Research Note

Environmental Factors Affecting Productivity of Brown-Headed Nuthatches

JOHN D. LLOYD,[1] *Ecostudies Institute, 512 Brook Road, Sharon, VT 05065, USA*

GARY L. SLATER, *Ecostudies Institute, P.O. Box 703, Mount Vernon, WA 98273, USA*

ABSTRACT Understanding the link between habitat use and components of fitness can yield useful insight into the environmental conditions necessary for population maintenance and can help promote effective habitat management. This information is especially important for species that are in decline or otherwise of conservation concern. Populations of brown-headed nuthatches (*Sitta pusilla*), an obligate cavity nester, have declined throughout their range, primarily due to extensive habitat loss and degradation. To help guide habitat management for this species, we identified habitat features associated with variation in the number of offspring fledged within 2 populations in southern Florida, USA. The most important predictor of productivity was the date on which a nest attempt began, with earlier nests producing more fledglings. The number of large pine (*Pinus elliottii* var. *densa*) snags and, to a lesser extent, the number of small pine trees surrounding a nest site were positively associated with productivity. We recommend that land managers in southern Florida focus on providing abundant large pine snags because doing so will increase productivity and also may increase nest-site availability and the percentage of individuals that breed each year. Prescribed burning may be an effective way to increase the abundance of large pine snags; however, land managers should exercise caution when doing so because of the trade-off between snag recruitment and snag consumption that accompanies the use of fire. We lack the data required to predict the fire-return interval that optimizes this trade-off, but until these data are available we recommend increasing the spatial heterogeneity in fire-return interval and lengthening the fire-return interval in some areas to 5–6 years. (JOURNAL OF WILDLIFE MANAGEMENT 71(6):1968–1975; 2007)

Habitat selection results in nonrandom, species-specific patterns of resource use. Within a species, variation among individuals in the use of habitat features often is associated with variation in components of fitness (Fretwell and Lucas 1970, Morris 1991, Badyaev 1995, Martin 1998, Murphy 2001). Consequently, examining the relationship between habitat use and fitness components can yield important insight into the environmental conditions necessary for population maintenance (Martin 1992). This information can be used to develop management strategies for plant or animal populations.

Identifying appropriate features for habitat management is especially important for species that are in decline or otherwise of conservation concern. The brown-headed nuthatch (*Sitta pusilla*), a cavity-nesting species of the open pine (*Pinus* spp.) forests of the southeastern United States, has experienced significant long-term population declines (Sauer et al. 2005) that have led to local extinctions (Withgott and Smith 1998) and is a species of conservation concern for the United States Fish and Wildlife Service (2002). Habitat degradation is thought to be the primary cause of population declines (Withgott and Smith 1998). Patterns of habitat use by brown-headed nuthatches are relatively well described; abundance is higher in older pine forests with open understories, relatively large trees, and numerous snags (Conner et al. 1983, O'Halloran and Conner 1987, Wilson et al. 1995, Slater 1997, Wilson and Watts 1999), but little is known of how variation in habitat affects survival or reproduction. However, the success of efforts to restore and maintain high-quality habitat for brown-headed nuthatches requires an understanding of how vital rates are likely to respond to habitat management, knowledge that can only be gained through direct examinations of reproduction or survival.

We examined how variation in vegetation structure at the nest site (density of small and large pine trees, density of pine snags, and % cover of hardwood shrubs), fire history, and hydrological conditions affected productivity of brown-headed nuthatches in the pine rocklands of southern Florida, USA. The objectives of this study were 2-fold: to identify habitat features that were associated with variation in productivity and to predict how variation in these habitat features would affect productivity. In addressing these objectives, we sought to provide land managers with information on how habitat can be manipulated to improve productivity and, in turn, stem the widespread population declines of this species.

STUDY AREA

We collected data on 2 brown-headed nuthatch populations: a population reintroduced in 1997 to Long Pine Key, Everglades National Park (25.3°N, 80.7°W), and the source population for the reintroduction, 40 km away in Raccoon Point, Big Cypress National Preserve (25.9°N, 80.9°W). Both sites were located in the pine rocklands, a fire-dependent, savannah-like ecosystem restricted to southern Florida and portions of Cuba and the Bahamas (Snyder et al. 1990). Pine rocklands were dominated by a single canopy species, South Florida slash pine (*Pinus elliottii* var. *densa*), and typically had an open understory supporting a diverse mix of tropical hardwoods, palms, and herbaceous plants. Average annual precipitation in this region was 130–150 cm,

[1] *E-mail: jlloyd@ecoinst.org*

with approximately 80% of rainfall occurring during the wet season, typically May–October (Snyder et al. 1990).

Long Pine Key was an 8,100-ha upland area within Everglades National Park that contained approximately 4,600 ha of pine forest (Snyder 1986). Long Pine Key was the only remaining area of pine rockland in Everglades National Park. Other plant communities embedded within the relatively continuous pine forest included *Muhlenbergia* prairie, hardwood hammock, and cypress (*Taxodium* spp.) forest. The pine forest was even-aged, a result of extensive logging in the 1930s and 1940s, and snags were abundant due to the widespread tree mortality associated with Hurricane Andrew in 1992. Since the mid-1990s, Everglades National Park has instituted an aggressive fire management program to reduce an overdeveloped shrub and palm (*Sabal palmetto* and *Serenoa repens*) understory and the resultant high fuel loads that have arisen after years of fire suppression and Hurricane Andrew. The overall target for fire-return intervals during this study was 3 years, although most areas were burned more frequently during the early years of the study in an effort to reduce high fuel loads that accumulated after Hurricane Andrew.

Raccoon Point contained approximately 9,000 ha of unlogged, old-growth pine forest within a cypress mosaic. Since 1992, a fire program that mimics the natural timing and frequency of fire has been maintained, with a fire-return interval of 3–6 years. This fire regime, coupled with the site's hydric condition, has resulted in a well-developed herbaceous understory with a moderate amount of saw palmetto (*Serenoa repens*) and hardwoods. Brown-headed nuthatches were moderately abundant at this site (1.1 individuals/10 ha [Slater 1997]; median abundance from 12 studies summarized in Withgott and Smith 1998 = 1.2 individuals/10 ha).

METHODS

We collected data in each of the breeding seasons from 1998 to 2003: 4 years during which individuals were translocated from Raccoon Point to Long Pine Key and 2 years posttranslocation. In Long Pine Key, we located brown-headed nuthatch breeding territories by walking systematic transects and using playback vocalizations in areas where individuals were released and, in subsequent years, in territories that had been established postrelease. As the population grew, we also conducted surveys in unoccupied areas where habitat appeared suitable. We used similar methods to locate nests within suitable habitat (i.e., patches of pine forests) at Raccoon Point. We initiated nest searches in both areas in mid-February, when individuals typically begin excavating nest cavities. However, at both sites, we also took advantage of the year-round territoriality of this species by conducting observations throughout the winter to ensure that we did not miss any breeding attempts.

Once we noted excavation and nest-building behaviors, an observer checked nest sites regularly until egg laying began. We defined a nesting attempt as beginning upon completion of the clutch, as indicated by incubation behavior. We

observed nests, usually for a 30-minute observation period, to determine status every 3–5 days until nestlings fledged or the nest failed. To avoid disturbing the birds, we observed activity at nests through binoculars from a distance of approximately 40 m. At this distance, we found that the presence of an observer had no obvious effect on adult breeding behavior (e.g., adults did not abort incubation feeding or nestling feeding attempts). Most adults in both populations were color banded, and thus we were able to follow individuals throughout the breeding season to determine if renesting occurred. Renesting was relatively rare, accounting for only 9.1% ($n = 13$) of all observed nesting attempts, and no pairs were known to make more than 2 nesting attempts in a season. Most renesting attempts (77%; $n = 10$) occurred following nest failure. We excluded renesting attempts from this analysis because they generally took place close to the original nest cavity, or very rarely in the same nest cavity, and thus may not reflect an independent trial of the effect of habitat on breeding productivity. We considered nesting attempts in the same territory in different years to be independent because brown-headed nuthatches almost always excavate new cavities in different trees (Withgott and Smith 1998).

We calculated productivity as the number of young fledged per nesting attempt. We focused on productivity because mark–recapture estimates of apparent adult survival did not vary among years, whereas productivity was highly variable among years and was a strong predictor of population size in the following year (G. L. Slater, Ecostudies Institute, unpublished data). Thus, it is a suitable metric for identifying habitat features that may affect population growth rate. We are confident that we found all nests within the study areas and that our estimates of productivity are unbiased: population sizes were small, most adults were color banded (77% [$n = 103$] of nest attempts had ≥1 banded bird), individuals are sedentary and occupy year-round territories, and we monitored territories intensively throughout much of the year. Because we found nests early in the nesting cycle—we located nearly all nests during cavity excavation or nest construction—our sample is not biased towards successful nests.

We examined variation in productivity as a function of vegetation structure around the nest site, fire-return interval, and hydrology. We chose to examine the effect of these variables on productivity because previous studies had shown them to be important in nest-site selection, or because our experience in this system suggested they might affect productivity. We did not consider characteristics of the nest tree or nest cavity (e.g., orientation or ht) because previous work in this system indicated that these variables were not useful in describing patterns of habitat selection or in distinguishing successful and unsuccessful nests (Slater 1997). We also chose to exclude landscape-level factors (e.g., patch size or distance to habitat edge) that may have influenced productivity because we were primarily interested in identifying habitat features that are amenable to management. Most of the variation in landscape-level features in

our study area arises from the naturally patchy distribution of plant communities in this ecosystem and is therefore not a suitable target for management.

We quantified vegetation structure around the nest site by measuring the following variables: the number of large pines (≥15 cm dbh), small pines (<15 cm dbh), and large pine snags (≥15 cm dbh) within an 11.3-m radius circle around the nest tree and the percent cover of hardwood shrubs (defined as all hardwoods 1.5–5 m above the ground), estimated visually, within a 1.8-m radius circle around the nest tree. We determined the number of fires within the past 5 years at each nest site using fire-history data obtained from Big Cypress National Preserve and Everglades National Park (National Park Service 2005a, b). We included 2 hydrology variables: mean water depth (i.e., stage ht minus elevation at the nest tree) on each territory during the winter prior to the breeding season (Dec and Jan) and during the breeding season (Mar–May). We estimated mean water depth for each period and each territory by determining mean daily stage height from 4 gauging stations surrounding Long Pine Key and one gauging station in Raccoon Point, and subtracting that value from the elevation at the nest tree. We determined the average elevation of each territory from elevation grids created from the United States Geological Survey (USGS) high-accuracy elevation data program (USGS 2006). In addition to the habitat variables, we also examined whether productivity varied as a function of the date on which incubation began, because seasonal declines in reproductive success are commonly reported for birds (Nilsson 1989, Hochachka 1990). We attempted to capture additional unexplained variation by including a dummy variable for year in our models.

Assuming that previously documented habitat preferences were adaptive, we expected a positive relationship between productivity and the number of large pines and large pine snags around the nest site. We also predicted a negative relationship between productivity and the number of small pines and the percent cover of hardwood shrubs. Furthermore, because the abundance of large snags and the density of mid- and understory vegetation are affected by the frequency of fire (Conner 1981, Wilson and Watts 1999), we expected a positive relationship between fire-return interval and productivity. Finally, although no previous study has examined links between hydrology and habitat selection in brown-headed nuthatches, we predicted that hydrology might have direct and indirect effects on food availability, which might in turn influence breeding productivity. For example, South Florida slash pine utilize relatively deep groundwater sources (Ish-Shalom et al. 1992) and thus seed production might be reduced when water levels are low, in turn reducing food availability and productivity of brown-headed nuthatches. Exceptionally low water levels might also reduce the abundance of insects (Wolda 1978), another important food source for brown-headed nuthatches.

We analyzed the relationship between productivity and habitat features using an information-theoretic, model-selection approach (Burnham and Anderson 1998). We created a candidate set of 10 models, based on linear combinations of variables, that we believed could reasonably explain variation in productivity based on our knowledge of the ecology of brown-headed nuthatches (Table 1). Every model contained a term for year and a term for date of incubation, and the first model contained only these terms. We included this most simple model to evaluate the degree to which adding information about habitat conditions improved the predictive power of our models. The next 2 models that we evaluated were also simple: one included a term for 5-year fire frequency (model 2), which we believed might influence productivity of brown-headed nuthatches through its effect on the plant community, and the other included a term for the number of large pine snags (model 3), which, as the factor limiting the availability of nest sites, might be sufficient by itself to explain variation in productivity. From these simplified models, we next evaluated models that considered productivity as a function of the 2 main elements through which we quantified nest-site vegetation: overstory vegetation (no. of large pines and large pine snags; model 4) and understory vegetation (hardwood shrub cover and no. of small pines; model 5). We evaluated these models separately to determine whether a more simplified description of nest-site vegetation might adequately explain variation in productivity. The next model (model 6) explained variation in productivity as a function of fire frequency, which can influence all of the vegetation variables that we considered important, and hydrology, which might modulate the effect that fire has on plant communities (e.g., Lockwood et al. 2003). In essence, this model suggested that broad categorical descriptions of habitat conditions (i.e., fire-return interval and $\bar{x}$ water level) could adequately capture the same variation described by our more detailed vegetation measurements. The next 3 models (models 7, 8, and 9) started with all of our nest-site vegetation measurements and added, respectively, effects of

Table 1. Candidate models explaining variation in productivity of brown-headed nuthatches in southern Florida, USA, from 1998 to 2003.

Model[a,b]	Model no.
Yr + date	1
Yr + date + fire frequency	2
Yr + date + no. of large pine snags	3
Yr + date + overstory nest-site vegetation	4
Yr + date + understory nest-site vegetation	5
Yr + date + hydrology + fire frequency	6
Yr + date + all nest-site vegetation	7
Yr + date + all nest-site vegetation + fire frequency	8
Yr + date + all nest-site vegetation + hydrology	9
Global	10

[a] The following variables were considered: yr, date that incubation began (date), no. of small pines (small pines), no. of large pines (large pines), % cover of hardwood shrubs (shrub cover), no. of large pine snags (large pine snags), 5-yr fire frequency, and water levels during the breeding (Mar–May) season and winter (Dec and Jan).

[b] All nest-site vegetation is small pines, large pines, shrub cover, and large pine snags; hydrology is breeding season and winter water levels; understory nest-site vegetation is small pines and shrub cover; and overstory nest-site vegetation is large pines and large pine snags.

Table 2. Observed values for habitat variables included in models of productivity for brown-headed nuthatches in southern Florida, USA, from 1998 to 2003.

Variable	$\bar{x}$	Range
No. of large pines[a]	5.7	0, 19
No. of large pine snags[a]	2.3	0, 11
No. of small pines[a]	1.4	0, 17
% cover by hardwood shrubs[b]	3.3	0, 70
No. of fires in previous 5 yr	1.4	0, 4
Water stage ht (m)		
Breeding season (Mar–May)	−0.7	−1.5, −0.2
Winter (Dec–Jan)	−0.3	−1.1, 0.6

[a] Measured in a 11.3-m-radius circle around the nest.
[b] Measured in a 1.8-m-radius circle around the nest.

fire and hydrology. We added the effects of fire and hydrology to models 8 and 9 because we were uncertain whether these terms would provide any additional information not already provided by the nest-site vegetation measurements. Finally, we tested a global model that included all of our variables.

We applied the following transformations to meet the assumptions of multiple linear regression: log (small pines, large pine snags, and date of incubation), square root (large pines), and arcsine (% cover of hardwood shrubs). We assessed the linearity of the relationship between dependent and transformed independent variables by examining plots of observed versus predicted values, we assessed normality via normal probability plots, and we verified homoscedasticity with plots of residuals versus predicted values. We also assessed the extent of multicollinearity among our independent variables by first calculating Pearson coefficients for all pair-wise comparisons, using a sequential Bonferroni correction to maintain the table-wide $\alpha = 0.05$ (Rice 1989). Next, we calculated a variance inflation factor (VIF) for each variable (Neter et al. 1996). Neter et al. (1996) suggested that a VIF ≥ 10 indicates the potential for problems with multicollinearity, but we adopted the more conservative rule of Graham (2003) that multicollinearity poses a problem for any VIF ≥ 2.

We evaluated the degree of support for each model using Akaike's Information Criterion (AIC; Akaike 1973), as corrected for small sample size (AIC$_c$; Burnham and Anderson 1998), and normalized Akaike weights (w_i). We based our inferences about sources of variation in productivity by considering models included in a 95% confidence set that we defined by summing w_i from largest to smallest until we reached 0.95 (Burnham and Anderson 1998). We only conducted further analyses with the suite of models in the 95% confidence set.

We interpreted the strength of each predictor variable by estimating model-averaged regression coefficients and 95% confidence intervals based on unconditional standard errors (Burnham and Anderson 1998). We calculated model-averaged regression coefficients as the average value of the regression coefficient across all models, weighted by w_i for each model. We considered variables for which the 95% confidence interval around the model-averaged regression

coefficient included zero unimportant in explaining variation in productivity. Using model-averaged estimates of regression coefficients allowed us to incorporate model-selection uncertainty and provided a more robust indication of the effect of each variable on productivity (Anderson et al. 2000). Unless otherwise noted, values presented are means with upper and lower 95% confidence interval limits.

We examined how changes in important predictor variables (i.e., those for which the 95% CI around the model-averaged regression coeff. did not overlap zero) affected productivity by substituting observed values for one variable while holding all other independent variables in the model constant at their observed mean (e.g., Stephens et al. 2005). We repeated this process for each model, and then calculated an overall estimate of productivity using the estimates generated from each model in the 95% confidence set, as weighted by w_i for each model (Burnham and Anderson 2002).

RESULTS

We located and monitored 141 nests during the course of this study, 50 in Long Pine Key and 91 in Raccoon Point. Relatively few nests failed (35%); nests generally produced 4 (22%), 3 (15%), or 2 (20%) fledglings. Nests with 1 (5%) or 5 (3%) fledglings were much less common. We could not determine clutch size for all nests, and thus it is unclear how much of the variation in productivity among successful nests is due to variation in clutch size versus attrition during the nesting cycle. With the exception of a few cases in which we observed the depredation of nests, we did not know the causes of nest failure. On average, successful nests produced 3.0 fledglings (95% CI = 2.7–3.2), and observed productivity from successful nests was similar in the reintroduced Everglades population at Long Pine Key (3.1 fledglings; 95% CI = 2.7–3.4) and the Big Cypress source population at Raccoon Point (2.9 fledglings; 95% CI = 2.6–3.2). Across all nests located during the course of the study, including those that failed, average productivity was 1.9 fledglings (95% CI = 1.7–2.2); total average productivity was similar at both sites (Long Pine Key: 2.0, 95% CI = 1.6–2.5; Raccoon Point: 1.9, 95% CI = 1.5–2.2). The observed estimate of total average productivity closely matched that predicted by the model-averaged estimate from the 95% confidence set of models (see below; model-averaged prediction of productivity = 1.8, 95% CI = 1.4–2.3).

Observed values for habitat features surrounding nest sites varied widely among nests (Table 2). As is the case with many ecological data sets, several of our independent variables were correlated, albeit weakly. The number of small pines was negatively correlated with the number of large pine snags ($r = -0.327$, $P \leq 0.001$), the number of fires within the previous 5 years was negatively correlated with the percent cover by hardwood shrubs ($r = -0.328$, $P = 0.002$) and positively correlated with the number of large pine snags ($r = 0.398$, $P \leq 0.001$), and mean water depth during the breeding and nonbreeding seasons were positively correlated ($r = 0.635$, $P \leq 0.001$). However, VIFs

Table 3. Akaike's Information Criterion values adjusted for small sample size (AIC_c) for candidate models explaining variation in productivity of brown-headed nuthatches in southern Florida, USA, from 1998 to 2003.

Model	K^a	$\Delta AIC_c^{b,c}$	w_i^d
Yr + date + all nest-site vegetation + hydrology	10	0	0.36
Global	11	0.7	0.26
Yr + date + hydrology + fire frequency	7	1.1	0.21
Yr + date + all nest-site vegetation	8	3.6	0.06
Yr + date + all nest-site vegetation + fire frequency	9	5.0	0.03
Yr + date + fire frequency	5	5.4	0.03
Yr + date + understory nest-site vegetation	6	5.9	0.02
Yr + date + no. of large pine snags	5	6.1	0.02
Yr + date	4	7.2	0.01
Yr + date + overstory nest-site vegetation	6	8.3	0.01

[a] K is the no. of parameters estimated by the model.
[b] ΔAIC_c is the difference between a given model and the model with the lowest AIC_c score.
[c] The lowest AIC_c score was 127.5.
[d] AIC_c wt (w_i) reflects the relative support for each model.

calculated for each independent variable in our data set ranged from 1.5 to 1.7, which indicates a negligible effect of multicollinearity on our estimates of β (Neter et al. 1996, Graham 2003).

There was substantial model-selection uncertainty in our analysis of variation in productivity, and the 95% confidence set of models included 6 of the 10 models in the candidate set (Table 3). The global model adequately fit the data ($F_{10, 131} = 3.16$, $P = 0.002$, adjusted $R^2 = 0.132$), and therefore our reduced models should fit the data as well (Anderson and Burnham 2002). Lacking a single best approximating model, we used model-averaged regression coefficients to examine the relationship between habitat features and productivity. Model-averaged regression coefficients indicated which habitat features had the strongest and most consistent effect on productivity.

The best predictor of fledgling production was the date on which incubation began (model-averaged β = −4.6, 95% CI = −1.7−−7.4). Model-averaged estimates of productivity predicted a steep decline as the breeding season progressed (Fig. 1); for example, averaged across all models and holding all other variables at their mean, we predicted a pair that began incubating at the beginning of the nesting season (Julian date 47) would produce, on average, 2.7 fledglings (95% CI = 2.5−2.8), whereas we predicted a pair at the end of the nesting season (Julian date 134) would produce 0.5 fledglings (95%CI = 0.4−0.6). The number of large pine snags surrounding the nest site had a strong positive effect on productivity (model-averaged β = 1.6, 95% CI = 0.1−3.0), although the effect was much weaker than that estimated for the date of nesting (Fig. 2). Finally, the number of small pines surrounding the nest site also had a weak positive effect on productivity (model-averaged β = 1.3, 95%CI = 0.4−2.2; Fig. 3). The 95% confidence intervals surrounding model-averaged regression coefficients for all of the other independent variables overlapped zero.
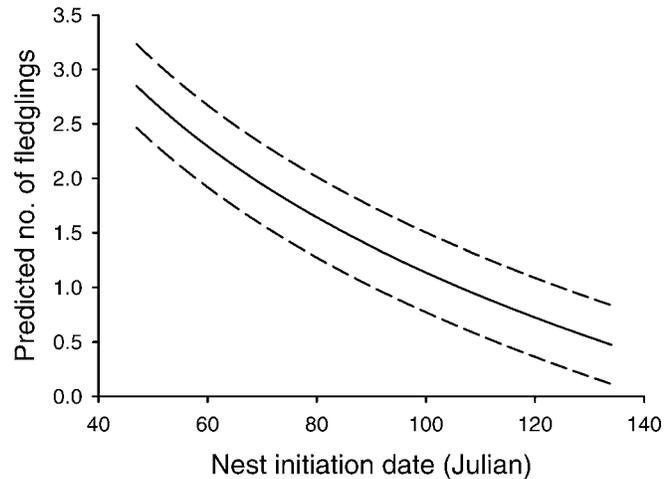

Figure 1. Predicted mean number (solid line; dashed lines are 95% CL) of fledglings produced from brown-headed nuthatch nests in southern Florida, USA (1998–2003), declines as a function of the date on which a nesting attempt began. We calculated the function by substituting different values for nest initiation date into 9 predictive models and generating an Akaike-weighted average across all models; all other independent variables were held at their mean observed value.

DISCUSSION

We found that one feature commonly identified as an important component of habitat for brown-headed nuthatches, the abundance of large pine snags, was positively associated with the number of offspring produced per nesting attempt. We do not know the mechanism underlying the positive association between productivity and the number of large pine snags, but choosing a nest site in an area with a greater number of potential nest sites may diminish the risk of predation (Martin 1988, Martin and
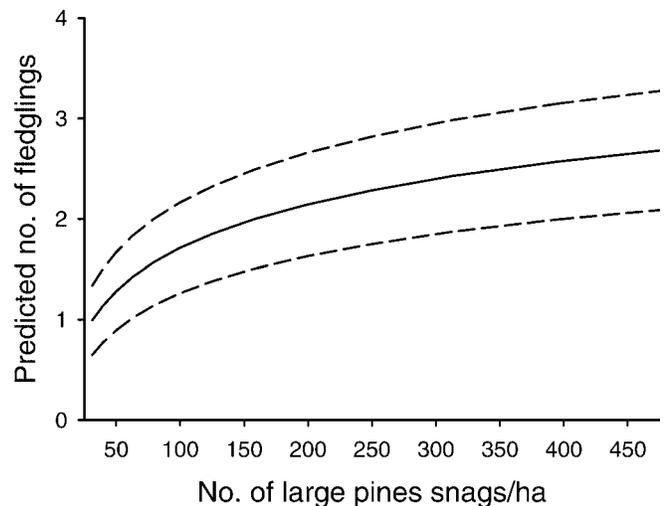

Figure 2. Predicted mean number (solid line; dashed lines are 95% CL) of fledglings produced from brown-headed nuthatch nests in southern Florida, USA (1998–2003), increases as a function of the density of large pine snags. We calculated the function by substituting different values for the number of large pine snags (limited to the range of obs values) into each predictive model containing a term for large pine snags, and then generating an Akaike-weighted average across all models. All other independent variables were held at their mean observed value.
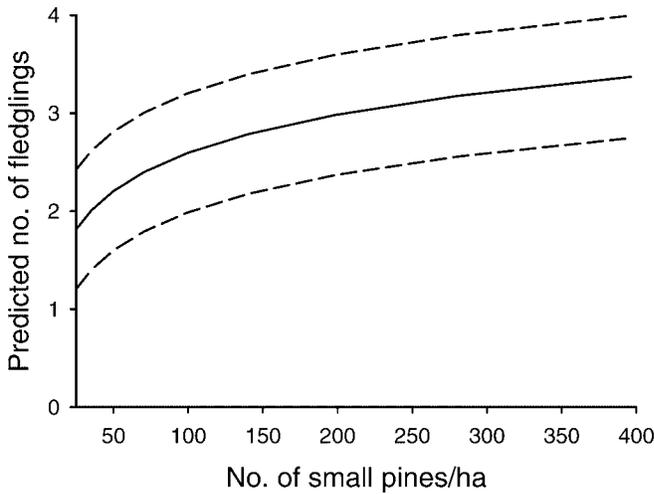
Figure 3. Predicted mean number (solid line; dashed lines are 95% CL) of fledglings produced from brown-headed nuthatch nests in southern Florida, USA (1998–2003), increases as a function of the density of small pine trees. We calculated the function by substituting different values for the number of small pines (limited to the range of obs values) into each predictive model containing a term for small pines, and then generating an Akaike-weighted average across all models. All other independent variables were held at their mean observed value.

Roper 1988, Li and Martin 1991). An increased number of snags also may reduce competition for nest sites with other cavity nesters, reducing the amount of energy that brown-headed nuthatches must expend defending their nest site (brown-headed nuthatches defend nest sites against conspecifics and other cavity-nesting species such as eastern bluebirds [*Sialia sialis*] and red-bellied woodpeckers [*Melanerpes carolinus*]; Slater 1997) and allowing breeding adults to invest more energy in caring for offspring, which may increase productivity.

We also found a positive relationship between the number of young fledged and the number of small live pine trees around the nest site. We lack a good biological explanation for this result because previous studies have found that brown-headed nuthatches prefer mature pine forests (Withgott and Smith 1998) with an open midstory (e.g., Hirth et al. 1991) and that they avoid nesting in areas with numerous small pine trees (Slater 1997). One possible explanation is that high densities of small pines around the nest site increased productivity by reducing the risk of nest predation; for example, dense patches of pines may hinder movement of potential nest predators or may increase concealment of the nest site (Martin 1992). However, we cannot rule out the possibility that the observed correlation was spurious.

The date on which incubation began was by far the most important predictor of productivity. This may be a result of variation in factors beyond the control of land managers, for example, seasonal changes in weather, clutch size, or the abundance of nest predators or competitors for nest sites. However, the seasonal decline in productivity also may have stemmed from seasonal changes in unmeasured components of habitat that influence productivity. Distinguishing among these alternatives is important, given the magnitude of the decline because components of habitat associated with this decline might be especially useful targets for management, perhaps more so than habitat features traditionally considered important (e.g., abundance of snags or openness of the understory).

None of the variables that we used to quantify fire history and hydrology had a measurable effect on productivity, although models that included an effect of hydrology tended to be well supported relative to models that ignored differences in hydrology. In addition, fire history contributed to variation in the density of large pine snags, which in turn was related to variation in productivity. Snag density was lowest in areas that had not burned in the previous 5 years, and thus the absence of fire was predicted to result in a gradual decline in productivity. We may have also underestimated the importance of hydrology by attempting to document a direct effect on productivity, as other research suggests that the most significant effect of hydrology may be its role as a modulator of fire effects on vegetation structure (Lockwood et al. 2003). For example, fire intensity may be greater in years when water levels are low, which may in turn lead to more pronounced changes in snag abundance (through effects on snag recruitment and mortality) or the condition of understory vegetation.

Fire, which is an important source of mortality in slash pine populations (Menges and Deyrup 2001), may be the most effective tool for increasing snag recruitment while at the same time promoting the understory conditions favored by brown-headed nuthatches (Conner et al. 1983). Typical recommendations for managing brown-headed nuthatch habitat focus on restoring frequent, low-intensity fires, generally at the beginning of the growing season (Dornak et al. 2004), but snag recruitment is lower in frequently burned stands (Menges and Deyrup 2001) and frequent fires may also consume existing snags and shorten snag retention time (e.g., Holden et al. 2006). Fire-return intervals of 1–2 years, as were implemented in the early years of this study, may be useful in restoring long-unburned pine rockland and reducing concomitant increases in fuel loads but, as a long-term management strategy, overly short fire-return intervals may reduce the abundance of snags. Fires in stands that have remained unburned for longer periods (e.g., 6–8 yr) will be significantly hotter and thus produce the greatest number of new snags (Menges and Deyrup 2001, Platt et al. 2002). Longer fire-return intervals likely will also increase snag retention time. At the same time, the density of midstory and understory vegetation increases as fire-return interval increases, and thus a compromise that allows for spatial heterogeneity in fire-return interval may be useful in creating and maintaining high-quality habitat for brown-headed nuthatches. Determining the range of fire-return intervals that will best resolve the conflict between optimal midstory and understory conditions and the number of large snags will require additional information about the role of fire in the population dynamics of snags, including a better understanding of how hydrological conditions and other disturbances (e.g., hurricanes or insect outbreaks) mediate

the effects of fire in the pine rocklands (e.g., Lockwood et al. 2003).

Our conclusions about the relationship between habitat features and productivity of brown-headed nuthatches are applicable throughout most of the remaining pine rockland in southern Florida because of the similar fashion in which these areas are managed. Fire-management targets for the pine rocklands in Everglades National Park and Big Cypress National Preserve generally call for fire-return intervals of 3–6 years, as was applied to our sites at Long Pine Key and Raccoon Point. The other significant tract of pine rockland that remains in southern Florida, in Florida Panther National Wildlife Refuge, had a fire-return interval of approximately 4 years, well within the range of return times observed on our study sites. The only pine rocklands to which our results may not apply are the small and highly fragmented patches that remain within the Miami-Dade County network of parks; however, our own ongoing surveys indicate that brown-headed nuthatches do not occupy these fragments.

MANAGEMENT IMPLICATIONS

Increasing snag density was associated with increased breeding productivity, suggesting that snag creation should be a target of future habitat management for brown-headed nuthatches. We recommend the continued use of fire as a management tool, although our results suggest that more attention should be paid to the trade-off between the length of the fire-return interval and the recruitment of new snags and retention of existing snags. In particular, we recommend increasing the variance in fire-return intervals so that some stands remain unburned for longer than the 3-year to 4-year rotation on which most of the pine rocklands are currently burned. Longer fire-return intervals in some stands will allow for longer snag retention times while increasing the number of snags created following fire. At present, little information exists on which to base precise management recommendations but, as a starting point and until further information is available on the relationship between snag population dynamics and fire-return interval, fire-return interval in some stands should be extended to 5–6 years.

ACKNOWLEDGMENTS

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Associate Editor: Rosenstock.