

OVENBIRD NEST SITE SELECTION WITHIN A LARGE CONTIGUOUS FOREST IN EASTERN PENNSYLVANIA: MICROHABITAT CHARACTERISTICS AND NESTING DENSITY¹

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ABSTRACT

Since 1982, Ovenbird breeding populations have been monitored on two forest plots within a contiguous forest of greater than 10,000 ha at Hawk Mountain Sanctuary in southeastern Pennsylvania. On these two plots, Owl's Head and River of Rocks, the number of Ovenbird territories remained stable and increased between 1982 and 2001, respectively, with an increase of greater than 20% between 1991 and 1999. On a third plot where surveys began later, the numbers of territories declined from 7.9 per 10-ha to 1.2 per 10-ha between 1991 and 1999 (Goodrich, unpubl. data). In this study, we evaluate if Ovenbirds select sites with certain vegetation and microhabitat characteristics for their nest sites and if that may explain nest selection and the differences in territory density found within this eastern Pennsylvania contiguous forest. We examined the microhabitat and vegetative characteristics of 11 Ovenbird nests from the two long-term study plots, Owl's Head and River of Rocks, together with 11 nearby random points within these plots (random-linked), and 12 random points within the less dense Visitor Center plot. We compared habitat variables using multiple ANOVA's and least square means test. Significant variables were placed in a model to predict nest occurrence and the best predictive model comparing Visitor Center to nest sites and random-linked to nest sites was selected using AIC values. Nest site areas had a significantly greater percentage of vegetation cover, number of plant stems, and number of plant species than did either the random-linked or Visitor Center plots. The best models to predict nest occurrence included percent vegetation cover within higher density areas (i.e., Owls Head and River of Rock's plots) and number of stems when comparing nests to lower density sites on the Visitor Center plot. Litter depth also was an important predictor of nest occurrence within nesting areas with nest sites. Our results suggest that microhabitat and vegetation characteristics can vary significantly within a contiguous forest and these differences influence Ovenbird nesting densities. Microhabitat differences within the Visitor Center site (e.g. percent

cover, number of species) may be mediated in part by higher frequency of white-tailed deer, greater abundance of invasive species, or other factors associated with its location near a forest opening. Disturbance factors that limit ground cover vegetation extent and diversity may limit the distribution of this forest-interior nesting species even within large forest blocks.

[J PA Acad Sci 83(1): 3–9, 2009]

INTRODUCTION

Ovenbirds (*Seiurus aurocapillus*) are neotropical migrant passerines that nest on the ground in small, dome-shaped nests in the interior of large forests. Robbins et al. (1989) found the species nesting in small forest fragments ranging from 100–850 ha as well as larger forests. Studies have shown that the breeding success of Ovenbirds is significantly lower in smaller forest fragments (Poneluzi et al. 1993, Robinson et al. 1995, Goodrich et al. *in prep*). Giocomo et al. (*in prep*) found that Ovenbird territory density is significantly lower in forest fragments less than 100 ha in size. Reasons for these differences may vary. In some cases it may result from increased nest predation by species utilizing the forest edge (Zegers et al. 2000). In other regions, the increased level of Brown-headed Cowbird parasitism (*Molothrus ater*) in fragments has been shown to cause forest bird declines (Robinson et al. 1995). Nesting territories in smaller fragments also may have reduced food supplies due to increased light reaching the forest floor (Burke and Nol 1998). Lower nesting densities of Ovenbirds may result if small forest fragments have inadequate habitat and food resources.

Long-term declines in Ovenbirds have been noted in a number of areas across their range, particularly in those areas most seriously affected by habitat fragmentation, such as Southern New England and the Cumberland Plateau (Sauer et al. 2003). Areas that still harbor abundant contiguous forest tracts such as Pennsylvania (Goodrich et al. 2002), are considered key regions for the long-term conservation of this and other forest-interior species.

However, contiguous forest tracts in Eastern North America also may vary in habitat quality and suitability for forest interior birds. Among the threats to birds in large forests in Pennsylvania are over-browsing by burgeoning white-tailed deer (*Odocoileus virginianus*) populations (DeGraaf et al. 1991, Horsely et al. 2003), acid rain effects on vegetation health, soil ecology, and invertebrate population dynamics

¹Received for publication 2 February 2008; accepted 20 May 2008.

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(Brotons et al. 1998, Hames et al. 2002), and habitat alteration through colonization by invasive species (Banko et al. 2002, Scheiman et al. 2003).

At Hawk Mountain Sanctuary, Berks County, Pennsylvania, within a greater than 10,000 ha tract of contiguous forest in the central Appalachians, nesting Ovenbirds have been monitored on two study plots, Owl's Head and River of Rocks, since 1982 (Porneluzi et al. 1993, Goodrich et al. 1998). The third plot, Visitor Center, was surveyed annually from 1991 through 1999.

Between 1991 and 1999, Ovenbirds averaged 6.3 ± 1.1 territories/10-ha and 5.4 ± 1.3 territories/10-ha on Owl's Head (OH) and River Rocks (ROR) plots and territory density increased non-significantly by 35% and 25% respectively (OH: $r = 0.23$, $df = 1$, $p = 0.50$; ROR: $r = 0.58$, $df = 1$, $p = 0.11$) (Goodrich et al. 1998, Barber and Goodrich, in prep.). In contrast, on the nearby Visitor Center plot adjacent to a 5 ha opening, the number of territories declined from an average of 7.7 territories/10-ha to only 1.12 territories/10-ha in 1999, a decline of 85% (Pearson correlation, $r = -0.89$, $p = 0.001$, $n = 9$). Nesting success on the Owls Head and River of Rocks plots has remained consistently high in the last 20 years, and significantly higher than nearby forest fragments suggesting that recruitment is not an issue within this forest landscape (Porneluzi et al. 1993, Goodrich et al. in prep). Ovenbird territory density has been shown to decline within forest adjacent to a clearcut during the three years after forest cutting (e.g., Wallendorf et al. 2006), however the Visitor Center opening was established in the mid-1970s, so decline in Ovenbird use in response to a new opening should have been detected earlier.

In this paper we examine if Ovenbirds select their nest sites within a contiguous forest based on microhabitat characteristics or if they place them at random, and if microhabitat differences may explain, in part, the significantly reduced densities of Ovenbirds observed in some areas. We investigate this question by quantifying the vegetative structure and other microhabitat characteristics near nest sites on the plots where densities increased, Owls Head and River of Rocks, and comparing them to random points paired with each nest site on the two sites where density increased and also with random points located on the nearby Visitor Center plot where nesting densities have declined.

METHODS

Study Area. The study was conducted at Hawk Mountain Sanctuary (HMS) in Berks County, Pennsylvania ($40^{\circ} 38'N$ and $75^{\circ} 59'W$). The 972 ha sanctuary is located within a larger >10,000 ha mixed deciduous forest on the Kittatinny Ridge of the central Appalachians in southeastern Pennsylvania. Our first plot, known as Owl's Head, is a 19.4 ha, 490×400 m rectangle on a ridge-top 408–448 m in elevation and dominated by oak-maple forest. The canopy is comprised mostly of chestnut oak (*Quercus prinus*) and red

maple (*Acer rubrum*), while the understory is made up of black gum (*Nyssa sylvatica*) and sassafras (*Sassafras albidum*). The shrub and ground cover layer is composed of huckleberry (*Gaylussacia baccata*), sheep laurel (*Kalmia angustifolia*), lowbush blueberry (*Vaccinium pallidum*), teaberry (*Gaultheria procumbens*), and highbush blueberry (*Vaccinium angustifolium*). The second plot, River of Rocks, is a 16.9-ha, 430×400 m rectangle on an eastward facing rocky slope 265 to 347m in elevation. It is also dominated by chestnut oak and red maple, but red oak (*Quercus rubra*) and sweet birch (*Betula lenta*) make up a larger portion of the canopy than on Owl's Head (Steckel 1998). Black gum and sassafras still dominate the understory, although mountain laurel (*Kalmia latifolia*) is found in dense stands in certain areas on the plot. The shrub layer is largely similar to that found on Owl's Head (Goodrich et al. 1998). The Visitor Center plot is a 5-ha, L-shaped plot (each leg is 300×100 m) approximately 396 m in elevation. The vegetation is similar to that on the Owl's Head plot. However, Visitor Center is adjacent to the HMS Visitor Center and much of the plot lies within 100 m of a building, parking lot, or small clearing. This plot was smaller than the other two plots as it was designed to be adjacent to the opening. All three plots lie within 1 km of each other.

Survey and Nest Search Protocol. Beginning in early May 2003, both the Owl's Head and River of Rocks plots were surveyed almost daily as either part of a continuing Breeding Bird Census conducted annually since 1982 (Ralph et al. 1993), or a separate study of long-term Ovenbird nesting biology (e.g., Porneluzi et al. 1993). Surveys were conducted between dawn and 10 am EST on each plot by systematically walking 30 meter grid lines across each study site. During these surveys, all Ovenbirds sighted or heard were marked on plot maps using the spot-mapping technique and sightings of previously color-banded males were mapped along with any associated mate. All color-marked males were followed for 10 or more minutes each to detect behavior by male or female suggesting nesting activity. Any nests located during surveys were flagged so they could be relocated easily. The Visitor Center plot, which had been eliminated from the long-term study in 1999, was surveyed three times in 2003 for Ovenbird use during June and early July. Locations of singing or sighted birds were mapped and tallied following standard Breeding Bird Census instructions to determine the number of territories present on each plot (Ralph et al. 1993).

Vegetation Survey Protocol. Vegetation characteristics were measured at each of the nests in mid to late July 2003, after the nestlings had fledged. Sampling was conducted after fledging to avoid disturbing the nests. As many of the plant species found on the floor in this forest were woody perennials, we assumed that any relative differences among the sites found in July would be representative of differences present in early May when most of the birds return and select nest sites. Canopy cover, canopy species composition, light levels and other forest characteristics were not measured as our pur-

pose was to compare the microhabitat at nest sites to other forest sites within the same forest at a finer scale.

A 1 m square frame was placed around the nests with the nest at the center and the four sides oriented in the cardinal directions. Within this square the litter depth, percent litter cover, percent bare ground, percent vegetation cover less than 1 m in height, and basal area were measured. All plant species within the 1 m plot and less than 1 m tall were identified, the number of stems counted, and the distance of the plot to the nearest tree in each of the cardinal directions measured and the tree species identified.

The percent nest concealment for each nest also was calculated by measuring the nest concealment from five different aspects: from 1 m away, at a height of 1 m, in each cardinal direction and also directly above the nest (Burke and Nol 1998). These five percentages were calculated as a proportion of 20 (i.e., 50% of 20 is 10) and then added together to reach a total percentage of 100. Slope, aspect, and distance to nearest edge for each nest were calculated by mapping GPS locations of the nests in ArcView 9.0, (ESRI 2003).

To compare habitat characteristics of nests to nearby locations within the study plot, vegetation also was measured at 11 random points placed at a randomly-selected angle at a distance of 30 m from each of the nests (hereafter referred to as random-linked sites). In addition, twelve random points were chosen on the Visitor Center plot by numbering the already marked 30 meter grid points for the plot and selecting random numbers to designate 12 randomly-selected grid points. Then, a 1 m plant survey site was placed in the center of the square to the northwest of this randomly selected grid point, to avoid placement along grid lines. For random points, the same vegetation and site characteristics were measured as for the nests with the exception of nest concealment, which was not calculated.

Statistical Analysis. Plots were placed into three separate groups: nest sites (pooling both River of Rocks and Owl's Head nests), random-linked sites 30 m away from nests, and random points in the lower-density plot, Visitor Center.

In order to initially assess the differences in habitat characteristics among the different groups, an ANOVA was conducted on each habitat variable measured. A least square means post-hoc test was conducted to determine which of the three groups differed from each other. The post-hoc test

was conducted for both significant and insignificant ANOVA results to assess patterns among the three groups. Any variable showing significant variation among the three groups in the ANOVA or posthoc tests were then evaluated in a set of nine competing logistic regression models to predict nest occurrence in a used area (comparing random-linked points to nest sites) and to predict overall nest occurrence (by comparing Visitor Center points (unused) to nest sites). Only variables showing initial significance were included in models as per Burnham and Anderson (2002). The Akaike's Information Criterion, adjusted for small sample size (AICc), and Akaike weights (Burnham and Anderson 2002), were used to identify the most parsimonious model in each model set. The best model selected from each set was used to estimate probabilities of nest occurrence based on the habitat values.

RESULTS

Breeding Densities and Nest Sites. Territories were not checked on Visitor Center from 2000 to 2002, however in 2003 the density of Ovenbirds remained low in comparison to other study areas, e.g. there were 9.7 territories / 10 ha on the Owl's Head plot, 5.6 territories / 10 ha on the River of Rocks plot, and 2.2 territories / 10 ha on the Visitor Center plot. In 1999 territory density was similarly low on the Visitor Center as compared to the other two sites. Because the pattern of lower density in 2003 was similar to 1999 (1.1 territories/10 ha) we assumed the lower density was not an anomaly.

Eleven nests were located on the Owl's Head and River of Rocks plots (e.g., 72% of 2003 nesting pairs on the plots). Thus, vegetation cover and site characteristics were compared between 11 nests and 11 random-linked sites within the two higher density plots, Owls Head and River of Rocks, and 12 random sites within the lower density plot, Visitor Center.

Habitat Analyses. A total of 22 plant species were recorded in the 1 m² plots with 0 to 3 unknown species recorded per plot. The percentage of vegetation cover significantly differed among the three plots (Table 1) ($F = 5.432$, $df = 2$, $p = 0.009$). Percent cover around nests ranged from 10 to 100 percent with an average of 62% per nest (Table 1). Bonferroni post-hoc pair-wise comparisons

Table 1. Microhabitat measurements of Ovenbird nests and random points on Owl's Head, River of Rocks, and Visitor Center plots at Hawk Mountain Sanctuary, 2003 (mean, standard error) (** Denotes value significantly greater than other site values ($p < 0.05$)).

Sites	Distance to Edge (m)	Litter Depth (cm)	% Vegetation Cover**	Number of Stems**	Number of Blueberry (sp.) Stems	Number of Red Maple Stems	Number of Tree Seedlings	Number of Species**
Nests (n = 11)	51.27, 15.35	4.55, 0.47	62.7, 25.3	38.64, 4.88	19.27, 2.08	2.18, 0.60	5.18, 1.17	7.73, 0.78
Random-Linked Points (n = 11)	57.00, 10.65	3.18, 0.42	33.6, 9.7	32.46, 6.49	13.82, 2.80	7.09, 4.55	10.91, 5.06	6.91, 0.56
Random Points- Visitor Center (n = 12)	43.25, 10.51	3.54, 0.48	26.7, 26.4	22.5, 2.68	11.92, 2.81	4.00, 1.44	5.50, 1.57	5.58, 0.31

** Denotes significant difference found among the three plots at $p < 0.05$ level.

Table 2. AIC Model selection results for comparing nest sites to unused sites in Visitor Center plot (n = 23).

MODEL	AICc	DIFF	WEIGHT
Number of stems	29.825	0.000	0.35470*
Percent vegetation	30.228	0.403	0.28997
Number of stems and percent vegetation	31.723	1.898	0.13731
Number of species	32.384	2.559	0.09867
Percent vegetation and litter depth	33.095	3.270	0.06915
Wood	35.931	6.106	0.01675
None	36.441	6.616	0.01298
Litter depth	36.772	6.947	0.01100
Four variables excluding litter depth	37.365	7.540	0.00818
All 5 variables	41.033	11.208	0.00131

*best model predicting nest location

revealed that vegetation cover was significantly higher at nest sites than at the random points in the Visitor Center plot (mean difference = 36.06%, $p = 0.011$, $df = 31$) and cover also was higher at nest sites compared to the random-linked sites (mean difference = 29.09%, $p = 0.057$, $df = 31$). However there was no significant difference between the random-linked and random Visitor Center sites (mean difference = 6.97%, $p = 1.0$). The average number of plant stems per plot varied significantly among the three samples ($r = 0.397$, $F = 2.894$, $p = 0.07$, $df = 34$; Table 1). Stem density at nest sites was higher than at Visitor Center points (Bonferroni pair-wise mean difference = 16.136, $df = 31$, $p = 0.07$), but was not greater than stem density at the random-linked sites (pair-wise mean difference = 6.182, $df = 31$, $p = 0.65$) (Table 1). The random-linked sites had more stems, but there was no significant difference between them and the Visitor Center sites ($p = 0.32$).

The average number of plant species per plot also varied significantly among the three sites ($r = 0.438$, $F = 3.678$, $p = 0.037$, $df = 31$) (Table 1). Post hoc Bonferroni pair-wise comparisons revealed that species diversity was greater at nest sites than at Visitor Center sites (mean difference = 2.144, $df = 31$, $p = 0.031$), but not at the random-linked sites ($p = 0.974$), and there was no significant difference between random-linked and Visitor Center sites ($p = 0.323$).

Litter depth, basal vegetation, and number of blueberry stems (*Vaccinium* sp.) were higher at nest sites compared to random points but the differences were not significant (Table 1). No other measurements exhibited significant differences between any of the sites ($p > 0.1$), including percent litter cover, distance to the nearest edge or trail, percent bare ground, basal area, the abundance of any of the individual species (e.g. red maple, mountain laurel, etc.), distance to nearest tree in the four cardinal directions, slope, and aspect. Bonferroni posthoc pair-wise comparisons were conducted on all insignificant habitat variables although none of the pair wise comparisons were significant ($p > 0.10$).

The average percent nest concealment for the 11 nests was 55% and did not differ between the two plots with nests (t-test, $p = 0.61$). Black gum was the most frequent tree on the three study plots comprising 42% of all trees, followed

by chestnut oak with 26%, red maple with 17%, and red oak with 10%. There was no difference in the frequency of these trees among the three plot sites.

Comparison of Variables. The number of stems, number of species, percent vegetation cover, litter depth, and basal area, were included in our set of competing logistic regression models to determine which variable or combination of variables was the best predictor of Ovenbird nest presence. We evaluated litter depth as a predictor of Ovenbird nest sites because it was marginally significant and has been shown to be important in other studies of Ovenbird nest sites (Burke and Nol 1998). Because of the small sample size ($n = 34$ total points sampled), we compared nest sites to the random-linked and Visitor Center points separately.

When comparing nests and Visitor Center sites, the number of stems and percent vegetation cover were both important predictors of nest presence, with Akaike weights of 0.411 and 0.336 respectively (Table 2). Of the two, the number of stems seemed most important. The probability of a nest being present was modeled as $\text{Log (odds)} = -4.4179 + 0.1500 * (\text{number of stems})$ ($P < 0.05$) for both the intercept and the number of stems, (standard error of intercept = 2.1528, standard error of number of stems = 0.0738). According to this model, the probability of an Ovenbird nest being present on a plot with <15 stems was <11% (Figure 1). But the probability of a nest being present on a plot with >38 stems was >80%. The percent vegetation cover model was also useful in modeling nest presence with the equation: $\text{Log (odds)} = -2.2266 + 0.4862 * (\text{percent vegetation cover})$ ($P < 0.05$ for both intercept and the percent cover, standard error of intercept = 0.9990, Standard error of % vegetation = 0.1948) (Figure 2).

For nest plots versus random-linked plots Akaike weights suggested that percent vegetation cover and litter depth were the two most important variables (0.3445 and 0.2417 Akaike weights respectively, Table 3). The best predictor model included only percent vegetation cover: $\text{Log (odds)} = -1.7205 + 0.3588 * (\text{percent vegetation})$ ($P < 0.08$ for the intercept and $P < 0.04$ for the percent vegetation; Standard error of intercept = 0.9554, standard error of percent vegetation = 0.1727). Using this equation, the probability of an

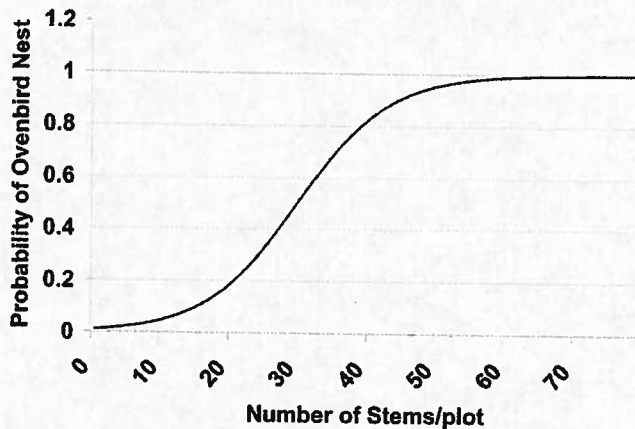


Figure 1. The probability of Ovenbird nest presence as function of the number of stems in a 1 m² plot when comparing nest sites to Visitor Center sites ($\text{Log (odds)} = -4.4179 + 0.1500 * (\text{no. of stems})$).

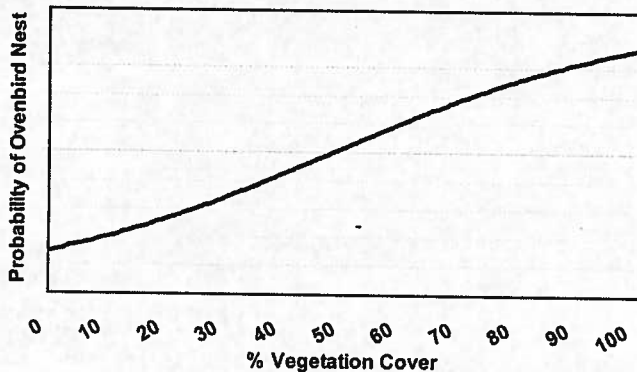


Figure 2. The probability of Ovenbird nest presence as function of percent vegetation cover in a 1 m² plot when comparing nest sites to random linked sites ($\text{Log (odds)} = -2.2266 + 0.4862 * (\% \text{ vegetation})$).

Ovenbird nest being present on a plot increased with the percent vegetation cover. With <10 percent vegetation cover per m², there was <20% chance of a nest being present (Figure 2). With >90 percent vegetation cover, there was >80% chance that a nest was present (Table 2, Figure 2).

DISCUSSION

Our study suggests that the microhabitat within a contiguous forest can vary substantially and that variation influences nest site selection by Ovenbirds. We found that in the Visitor Center plot where Ovenbird density has declined, there were significantly fewer plant species, lower stem densities, and less vegetation cover overall as compared to nest sites. In addition, litter depth and number of blueberry stems were also lower than at the plots still occupied by Ovenbirds, although the difference was not significant. The best predictors of Ovenbird nest locations within the contiguous forest were vegetation cover and stem density.

The reasons causing the within-forest differences in vegetative structure are unknown. One possible explanation is the increased numbers of white-tailed deer and their concentration near openings in the contiguous forest, such as the Visitor Center area. Pennsylvania Game Commission (2001) data for the study area (e.g., Berks County) placed the density of white-tailed deer at >14.2 deer/km² for each year since 1982 and as high as 28.8 deer/km² during some years of the study period. The estimated regional deer population increased significantly during the study period suggesting deer browsing activity may have increased ($r = 0.474$, $n = 19$, $p = 0.041$) (Pennsylvania Game Commission 2001).

Deer densities of this level have been shown to cause changes in the ground cover and shrub vegetation. Declines in seedling numbers, stem density in most plants, and overall floral diversity have also been noted in areas of high deer density (e.g., Horsley et al. 2003). In addition, a forest health survey conducted at Hawk Mountain in 1998 reported heavy deer browse with little forest regeneration occurring, with greater impacts noted near openings (Steckel 1998).

Bird populations can be affected by higher deer densities, particularly those species nesting in the intermediate canopy (DeCalesta 1994). Although, DeCalesta and others have not found decreases in nesting populations of ground and canopy nesters linked to increases in deer, if deer occur at high levels for long periods they may significantly impact overall plant species diversity and stem density of shrub and herbaceous layers, causing effects such as those noted by

Table 3. AIC model selection results for comparing nest sites to random-linked points within the study plots ($n = 22$).

MODEL	AICc	DIFF	WEIGHT
Percent vegetation	32.495	0.000	0.34455*
Litter depth	33.204	0.709	0.24171
Percent vegetation and litter depth	34.402	1.907	0.13279
None	35.130	2.635	0.09227
Number of stems and percent vegetation	35.179	2.684	0.09004
Number of species	37.044	4.549	0.03544
Number of stems	37.204	4.709	0.03271
Wood	37.740	5.245	0.02502
Four variables excluding litter depth	41.059	8.564	0.00476
All five variables	44.895	12.400	0.00070

* best model predicting nest location

our results (Horsley et al. 2003). The Visitor Center plot is within 100 m of the Hawk Mountain Visitor Center and its parking facilities, while the other two plots are both > 1 km away from this opening, and deer may be more frequent in this area.

Another possible impact in the Visitor Center area of the forest is the invasion of non-native species along openings. Non-native plants, such as stilt grass (*Microstegium vimineum*), have begun to enter much of the forest interior along drainage swales adjacent to the Visitor Center and are altering the composition of the nearby forest ground cover (and its associated invertebrate populations). Non-native earthworms also have been invading the Hawk Mountain forest in recent years, particularly adjacent to disturbed areas (Maerz, J., pers. comm.). Recent research suggests that non-native earthworms may reduce the leaf litter mass which may affect both nest site suitability and prey availability as the worms appear to deplete the forest floor invertebrate population and reduce plant species richness (Holdsworth et al. 2007, Maerz, J., pers. comm.) Because Ovenbirds feed predominantly on forest floor invertebrates (Van Horn and Donovan 1994), non-native species that cause reduction in invertebrate densities could indirectly reduce the quality of nesting habitat available.

A final consideration is ground predators. Just as with deer, there may be more medium-sized and small mammals near the Visitor Center plot due to the plot's proximity to the HMS Visitor Center facilities, their openings, and their bird feeding stations. Studies on other ground-nesting birds have shown greater nest densities and greater nest survivorship in areas with lower small mammal numbers (Morton 2005, Schmidt et al. 2006).

Microhabitat differences appear to have important consequences for patterns of nest density in forest-nesting birds even within large areas of contiguous forest. Burke and Nol (1998) found that pairing success on small forest fragments was at times 0% while on the largest fragments it reached 100%. They attribute this drastic difference to the nest site microhabitat characteristics that females prefer, suggesting that females choose sites with deep litter and other characteristics that will increase their reproductive success. Coupled with our findings, this suggests that there may be certain microhabitat features that when absent may preclude nesting attempts. As suggested by Burke and Nol (1998), these characteristics may be indicative of habitat quality for invertebrate prey populations, but they may also be important for nest concealment and predator avoidance. In contrast, Van Horn and Donovan (1994) report little is known about nest site selection in Ovenbirds but they nest "in areas where the forest floor is open and shrubs are sparse"; they also note some nests are placed in "moderately dense herbaceous vegetation". Results of this study suggest Ovenbirds may prefer to place their nests in moderate dense cover and selection of sites in open areas may be a response to a lack of available cover or other aspects over-riding this preference such as litter depth.

This study highlights the need for a detailed understanding of the microhabitat characteristics needed for a healthy species population in conservation planning, not merely the overall habitat type or patch size most frequently used.

ACKNOWLEDGMENTS

We thank Ben Baiser, Kate Coddington, and Sue Wolfe for their help in data collection and Margaret Brittingham, Stan Senner, Cathy Viverette and Jim Bednarz for research assistance during the long-term forest bird studies at Hawk Mountain. We thank the Pennsylvania Game Commission for the use of the property for one of the study sites. We thank Dr. Keith Bildstein and several anonymous reviewers for their help with earlier drafts of this paper. Also thanks to Mr. Sarkis Acopian for his generous donations that have allowed for the continuation and expansion of the internship program at Hawk Mountain Sanctuary. Long-term Ovenbird research has been partially supported by the Wild Research Conservation Fund and National Fish and Wildlife Foundation. This is Hawk Mountain Sanctuary contribution number 105.

LITERATURE CITED

- Banko, P. C., P. T. Oboyski, J. W. Slotterback, S. J. Dougill, D. M. Goltz, L. Johnson, M. E. Laut, and T. C. Murray. 2002. Availability of food resources, distribution of invasive species, and conservation of a Hawaiian bird along a gradient of elevation. *Journal of Biogeography* 29: 789–808.
- Barber, D. R., and L. J. Goodrich. *In prep.* Relative densities and population trends of forest nesting birds in Pennsylvania.
- Brotans L., M. Magrans, L. Ferrus, and J. Nadal. 1998. Direct and indirect effects of pollution on the foraging behaviour of forest passerines during the breeding season. *Canadian Journal of Zoology* 76: 556–565.
- Burke, D. M., and E. Nol. 1998. Influence of food abundance, nest-site habitat and forest fragmentation on breeding Ovenbirds. *Auk* 115: 96–104.
- Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach, 2nd edn. Springer-Verlag, New York.
- DeCalesta, D. S. 1994. The effect of white-tailed deer on songbirds in managed forests in Pennsylvania. *Journal of Wildlife Management*. 58: 711–718.
- DeGraaf, R. M., W. M. Healy, and R.T. Brooks. 1991. Effects of thinning and deer browsing on breeding birds in New-England oak woodlands. *Forest Ecology and Management* 41: 179–191.
- ERSI (Environmental Systems Research, Inc.). 2003. ArcGIS 8.0. ESRI, Redlands, California, USA.
- Giocomo, J. J., M. C. Brittingham, and L. J. Goodrich. *In prep.* Effects of internal openings on nest success of forest songbirds.

- Goodrich, L. J., C. B. Viverette, S. E. Senner, and K. L. Bildstein. 1998. Long-term use of Breeding Bird Census plots to monitor populations of neotropical migrants breeding deciduous forests in eastern Pennsylvania, USA. Pages 149–165 In *Forest biodiversity in North, Central and South America and the Caribbean: research and monitoring* (F. Dallmeier and J. A. Comiskey, eds.). *Man the Biosphere Series*, Smithsonian. Vol. 21. Parthenon Publishing Group. Pp. 1–768.
- Goodrich, L. J., M. Brittingham, C. B. Viverette, and J. C. Bednarz. *In prep.* Effects of forest fragmentation on long-term breeding success and return rates of Ovenbirds in eastern Pennsylvania.
- Hames, R. S., K. V. Rosenberg, J. D. Lowe, S. E. Barker, and A. A. Dhondt. 2002. Adverse effects of acid rain on the distribution of the Wood Thrush *Hylocichla mustelina* in North America. *Proceedings of the National Academy of Sciences of the United States of America* 99: 11235–11240.
- Holdsworth, A. R., L. E. Frelich, and P. B. Reich. 2007. Effects of earthworm invasion on plant species richness in northern hardwood forests. *Conservation Biology* 21: 997–1008.
- Horsley, S. B., S. L. Stout, and D. S. DeCalesta. 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. *Ecological Applications* 13: 98–118.
- Morton, E. S. 2005. Predation and variation in breeding habitat use in the Ovenbird, with special reference to breeding habitat selection in northwestern Pennsylvania. *Wilson Bulletin* 117:327–335.
- Pennsylvania Game Commission. 2001. *Pennsylvania Deer Statistics 1982–2000*. Pennsylvania Game Commission, Harrisburg, Pennsylvania.
- Porneluzi, P., J. C. Bednarz, L.J. Goodrich, N. Zawada, and J. Hoover. 1993. Reproductive performance of territorial Ovenbirds occupying forest fragments and a contiguous forest in Pennsylvania. *Conservation Biology* 7: 618–622.
- Ralph, C.J., G.R. Geupel, P. Pyle, T.E. Martin, and D.R. DeSante. 1993. *Handbook of field methods for monitoring landbirds*. Gen. Tech. Rep. PSW-GTR-144. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; 41 pp.
- Robbins, C. S., D. K. Dawson, and A. Dowell. 1989. Habitat area requirements of breeding forest birds of the Middle Atlantic States. *Wildlife Monographs* No. 103.
- Robinson, S. K., F. R. Thompson III, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* 267: 1987–1990.
- Sauer, J. R., J. E. Hines, and J. Fallon. 2003. *The North American Breeding Bird Survey, Results and Analysis 1966–2002*. Version 2003.1, U.S.G.S. Patuxent Wildlife Research Center, Laurel, Maryland.
- Scheiman, D. M., E. K. Bollinger, and D. H. Johnson. 2003. Effects of leafy spurge infestation on grassland birds. *Journal of Wildlife Management* 67: 115–121.
- Schmidt, K. A., R. S. Ostfeld, and K. N. Smyth. 2006. Spatial heterogeneity in predator activity, nest survivorship, and nest-site selection in two forest thrushes. *Oecologia* 148:22–29.
- Steckel, D. 1998. *Pennsylvania Forest Stewardship Plan for the Property of the Hawk Mountain Sanctuary Association*. Natural Lands Trust, Inc. Media, Pennsylvania.
- Van Horn, M. A., and T. M. Donovan. 1994. Ovenbird (*Seiurus aurocapillus*). *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/088>.
- Wallendorf, M. J., P. Porneluzi, W. Gram, R. Clawson, and J. Faaborg. 2006. Bird response to clear cutting in Missouri Ozark forests. *J. of Wildlife Management* 1899–1905.
- Zegers, D. A., S. May, and L. J. Goodrich. 2000. Identification of nest predators at farm/forest edge and forest interior sites. *Journal of Field Ornithology* 71: 207–216.