



RESEARCH ARTICLE

Resource configuration and abundance affect space use of a cooperatively breeding resident bird

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ABSTRACT

Movement and space use of birds is driven by activities associated with acquiring and maintaining access to critical resources. Thus, the spatial configuration of resources within home ranges should influence bird movements, and resource values should be relative to their locations. We radio-tracked 22 Brown-headed Nuthatches (*Sitta pusilla*) and related their space use and home range sizes to available resources while taking nest site locations into account. We developed utilization distributions (UDs) from nuthatch locations, and treated 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, and used lognormal regression to relate intensity of use to resource metrics at random points by ranking linear mixed models. Nuthatch home ranges typically had two centers of activity. Areas of high use were associated with the density of recently killed snags (likely a 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 higher nest snag density. Predicted home range sizes decreased by 77% and 69%, respectively, when percent pine and nest snag density were maximized. Our results illustrate that movement decisions within home ranges are driven by both the availability and spatial distribution of resources, while ongoing savannah-woodland management is providing resources that are used by Brown-headed Nuthatches.

Keywords: home range size, optimal foraging theory, resource selection, *Sitta pusilla*, utilization distributions

La configuración del recurso y la abundancia afectan el uso del espacio de un ave residente de cría cooperativa

RESUMEN

El movimiento y el uso del espacio en las aves están determinados por actividades asociadas con la adquisición y el mantenimiento de recursos críticos. Por ende, la configuración espacial de los recursos adentro del ámbito de hogar debería influenciar los movimientos de las aves y el valor de los recursos debería guardar relación con sus ubicaciones. Seguimos con radio transmisores 22 individuos de *Sitta pusilla* y relacionamos el uso del espacio y los tamaños de los ámbitos de hogar con la disponibilidad de recursos, tomando en consideración la localización de los nidos. Desarrollamos distribuciones de utilización (DUs) a partir de la localización de individuos de *S. pusilla* y tomamos el área de cada isolinia de 95% como el tamaño del ámbito de hogar y el peso de la DU como una probabilidad relativa de uso. Ajustamos los modelos relacionando el tamaño del ámbito de hogar con las estimaciones promedio de recursos adentro del ámbito de hogar y empleamos regresiones logarítmicas normales para relacionar la intensidad de uso con las medidas de recursos en puntos al azar, mediante la priorización de modelos lineales mixtos. Los ámbitos de hogar de los individuos de *S. pusilla* tuvieron típicamente dos centros de actividad. Los ámbitos con mucho uso estuvieron asociados con la densidad de tocones recientemente muertos (probablemente un recurso alimenticio), prescripciones de fuego recientes, dominancia de pino, bajas tasas de siembre de árboles y cobertura herbácea. Los ámbitos de hogar fueron generalmente grandes (media 7.1 ha, rango 0.3–47.6 ha) y los ámbitos de hogar más pequeñas estuvieron asociadas con la dominancia de pino y una mayor densidad de tocones nido. Los tamaños predichos del ámbito de hogar disminuyeron 77% y 69%, respectivamente, cuando se maximizaron el porcentaje de densidad de pino y de tocones nido. Nuestros resultados muestran que las decisiones de movimiento adentro de los ámbitos de hogar estuvieron determinadas por la disponibilidad y la distribución espacial de los recursos mientras que el manejo continuo de la sabana y del bosque provea los recursos que utilizan los individuos de *S. pusilla*.

Palabras clave: distribuciones de utilización, selección de recursos, *Sitta pusilla*, tamaño del ámbito de hogar, teoría de forrajeo óptimo

INTRODUCTION

Foraging substrates and nest sites are among the critical resources needed by all birds (Newton 1998); acquiring and maintaining access to these resources drives movement and space use. The relationship between resources and space use is especially strong for resident species. Many such species move to permanent locations during natal dispersal, and birds then remain on all-purpose home ranges throughout the year (Jackson 1994, Golabek et al. 2012). Several studies have also documented extensive predispersal prospecting movements in resident and cooperatively breeding birds, reinforcing the importance of 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 most influence bird movement within home ranges during the nesting season. Central-place foraging influences movements because individuals return to a focal location after each foraging bout (Orians and Pearson 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 home range as an assemblage of uniformly valued resources may be inappropriate during nesting because some resources are more distant from the nest and are thus more costly.

Few researchers have evaluated how animal movements are influenced by the distribution of resources and the associated effort 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., third-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 seldom assessed in areas perceived by researchers to be uniform (Levin 1992, Rhodes et al. 2005).

Similarly, animal home ranges 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 could identify possible limiting factors. Our objective was to determine 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 resource utilization functions suitable for a central-place forager (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 fire-maintained savannah-woodland, and is endemic to the southeastern United States (Slater et al. 2013). The species co-occurs with the endangered Red-cockaded Woodpecker (*Picoides borealis*) and is widely presumed to benefit from habitat management for that species (Wilson et al. 1995, Slater et al. 2013). Nuthatches are small (10 g), obligate cavity-nesters and primary excavators, requiring well-decayed snags for nesting (Slater et al. 2013). Limited nest-site availability may drive cooperative breeding in nuthatches as it does in the Red-cockaded Woodpecker, which uses similar habitats (Brawn and Balda 1988, Walters et al. 1992, Slater et al. 2013). Nuthatches use all-purpose home ranges throughout the year and can spend $\geq 90\%$ of their time engaged in foraging behaviors (Yaukey 1997), suggesting that home-range selection may be influenced by food abundance in addition to nest site availability (Slater et al. 2013).

Study Site

We studied Brown-headed Nuthatches in the Pine-Bluestem Ecosystem Management Area of the Ouachita National Forest in Arkansas, USA (34.82°N, 94.21°W), where Brown-headed Nuthatches are common (James and Neal 1986, Hedrick et al. 2007). Current forest management includes prescribed fire, midstory reduction, and stand thinning to restore pine savannah-woodland conditions (Wilson and Watts 1999, Hedrick et al. 2007). The Pine-Bluestem Ecosystem Management Area is $\sim 101,000$ ha; $\geq 57\%$ has been treated with prescribed fire on ≥ 1 occasion and $\geq 7.5\%$ is in “substantially restored” condition (Hedrick et al. 2007).

Field Methods

Capture, marking, and radio-tracking. We captured, marked, and radio-tracked nuthatches from March 21 to May 20, 2011, and from March 12 to May 23, 2012. We captured nuthatches with mist nets and by using calls modified from Spencer (2009a, 2009b) in program Audacity (Audacity Development Team 2011). Each bird was banded with a unique combination 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 by Avian Biotech International (Tallahassee, Florida, USA)

and Kin Han (Department of Biology, University of Florida, Gainesville, Florida, USA). We also estimated sex using brood patches, cloacal protuberances, and behavioral cues (Pyle 1997).

We attached radio-transmitters to the two central rectrices using gel-type ethyl cyanoacrylate glue and an accelerant applied to the feathers using a cotton swab (Instacure⁺ and Instaset, BSI, Atascadero, California, USA; Mong and Sandercock 2007, Kesler et al. 2010). Transmitters weighed ~ 0.27 g (2–3% of a nuthatch's mass) and had battery lives of roughly 17 days in 2011 (model LB-2X, Holohil, Carp, Ontario, Canada; dimensions: 8 mm L \times 5.3 mm W \times 2.8 mm H) and 45 days in 2012 (model A2414, Advanced Telemetry Systems, Asanti, Minnesota, USA; dimensions: 12 mm L \times 5 mm W \times 2.5 mm H). Transmitter attachment took approximately 90 s and maximum holding time was < 5 min. Transmitters could be detected up to ~ 600 m away under field conditions. If a transmitter came off before the bird had been located ≥ 30 times, we attempted to recapture it and replace the transmitter by attachment to the two innermost remaining rectrices. We noted any abnormal behavior including nest abandonment subsequent to radio-tagging.

We located birds using the homing method with a handheld receiver and Yagi-Uda antenna (R-1000 receiver, RA-165 antenna, Communications Specialists, Orange, California, USA; Uda 1927, Yagi 1928, White and Garrott 1990). We attempted to locate each bird 1–3 times each day > 1 day postcapture until the transmitter failed, reached the end of its predicted battery life, or came off a bird with ≥ 30 locations. Successive locations were separated by > 1 hr to ensure behaviorally independent samples and to reduce temporal autocorrelation (Seaman et al. 1999), and we located birds in a different sequence during each tracking bout to ensure sampling throughout the day. We recorded bird locations with a handheld global positioning system (GPS; Garmin eTrex Vista HXC, Garmin, Olathe, Kansas, USA). We only located birds in conditions of low wind (< 15 km hr⁻¹) and no precipitation 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 define “attending the nest” to mean either perching within view of the nest tree while engaged in a combination of vigilance and preening behaviors, or being in the nest cavity. 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, in 2012 we revisited on ≥ 1 occasion home ranges that had been occupied in 2011 to verify that these sites were still occupied. We counted these

sites as occupied if we saw ≥ 1 color-banded bird in a 2011 home range at any point in 2012.

We searched exhaustively for two birds that were not located immediately by the homing method. 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 min at both the capture location and the nest site attempting to resight each missing bird. These two birds were not located despite these efforts, but had live transmitters during a roost check the same evening. Missing observations can result in 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 in a new home range, so we excluded its initial observations and analyzed only its post-movement space use (per Burt 1943). All other birds in the study were invariably located at will.

Developing utilization distributions. We developed a fixed-kernel utilization distribution for each bird (UD; Marzluff et al. 2004; e.g., Figure 1). The UD is a probability density function developed from location coordinates using kernel smoothing methods (Worton 1989, Millspaugh et al. 2006). Each UD was bounded by the 95% isopleth and we treated the area of each UD as the size of a nuthatch home range. Bandwidth selection was calculated using the plug-in method (Gitzen et al. 2006). We determined that birds with ≥ 17 locations 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 correlation between the number of locations 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 these locations (R Development Core Team 2012). We measured live trees and ground cover at each vegetation sampling point in 2011 and 2012. In 2012, we also measured snags at the vegetation sampling points, but we had to revisit locations where we had tracked birds in 2011 to measure snags and thus we measured snags at a different set of random locations than those used to collect the other vegetation data in 2011. 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 ArcGIS 9.3 (Environmental Systems Research Institute, Redlands, California, USA). We used the area-weighted mean snag density from up to 5 random locations within 150 m of a vegetation sampling point with a distance weighting power function of 2.

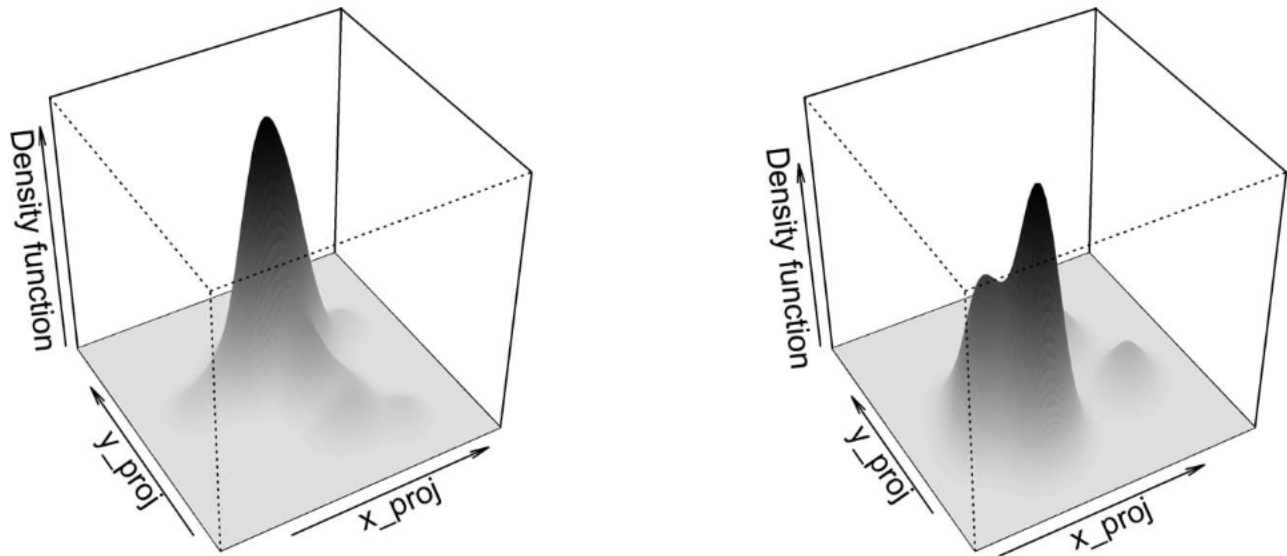


FIGURE 1. Illustrative utilization distributions (UDs) of Brown-headed Nuthatches in Arkansas, USA, 2011–2012. The UD on the left approximates the Rosenberg and McKelvey (1999) null model where resources are uniformly distributed and therefore selected as a function of distance from the nest site. The UD on the right is a more typical UD where resource configuration is patchy and resource selection is shaped by both distance from the nest site and resource configuration.

We measured tree diameters, grassy herbaceous cover, shrub cover, and snags at vegetation sampling points. We selected trees using a 10-factor wedge prism, measured the diameter at breast height (DBH) of all selected trees to the nearest 5 cm class with a Biltmore stick (Jackson 1911, Grosenbaugh 1958), 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 the distance to every visible snag detected from each point using a laser rangefinder (Bushnell Yardage Pro Sport, Overland, Kansas, USA) and measured each snag's DBH. Field observers visually inspected snags and classified them as fresh or punky by matching snag condition to a series of illustrations and criteria adapted from Maser et al. (1979). Fresh snags were freshly killed (stages 4 and 5); snags and punky snags were well-decayed with broken crowns (stages 6 and 7; 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. Tree stocking is a measure used by foresters to maximize timber production; thus, 100% stocking is optimal from a forestry perspective but higher values commonly occur (Johnson et al. 2009). We calculated percent stocking from our tree diameters using equations for mixed hardwoods (Gingrich 1967 in Johnson et al. 2009) and Shortleaf Pine (*Pinus echinata*; Rogers 1983 in Johnson et al. 2009). 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. 1993, Fiske and Chandler 2011). We pooled data from a concurrent study of occupancy and abundance in the same area, and developed separate models for fresh and punky snags with DBH ≥ 10.2 cm. We fitted hazard-rate and half-normal detection models with appropriate site-level covariates for each snag class. As covariates, we considered local shrub cover and percent tree stocking for punky snags, which can be shorter than surrounding shrubs. We only considered percent tree stocking for fresh snags, which are invariably taller than surrounding shrubs but may be harder to see in dense stands. We calculated snag density estimates for each point by correcting our observed values based on the best-supported detectability model for each snag type.

We extracted years since prescribed fire and fire season (season in which fire occurred, growing: May–October, or dormant; Sparks et al. 1998, Beyer 2004, USDA Forest Service 2012) for each point from a GIS database. Locations where fire last occurred ≥ 10 yr ago were coded as 10 to prevent high leverage of model results by outliers; stands ≥ 10 yr after a prescribed fire and stands with no history of prescribed fire have a similar structure. We classified a home range as having been impacted by a growing season burn if ≥ 1 vegetation sampling point 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.

TABLE 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.

| Covariate | Description | Intensity of use | Home range size |
|------------------|--|------------------|-----------------|
| Distance | Ln(Distance of sampling location from nest), m | ✓ | |
| Grass | Grassy herbaceous cover, % | ✓ | ✓ |
| Pine | Proportion of total stocking rate that was pine, % | ✓ | ✓ |
| Stocking | Total tree stocking rate, % | ✓ | ✓ |
| Punky snags | Punky snag density, stems ha ⁻¹ | | ✓ |
| Fresh snags | Fresh snag density, stems ha ⁻¹ | ✓ | |
| Fire season | Season in which fire occurred, growing vs. dormant | ✓ | ✓ |
| Years since fire | Most recent fire, 0–10 years | ✓ | |

Analyses

Home range size and resource availability. For each bird, we fit lognormal linear models relating home range size to mean resources available (Table 1; Barton 2012). We fit all linear combinations of models with covariates we hypothesized to be associated with home range size for a total of 32 models. Our choice of covariates was based on a thorough review of nuthatch studies, which indicated that snags, tree stocking, tree species, and time since prescribed fire were influential (Slater et al. 2013). We were concerned that previous studies did not distinguish between different snag types and their respective functions, and decided to treat them separately. We excluded fresh snags, which are of unknown value to nuthatches, from this analysis, but we included punky snags, which are used for nesting and thus may be a defended resource. We also considered fire season because of increased interest in growing-season prescribed fire and its effects (Sparks et al. 1998). There was very little variation in years since fire among home ranges (1–2 yr), so we concluded that modeling years since fire as a function of home range size was inappropriate.

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. The resource utilization functions were linear mixed models in which we treated the standardized height of the UD at each randomly selected point as a normally distributed response variable (Bates et al. 2012). We used mixed models and included individual identity as a random effect to account for nonindependent responses within individual UDs (Bolker et al. 2009). We fit a priori models that included log-transformed distance to nest in all models and all single and additive combinations of relevant habitat and fire management covariates (Table 1) as linear fixed effects, for a total of 64 models (Burnham and Anderson 2002). Our choice of covariates was again based upon findings of prior studies, a desire to treat fresh and punky snags separately, and a concern for the possible effects of growing-season prescribed fire. We did not consider density of punky snags, which serve only as nest sites for nuthatches. Thus, any correlation between intensity of space use and punky

snags would have been either spurious or an artifact of territoriality. We considered fresh snag density instead, hypothesizing that they might be a food source.

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, i.e. 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.

Model evaluation and predictions. We ranked models for all analyses using Akaike's Information Criterion adjusted for small sample size (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). We also did not consider models with ΔAIC_c less than or equal to that of the null model to be competitive. Results from 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) based on all competitive models. Confidence intervals for the mixed-model analysis and associated predictions were based on 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 for inclusion the ~85% confidence intervals of these covariates should not include zero (Arnold 2010). We refer to these covariates as “less supported” if their 95% confidence intervals overlapped zero. We considered 95% confidence intervals that did not overlap zero as additional evidence that a given covariate influenced nuthatch space use (hereafter “more supported”).

We present predicted 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

TABLE 2. (A) 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; and (B) summary of vegetation and snag characteristics sampled at 965 sampling points in 22 Brown-headed Nuthatch home ranges in Arkansas, USA, 2011–2012. Variables are described in Table 1.

| | %Shrubs | %Grass | %Litter | %Pine | %Stocking | Fresh snags ha ⁻¹ | Punky snags ha ⁻¹ |
|---|---------|--------|---------|--------|-----------|------------------------------|------------------------------|
| (A) Resource characteristics of home ranges | | | | | | | |
| 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 |
| (B) Resource characteristics of all sampled points | | | | | | | |
| Mean | 35.46 | 38.45 | 26.09 | 75.14 | 26.68 | 1.59 | 2.47 |
| σ | 24.01 | 22.76 | 25.60 | 33.41 | 16.13 | 2.27 | 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 | 22.61 | 73.49 |

1999). Model fit for the global lognormal regression model was assessed by ANOVA test and \hat{c} , a measure of overdispersion. Values of $\hat{c} > 1$ indicate unmodeled heterogeneity in the data, suggesting that relevant covariates may have been left out (Etterson et al. 2009). All analyses were conducted in R version 2.15.2 (R Development Core Team 2012).

RESULTS

We captured 40 nuthatches and attached transmitters to 30. We excluded 8 radio-tagged birds from analyses because they were either not adequately sampled or were not independent because they were part of the same group. The remaining 22 nuthatches were from different groups and we relocated them 17–63 times (mean: 42). One group abandoned an incomplete clutch after transmitter attachment and several antennae were preened. No other behavioral effects of transmitter attachment were observed. All groups were territorial and attempted to breed. All groups tracked in 2011 remained in the same home ranges in 2012. Eighteen of 22 groups were composed of ≥ 3 members. Our sample was 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 11–41% total tree stocking and 41–91% pine (Table 2). Both fresh and punky snags averaged < 2.5 ha⁻¹ across home ranges (Table 2). Resources such as snags were more variable among sampling points within home ranges than among averages across home ranges (e.g., punky snags ranged from 0–73 ha⁻¹, $n = 965$; Table 2).

Home ranges were 0.3–47.6 ha (median: 7.1 ha, $n = 22$). Fourteen of 22 (64%) nuthatch utilization distributions had two centers of activity, indicating that birds were primarily using two distinct locations. There was no evidence of lack of fit of the global model predicting home range 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 Table 6). Home range size had a more supported relationship with percent pine and punky snag density, a less supported relationship with percent grassy herbaceous cover, and no apparent relationship with total stocking or fire season (top three models, $w_i = 0.85$; Table 3). There was also support for the null model ($\Delta AIC_c = 2.01$, $w_i = 0.15$; Table 3). Model-averaged predicted home range size declined 71% and 77% across the range of punky snag density and percent pine, respectively (Figure 2). Grassy herbaceous cover was associated with larger predicted home range sizes, which increased by 113% when grassy herbaceous cover was maximized (Figure 2). Model-averaged coefficients \pm SE and 95% confidence intervals for pine, punky snags, and grass were: pine, -0.039 ± 0.015 , -0.068 to -0.010 ; punky snags, -0.303 ± 0.129 , -0.556 to -0.050 ; grass, 0.028 ± 0.015 , -0.001 to 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 ($\chi^2_6 = 38.68$, $P < 0.001$). We fitted 64 third-order resource selection models (Appendix Table 7) and three were competitive for inference (Table 4). Distance from nest, fresh snag density, and years since last fire had a more supported association with nuthatch use, whereas percent pine, total stocking, and grassy herbaceous cover had a less supported association, and fire season had no apparent relationship (Table 5). Fresh snag density, percent pine, and grassy herbaceous cover were positively associated with relative probability of use (Figure 3), whereas use declined with increasing total stocking and years since prescribed fire (Figure 3). Resources differed in their apparent importance to nuthatches. For example, the standardized model-averaged coefficient for fresh snags

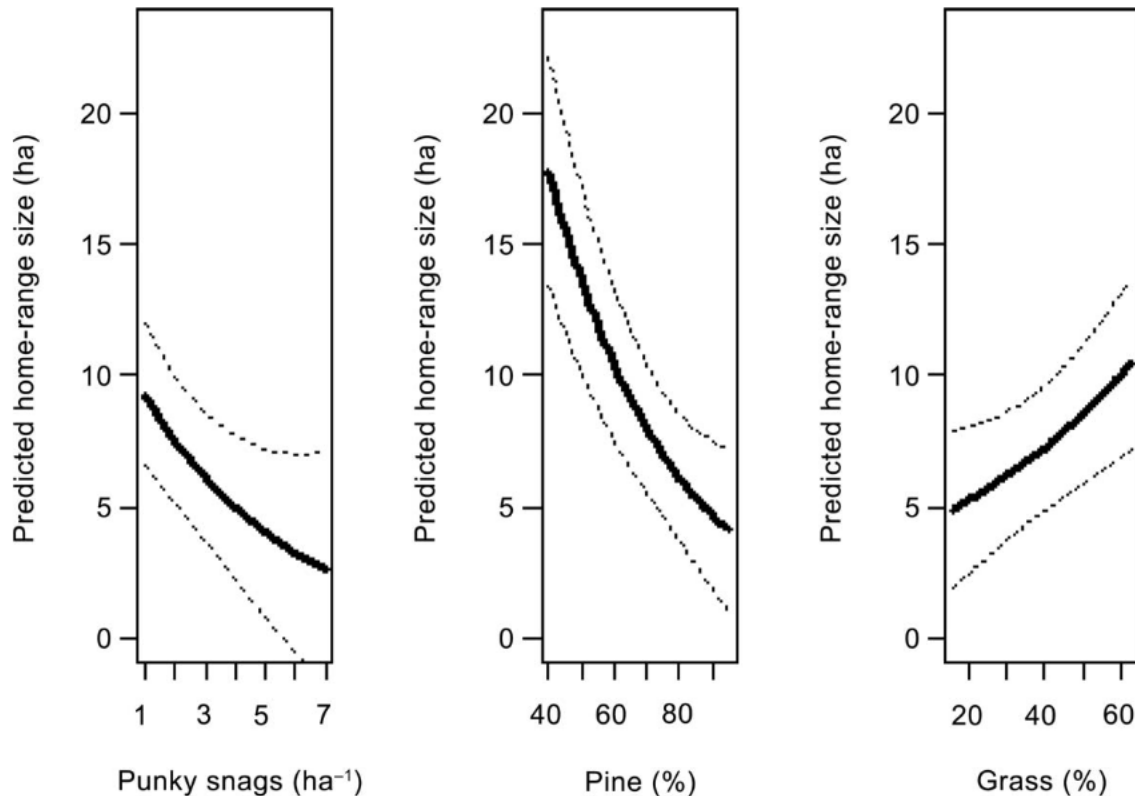


FIGURE 2. Model-averaged predicted home range size at different levels of punky snag density, percent pine, and percent grassy herbaceous cover in Brown-headed Nuthatch home ranges in Arkansas, USA, 2011–2012. Dotted lines are 95% confidence intervals.

was 2.4 times larger than the same coefficient for total stocking (Table 5).

DISCUSSION

Home range size of Brown-headed Nuthatches was related to punky snags suitable for nesting, pine trees needed for foraging, and grassy herbaceous cover that might influence nuthatch invertebrate prey (James et al. 2001, Slater et al. 2013). Space use within home ranges was heavily dominated by the influence of a central place, yet several resources were also associated with nuthatch use. Nut-

hatches avoided areas within home ranges where fire had not occurred and where tree stocking was high, preferring abundant recently killed snags and grassy herbaceous cover. Most nuthatches had two centers of activity within their home ranges. We believe that these activity centers are indicative of centers of foraging activity, because we only recorded locations for nuthatches that were not attending the nest site and nuthatches were nearly always actively foraging when located. The high level of foraging activity that we observed is consistent with the only extant study of the subject (Yaukey 1997).

TABLE 3. Support for models relating home range size of Brown-headed Nuthatches to mean resource metrics and recent prescribed fire in Arkansas, USA, 2011–2012. K is the number of parameters in each model, Loglik is the negative log-likelihood, ΔAIC_c is the difference in corrected Akaike's Information Criterion value for each model from the top-supported model, and w_i is the Akaike weight for each model. Only the null model and models with $\text{AIC}_c \leq$ the null model are presented.

| Model ^a | K | Loglik | ΔAIC_c ^b | w_i |
|------------------------|-----|--------|-----------------------------------|-------|
| Pine+punky snags+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 |

^a Covariates are described in Table 1.

^b The AIC_c value of the top model was 62.5.

TABLE 4. 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. K is the number of parameters in each model, Loglik is the negative log-likelihood, ΔAIC_c is the difference in corrected Akaike's Information Criterion value for each model from the top-supported model, and w_i is the Akaike weight for each model. Only models within 4 AIC_c of the top model are presented in comparison with the distance and null models.

| Model ^a | K | Loglik | ΔAIC_c ^b | 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 |

^aCovariates are described in Table 1.

^bThe AIC_c value of the top model was 2460.7.

The distribution of suitable nest sites may limit the carrying capacity of managed pine-bluestem habitats for Brown-headed Nuthatches. For 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 that we suspected to be limiting, punky snags, had a strong relationship with nuthatch home range size. We hypothesize that the mechanism for this relationship is territoriality; nuthatches may defend a surfeit of cavities throughout the year, which would then be available for future use.

We also found support for a relationship between home range size and percent pine. Home ranges decreased 77% across the range of percent pine. A post-hoc analysis, however, indicated that high punky snag density co-occurred only with low percent pine values (Figure 4). 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. Also, there may be a tradeoff between nest sites and foraging substrates that affects home range selection in nuthatches. Predicted home range size increased 113% across the range of observed values for grassy herbaceous cover. However, the relationship was in the opposite direction to that hypothesized and the 95% confidence interval overlapped zero. Grassy herbaceous cover also had a less-supported,

weak positive association with nuthatch space use within home ranges (Table 5) and no apparent relationship with nuthatch site occupancy (Stanton 2013). Overall, the evidence suggests that grassy herbaceous cover may be unimportant to Brown-headed Nuthatches, in contrast to its importance to Red-cockaded Woodpeckers, which are often found in similar fire-maintained habitats (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 and a confidence interval that did not overlap zero (Table 5). However, fine-scale variation in resources also influenced space use by nuthatches as shown by overall model selection results and model-averaged confidence intervals that did not overlap zero for several covariates (Table 5). Pine savannahs and woodlands can look very homogeneous 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), and it is difficult for us to measure 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

TABLE 5. Model-averaged standardized and unstandardized parameter estimates and unstandardized standard errors for covariates relating intensity of space use of 22 Brown-headed Nuthatches to resource and fire management metrics in Arkansas, USA, 2011–2012. Covariates are described in Table 1.

| Parameter | β (standardized) | β (unstandardized) | 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 |

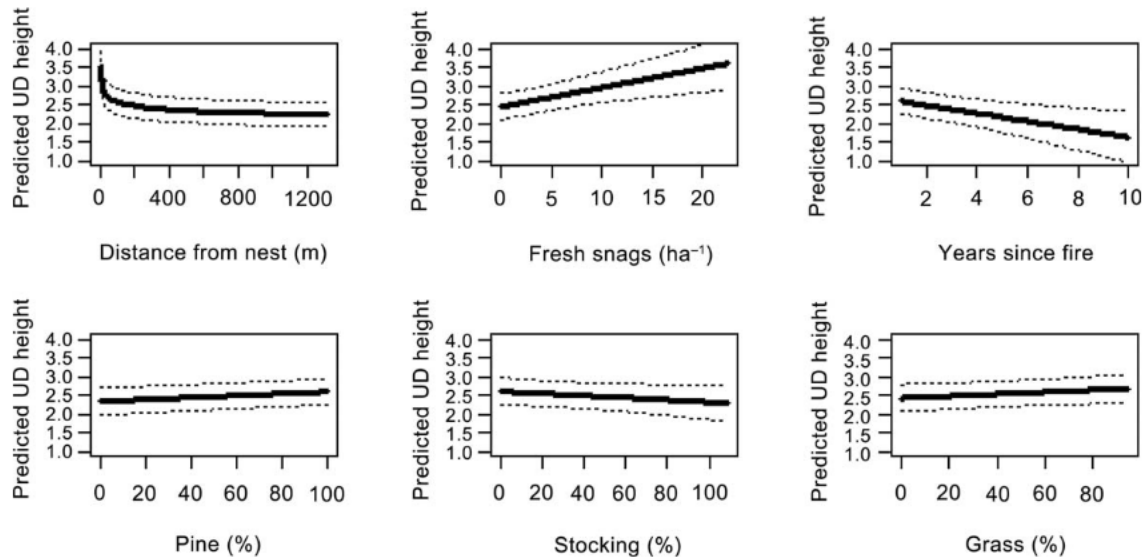


FIGURE 3. Predicted utilization distribution (UD) heights (a measure of relative probability of use) at different levels of habitat and fire management covariate values within Brown-headed Nuthatch home ranges in Arkansas, USA, 2011–2012. The y-axis range is minimum–maximum and units are SDs. Dotted lines are 95% confidence intervals. Covariates are described in Table 1.

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; that it was supported in our analyses in addition to vegetation structure 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 prey taken by nuthatches (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 (e.g., Figure 1). Nuthatches were almost invariably foraging when located, so we believe this pattern was likely generated by foraging behavior. Foraging in two distinct locations may be common for nesting passerines, as it is for seabirds (e.g., Jakubas et al. 2012). When animals 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).

We did not study prey availability, but wanted to explore post-hoc whether there were any differences between home ranges with one or two centers of activity. We used Welch's *t*-tests and Holm's correction for multiple comparisons to determine whether home ranges differed in size or resource density according to how many centers of activity were present (Welch 1947, Holm 1979). We found that home ranges with two centers of activity had lower mean tree stocking, 24% versus 32%, a possible

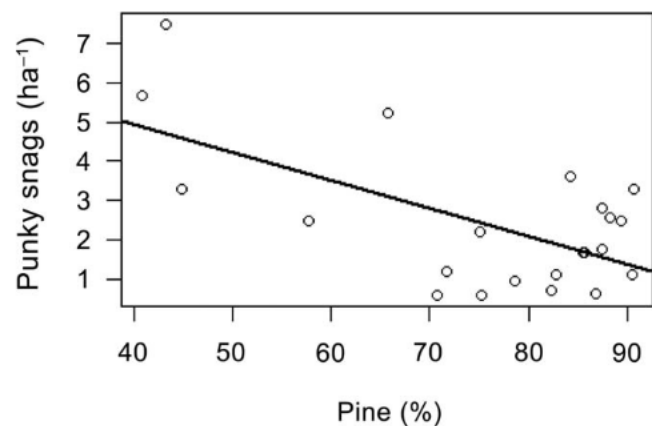


FIGURE 4. Observed mean percent pine within 22 Brown-headed Nuthatch home ranges in Arkansas, USA, 2011–2012, plotted against mean observed punky snag density. The best-fit line is from a linear regression ($r^2 = 0.39$, 20 df, SE = 0.02, $P < 0.01$).

indicator of lower habitat quality for a species that forages on trees ($t_{17,2} = 3.1$, $P = 0.04$). However, the difference was small and no other differences were apparent (all $P > 0.05$).

Our sample was markedly male-biased ($\geq 68\%$). Male nuthatches are more aggressive and deliver food to incubating females (Slater et al. 2013), making them far easier to capture. However, populations of Brown-headed Nuthatches can be male-biased (Norris 1958). Thus, the bias in our sample may not be entirely attributable to our capture methods. Regardless, sex differences in resource selection can occur and our results may not apply to females (Manly et al. 2010). Likewise, molecular sexing from feathers was unsuccessful in 18% of cases. Future researchers should investigate improved sexing and capture methods to achieve a more representative sample.

Brown-headed Nuthatches have been declining in abundance, with the greatest declines at the southern limits of their range (Sauer et al. 2012). The species has simultaneously extended its range northward, perhaps in response to climate change and habitat restoration (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 recolonization of suitable habitat will occur in places such as the Missouri Ozarks (~400 km northeast of our study area) without human assistance (Slater 1997, Haas et al. 2010, Stanton 2013). 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 woodlands and savannahs require ongoing active management (Wright and Bailey 1982). The relationships that we found support the value of prescribed fire and other active pine restoration efforts for Brown-headed Nuthatches during the breeding season.

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Commission (permits # 030720114 and 010920121), and the U.S. Geological Survey (permit # 23574); we also received written authorization for our research from the Ouachita National Forest (File code 2620/2700). Research protocols were approved by the Institutional Animal Care and Use Committee of the University of Missouri (reference # 7006). Use of trade, product, or firm names does not imply endorsement by the U.S. Government.

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APPENDIX

See Table 6 and Table 7.

TABLE 6. 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. Covariates are described in Table 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 | <i>K</i> | Loglik | ΔAIC_c^a | 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 |
| 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 | 0.00 |
| Pine+stocking+fire season | 5 | −28.15 | 7.60 | 0.00 |
| Pine+punky snags+grass+stocking+fire season | 7 | −24.09 | 7.73 | 0.00 |
| Pine+grass+stocking+fire season | 6 | −26.74 | 8.63 | 0.00 |
| Punky snags+grass+stocking+fire season | 6 | −26.86 | 8.87 | 0.00 |

^aThe AIC_c value of the top model was 62.5.

TABLE 7. Complete ranked candidate model set relating standardized utilization distribution height at a point (a measure of relative probability of use) to available resources in Arkansas, USA, 2011–2012. Covariates are described in Table 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 | <i>K</i> | Loglik | ΔAIC_c^a | 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 |

TABLE 7. Continued.

| Model | K | Loglik | ΔAIC_c^a | w_i |
|--|---|----------|------------------|-------|
| 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 |
| 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 |
| 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 |

^a The AIC_c value of the top model was 2460.7.