

LANDSCAPE CONFIGURATION EFFECTS ON DISTRIBUTION AND ABUNDANCE OF WHIP-POOR-WILLS

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ABSTRACT.—We examined the influence of landscape configuration created by forest regeneration practices on distribution of Whip-poor-wills (*Caprimulgus vociferous*) during the breeding season by comparing relative abundance and space use between forest areas (stands ≥ 17 years of age) and regenerating forest edges (regeneration stand ≤ 6 years of age adjacent to forest area). Regenerating forest edges contained greater ($P < 0.001$) abundance of Whip-poor-wills ($\bar{x} \pm SE = 2.4 \pm 0.30$ birds/10 ha) than forest areas (0.8 ± 0.11 birds/10 ha). Eighty-four percent of detections at regenerating forest edges were from within the regenerating stand. However, Whip-poor-wills within regenerating stands were detected within 100 m of the forested edge with a greater probability ($P < 0.001$) than expected by chance. The positive response of Whip-poor-wills to forest edges is likely due to proximity and use of foraging habitats. The relatively high number of habitat openings created by some forest regeneration practices provide Whip-poor-wills with foraging opportunities not present in less intensively managed forest systems. Forest management for Whip-poor-wills should consider harvest strategies that maintain the availability of regenerating patches in close proximity to mature forests. Received 18 August 2006. Accepted 30 January 2008.

The distribution and abundance of species that depend on resources that are not contained within a single patch type are likely influenced by the spatial organization of all required habitat types (Szaro and Jackle 1985, Dunning et al. 1992, Pearson 1993, Watts 1996, Sisk et al. 1997, Ries and Sisk 2004). This is because species that depend on more than one habitat type must broaden their use of a landscape to include all patch types needed to meet their requirements. The use of a habitat patch within a heterogeneous landscape for these species is influenced both by the characteristics of the patch (e.g., food supply, predation risk, competitive pressure, behavioral constraints) and the characteristics of surrounding patches (Hansson 1977, Foster and Gaines 1991, Johnson et al. 1992, Rodewald and Yahner 2001). Ultimately it is likely that spatial association of required habitat patches serves as the most important characteristic in affecting distribution and abundance of a species in a landscape (Szaro and Jackle 1985, Dunning et al. 1992, Pearson 1993, Watts 1996, Sisk et al. 1997, Ries and Sisk 2004).

Whip-poor-wills (*Caprimulgus vociferous*) are nocturnal insectivorous birds that typically nest in forested habitat but frequently use open habitats including fallow fields, crop-

land, shrubland, and regenerating pine (*Pinus* spp.) stands for foraging (Bent 1940, Cooper 1981, Eastman 1991, Peterjohn and Rice 1991). That Whip-poor-wills use resources that can occur in distinctly different habitat types implies their distribution and abundance may be influenced by the spatial configuration of patches within a broader landscape. Thus, Whip-poor-will abundance would be predicted to respond positively to landscapes where the required patches are in close proximity (Ries and Sisk 2004).

Forested landscapes under intensive management often contain a spatial mosaic of different age stands where adjacent stands (i.e., patches) are separated by abrupt edges (Thompson et al. 1995). Landscapes that are frequently disturbed by forest regeneration practices may provide Whip-poor-wills with habitat opportunities not available in less-intensively managed forest systems. The objective of our study was to investigate the effect of the spatial arrangement of habitat patches created by regeneration forest management on the distribution and abundance of Whip-poor-wills.

METHODS

Study Area.—Our study was conducted on a 30,000 ha forested tract in eastern North Carolina ($\sim 35^{\circ} 30' N$, $76^{\circ} 60' W$) that is managed primarily as a loblolly pine (*Pinus taeda*) plantation. The tract is divided among 1,010

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forest stands that are individually managed on a 30–35 year rotation schedule. Pine stands were initially planted as seedlings in parallel rows with a stocking level of 800 to 1,200 pine stems/ha. Young regenerating stands (1–5 years after planting) are characterized by a dense cover of shrubby plants, a high percentage of ground cover of grasses and forbs, and no overstory (i.e., open). Dominant plants include switch cane (*Arundinaria gigantea*), sweet pepperbush (*Clethra anifolia*), highbush blueberry (*Vaccinium corymbosum*), and blackberry (*Rubus sp.*). Pines reach a height of ~2.5 m after 6 years. Stands are commercially thinned two times (at ~12–15 years and 19–21 years after planting) before final harvest. Mature stands are characterized by dense understory vegetation dominated by switch cane, sweet pepperbush, highbush blueberry, fetterbush (*Lyonia lucida*), and gallberry (*Ilex glabra*). Dominant hardwood trees include red maple (*Acer rubrum*), sweetgum (*Liquidambar styraciflua*), red bay (*Persea borbonia*), sweet bay (*Magnolia virginiana*), and tulip poplar (*Lirodendron tulipifera*). Mature stands are harvested by clear-cutting. A network of logging roads cross the landscape. The staggered regime of harvesting and thinning creates a spatial mosaic of different age stands separated by distinct boundaries (Wilson and Watts 1999).

Study Design.—The influence of the configuration on stands of different age was examined by comparing the number of Whip-poor-wills at survey points along the boundary between two mature forest stands (forested area) to survey points along the boundary between one mature forest stand and one open, regenerating stand (regenerating edge). All mature forests had been planted 17–28 years prior and had been commercially thinned at least once. Regenerating stands were planted with pines within the last 1–5 years. Twenty-nine forested areas and 28 regenerating edges were selected as spatial replicates for study. Criteria for selection included stand size and shape. Small, narrow stands were avoided to reduce contagious effects from edges of other stands not selected for study. We selected a replicate for survey only if adjacent stands shared at least 350 m of edge. Each spatial replicate contained one point count station positioned on a logging road and along the edge between

the two focal stands. The location of survey points was chosen to maximize the distance between the boundaries of other stands not selected for study.

Bird Surveys.—The 57 survey points were divided into two groups (31 and 26 points, respectively) that were sampled on different nights between 13 May and 17 July 1999. All points were visited seven times during this period. Whip-poor-will activity is known to vary with lunar light intensity (Mills 1986, Wilson and Watts 2006); thus the two groups of points were surveyed on sequential nights over different periods of the lunar phase (new moon, first quarter, full moon, last quarter). Surveys began at 0.5 hrs after dusk and ended at least 1 hr before sunrise, and were conducted by driving between points on a predetermined route. The order in which points were visited was reversed between successive visits to reduce bias due to time of night. Surveys were not conducted during rain or winds >15 km/hr. One observer stood at the survey point during each point visit and recorded all birds that performed at least one syllable of the onomatopoeic “whip-poor-will” vocalization for a period of 5 min. Surveys may be biased to detect calling males because females are not known to routinely use this specific vocalization (Cink 2002). Visual detections and other vocalizations, such as grunt calls (Cink 2002), were not recorded to avoid biasing counts near the road edge or by stand type. The positions of all birds were mapped so detections could be summarized by the distance from the observer, distance from the edge of the two focal stands, or distance from the edge of any other stand within the vicinity.

We attempted to verify the observer’s accuracy of estimating the location of Whip-poor-wills from call-count surveys by comparing these data to locations estimated from radio-marked birds at this site the following year (Wilson 2003). This is not a direct measure an observer’s ability to estimate location because it compares data collected independently, but we believe it offers the only opportunity to validate an observer’s ability to identify the location of Whip-poor-wills at night. We summarized the estimated distance of Whip-poor-wills to the nearest forest edge for all observations in each data set into 100-m intervals and compared them for indepen-

dence using χ^2 analysis. There was no significant difference ($\chi^2_3 = 3.27$, $P > 0.10$) between locations estimated by using call counts and locations estimated by using radio telemetry. We assume that Whip-poor-wills used space in a consistent manner between years and this space use can be measured effectively using each technique.

Statistical Analyses.—Density values ($\bar{x} \pm$ SE) used to compare abundance between forest areas and regenerating edges were calculated using only the detections within a specified transect. The width of each transect was standardized among all survey points to limit detections used for this analysis to those observed within a 100 m perpendicular distance measured from the boundary between stands selected for study. The length of each transect was allowed to vary between individual survey points to concentrate the investigation within a zone between stands selected for study, and to eliminate observations that might have been influenced by other stand edges not selected for study. This was accomplished by changing the lengths of each transect so it terminated at a distance of 150 m from the edges between other stands not selected for study. The survey visit with the highest recorded abundance within each transect was used for the density estimate. Density values were standardized to number of birds/10 ha (i.e., 500 m length \times 200 m width rectangular transect) before analysis to accommodate variation in transect length. Density was compared between edge types using a one-way ANOVA (Statistica 6.1, Statsoft Inc. 1984–2005).

Whip-poor-will distribution was also compared between two stands that shared a common edge by summing all detections collected during the entire study into 100-m distance classes. This overall sum represents an accumulated pattern of space use through time rather than a population index since the samples are not independent. The total number of detections varied among survey nights due to changes in lunar light conditions (Wilson and Watts 2006). However, detection frequencies between distance classes were statistically indistinguishable across lunar conditions (i.e., <25%, 26–50%, and >50% of moon face illuminated) (3×2 contingency tables for all

χ^2 values < 4.5 , all $P > 0.20$) and the data were pooled.

We also compared the influence of stand age on edge use (Whip-poor-will detections) between forested stands and regenerating stands using χ^2 contingency tables. We used detections for this comparison only within 100 m of the boundary between two adjacent focal stands. Stands of each forested area were randomly assigned to one of two groups for this comparison. We examined the influence of stand type on relative edge use by testing for independence between detections 0–100 m and 101–200 m from the edge of adjacent forested stands, and adjacent forest and regenerating stands using χ^2 contingency tables.

The distribution of Whip-poor-wills within regenerating stands was further examined by comparing the distance of all observations from the nearest forest edge to an expected random distance using χ^2 analysis. This comparison included the entire perimeter of the regenerating stand and not only the boundary that was selected for density comparisons. Distances were expected to vary geometrically with stand area and shape; thus, separate statistical comparisons were made from five stand size classes; (1) <20 ha ($n = 2$), (2) 21–30 ha ($n = 4$), (3) 31–40 ha ($n = 8$), (4) 41–50 ha ($n = 4$), and (5) stands ≥ 51 ha ($n = 10$). Expected values were generated by creating 30 random locations within each open stand from digitized stand maps using ArcView 3.2 GIS software (ESRI 1992) and the animal movement extension of Hooze et al. (1999). The distance of random points to the nearest stand edge was measured from GIS coverage. The distances of both observed and random locations from the nearest forested stand edge were classified by 100-m intervals before comparison.

RESULTS

Regenerating edges supported a significantly greater ($F_{1,55} = 27.6$, $P < 0.001$) average density of Whip-poor-wills compared to forested areas ($\bar{x} \pm$ SE, 2.4 ± 0.30 birds/10 ha and 0.8 ± 0.11 birds/10 ha, respectively). The distribution of Whip-poor-wills between adjacent stands was influenced by edge type ($\chi^2_1 = 46.4$, $P < 0.001$). The frequency of all Whip-poor-wills detected in forest areas was evenly distributed between adjacent mature

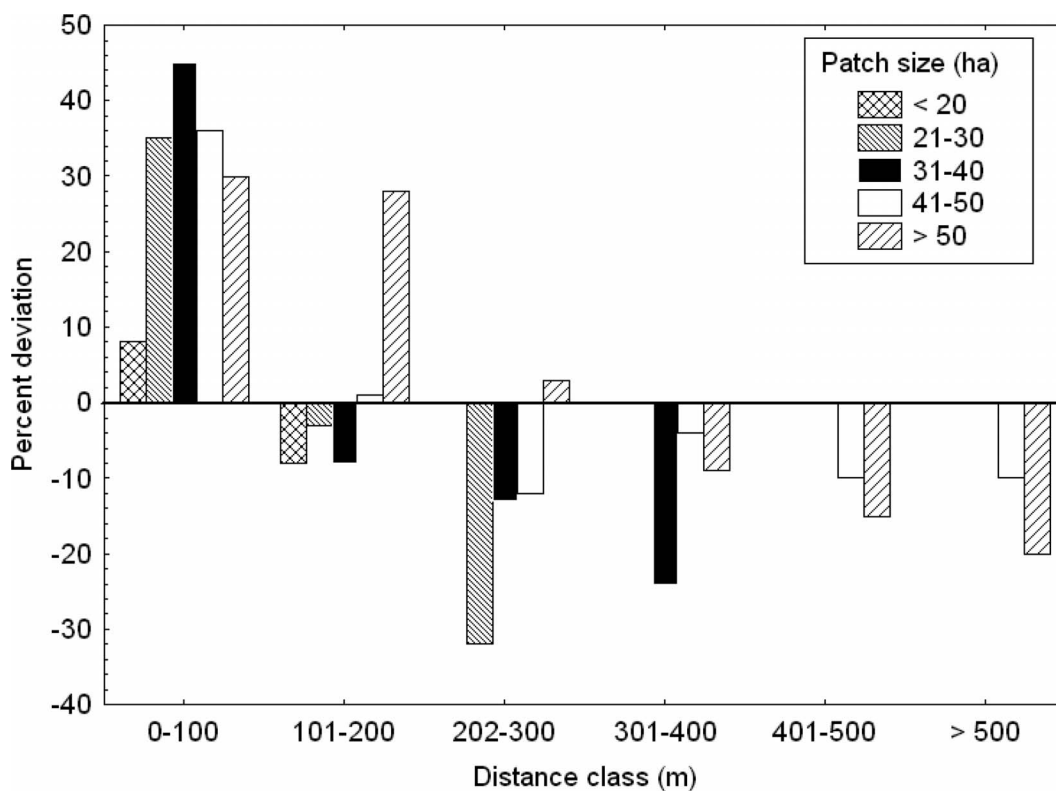


FIG. 1. Deviation (%) between observed locations of Whip-poor-wills within regenerating forest stands and an expected random distribution after classification into distance categories from the nearest forested edge. Positive deviations indicate distance categories where Whip-poor-wills were detected with greater frequency than expected by chance and negative deviations indicate the distance categories where Whip-poor-wills were detected less frequently than by chance.

forest stands ($\chi^2_1 = 0.74$, $P = 0.61$) with 45% and 55% of detections occurring in one of two randomly assigned groups, respectively. Whip-poor-wills in regenerating edges were over five times more likely ($\chi^2_1 = 100.4$, $P < 0.001$) to be detected within the regenerating stand (183 of 218 observations, 84%) compared to the adjacent forest stand.

Stand age had a significant influence on space use between distance observations of 0–100 m and 101–200 m ($\chi^2_1 = 3.8$, $P = 0.050$) from the stand edge. Whip-poor-wills at regenerating edges had a greater probability ($\chi^2_1 = 26.6$, $P < 0.001$) of being detected within a distance of 0–100 m from the forest edge than a distance of 101–200 m from the nearest forest edge. Sixty-four percent (217 of 339) of observations occurred within 100 m of the forest edge. The distribution of Whip-poor-wills did not differ ($\chi^2_1 = 1.4$, $P = 0.76$) be-

tween 0–100 m and 101–200 m in forest areas. Fifty-four percent (86 of 157) of observations were recorded within a distance of 100 m from the stand edge.

The distribution of Whip-poor-wills within regenerating stands was highly skewed to forest edges. Whip-poor-wills within regenerating stands were more likely to be detected within 200 m of a forest edge than further away. This result was most pronounced in patches >20 ha where birds were more likely to be detected within 200 m of the forest edge compared to an expected random distribution among all available classes (all $\chi^2_3 = 91.6$, $P < 0.001$; $\chi^2_4 = 76.2$, $P < 0.001$; $\chi^2_5 = 79.9$, $P < 0.001$; and $\chi^2_5 = 85.8$, $P < 0.001$ for stands that were 21–30 ha, 31–40 ha, 41–50 ha, and > 50 ha, respectively) (Fig. 1). Detections within regenerating stands < 20 ha did not differ from random when compared

between 0–100 m and 101–200 m distance classes ($\chi^2_1 = 0.30$, $P = 0.58$). The shortest distance between opposing stand edges in patches < 20 ha was generally not > 400 m.

DISCUSSION

The presence of open regenerating stands had a positive effect on the density of Whip-poor-wills using this forested landscape. This suggests that regenerating stands provide some resource that Whip-poor-wills prefer for foraging or breeding. One possible explanation for high use of open habitats is that it provides greater access to prey. Both abundance and richness of adult lepidopteran insects, the primary food item of Whip-poor-wills (Cink 2002), can be influenced by timber management and have been shown to be greater in clear-cuts than forest interiors (Jokimaeki et al. 1998, Summerville and Crist 2002). Whip-poor-wills forage on aerial prey almost exclusively using a visual field with short, upward-directed flights initiated from on or near the ground. Foraging activity increases with lunar light intensity for this species (Mills 1986), possibly an adaptation for finding food by exploiting back-lit insects. Open habitats receive more lunar illumination and probably provide better opportunities for visual detection of prey. Regenerating stands may therefore provide both a richer prey base and better foraging conditions compared to mature forest stands with well-developed canopies.

Whip-poor-wills are ground nesters that require forested habitats (Bent 1940, Peck and James 1983, Cink 2002) with ground vegetation for nesting. The density of ground vegetation in our study area varied markedly between forest and regenerating patches. Forest patches contained dense, continuous thickets of ground-level vegetation and regenerating stands had sparse patchy ground vegetation.

Regenerating pine stands had a positive effect on use of adjacent mature stands by Whip-poor-wills. Responses to habitat adjacency often result from resource complementation when two adjacent patches contain distinctly different resources (Forman and Godron 1986, Dunning et al. 1992, Ries and Sisk 2004). This is consistent with the general belief that Whip-poor-wills require forested patches for nesting but use open areas includ-

ing agricultural fields, scrub, and marshes for foraging (Cooper 1981, 1982; Alexander and Creswell 1990; Eastman 1991; Peterjohn and Rice 1991; Wang and Brigham 1997). Regenerating forests that are directly adjacent to mature stands may provide Whip-poor-wills the opportunity to exploit foraging and nesting habitats in close proximity.

The distribution of Whip-poor-wills near regenerating stands is consistent with a resource complementation argument. Whip-poor-will distribution within large regenerating stands was skewed to the edges that were adjacent to mature forest areas suggesting that territory placement was influenced by openings created by forest harvesting. This pattern would allow birds to effectively exploit resources from both habitat types. Observations of radio-tracked Whip-poor-wills from a separate study (Wilson 2003) support this suggestion. Males with both forested and regenerating habitats in close proximity typically roosted in forest habitat during the day, although they spent a disproportionately high amount of time foraging in regenerating stands at night.

The response of Whip-poor-wills to forest edges has direct implications for management of Whip-poor-will breeding populations in forested landscapes. Forest harvesting strategies that provide sustained yield of edge habitat by interspersing harvested patches with mid-rotation patches will favor Whip-poor-will populations. The amount of edge habitat available on a landscape scale is sensitive to both patch size and the level of interspersion between patch types (Franklin and Forman 1987). Management scenarios that use small to moderate patch sizes and spatially orchestrate harvests to maximize interspersion of patch types should be most useful.

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