.65	1.11E-14
Ψ (stock) *p* (phen)	5	-352.28	59.73	1.06E-14
Ψ (years from fire+BP2k+pine+grass) *p* (phen)	8	-349.28	60.04	9.10E-15
Ψ (BP2k+pine+grass) *p* (phen)	7	-350.85	61.07	5.44E-15
Ψ (years from fire+BP2k) *p* (phen)	6	-352.45	62.17	3.14E-15
Ψ (punky snags+years from fire) *p* (phen)	6	-353.03	63.32	1.76E-15
Ψ (years from fire+BP2k+grass) *p* (phen)	7	-352.18	63.72	1.45E-15
Ψ (BP2k) *p* (phen)	5	-354.37	63.91	1.32E-15
Ψ (years from fire+pine) *p* (phen)	6	-353.45	64.15	1.16E-15
Ψ (punky snags+pine) *p* (phen)	6	-353.63	64.52	9.66E-16
Ψ (punky snags+years from fire+grass) *p* (phen)	7	-352.73	64.82	8.32E-16

Model	K	**logLik**	$\Delta\mathrm{AIC}_c$	w_i
Ψ (BP2k+grass) *p* (phen)	6	-353.82	64.89	8.04E-16
Ψ (years from fire+pine+grass) *p* (phen)	7	-352.78	64.92	7.94E-16
Ψ (punky snags+pine+grass) *p* (phen)	7	-352.96	65.28	6.61E-16
Ψ (years from fire+grass) *p* (phen)	6	-356.38	70.02	6.20E-17
Ψ (years from fire) *p* (phen)	5	-357.48	70.13	5.86E-17
Ψ (punky snags+grass) *p* (phen)	6	-356.84	70.95	3.90E-17
Ψ (punky snags) *p* (phen)	5	-358.04	71.25	3.34E-17
Ψ (pine+grass) *p* (phen)	6	-358.05	73.36	1.17E-17
Ψ (pine) *p* (phen)	5	-360.51	76.18	2.84E-18
Ψ (grass) *p* (phen)	5	-361.85	78.88	7.38E-19
Ψ (.) *p* (phen)	4	-365.15	83.40	7.71E-20