SPATIAL INCIDENCE OF BARRED OWL (*STRIX VARIA*) REPRODUCTION IN OLD-GROWTH FOREST OF THE APPALACHIAN PLATEAU

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Abstract.—Barred Owl (*Strix varia*) occurrence and breeding were evaluated in old-growth forest using Poisson and binomial models constructed with seven spatially-explicit parameters derived from territorial density. Reproduction was evidenced by owl chicks heard inside cavity nests or being fed by adults in old-growth deciduous (beech-maple, oak-hickory) and old-growth mixed forest types (hemlock-white pine-deciduous). Barred owls nested on 64% of 11 relatively small (6–33 ha) study plots. Probabilities of obtaining this many cases of breeding or occurrence by chance alone were extremely low in all model executions, ranging to as little as $P = 1.6 \times 10^{-7}$. Compared to managed forests, old-growth forests used by breeding owls typically had higher snag densities and basal areas, large (≥45 cm dbh) eastern hemlock (*Tsuga canadensis*), some large live trees 50–100 cm dbh, and reduced understories. Among old-growth stands, vertical ($P = 0.06$) and horizontal complexity ($P < 0.01$) of the canopy differed significantly between areas used and not used for breeding. As in other *Strix*, I infer that spatial juxtaposition of structural features in late successional forest favors localizing reproductive effort within a small subset of the owl's home range. Older forest provides large cavities for nesting, a dense canopy for thermoregulation and protection from mobbing, and sparse ground cover that may facilitate prey detection and capture. All of these structural features are enhanced by life history characteristics of eastern hemlock.

Key Words: *Barred Owl; Strix varia; reproduction; breeding season habitat; habitat use; eastern old-growth; Pennsylvania.*

Incidencia espacial de Búhos (*Strix varia*) reproducción en bosques viejos en el Appalachian Plateau

Resumen.—Ocurrencia y crianza del Búho (*Strix varia*) fueron evaluados en bosque de crecimiento-viejo usando modelos Poisson y binomial construidos con siete parámetros explícitos derivados de densidad territorial. Reproducción fue indicado por búhos chicos oídos dentro de la cavidad de nidos o por los adultos dándoles de comer en crecimiento-viejo de bosques de hoja caduca (beech-maple, oak-hickory) y bosque mixtos de crecimiento-viejo (hemlock-white pine-deciduous). Búhos estabán en nidos en 64% de 11 lugares de estudio relativamente pequeños (6–33 ha). Probabilidades de obteniendo tantas situaciones de cría y ocurrencias por chanza sola eran muy bajas en modelo executaciones, desde tan poco come $P = 1.6 \times 10^{-7}$. Comparado con bosques manejados, bosques de crecimiento-viejo usados por búhos que crían típicamente tenían densidades altas y áreas (basal), grandes (≥45 cm dbh) *Tsuga canadensis*, unos árboles grandes 50–100 cm dbh, y vegetación reducidas por de bajo. Dentro de áreas de bosques de crecimiento-viejo, vertical ($P = 0.06$) y complejidad horizontal ($P < 0.01$) del dosel vario mucho entre áreas usadas y áreas no usadas para cría. Como en otras *Strix*, Yo digo que espacial yuxtaposición de elementos estructurad en bosques sucesional tardes hace favor de localizar esfuerzos reproductivo dentro de un lugar chico en el arreo de los búhos. Bosques maduros mantienen cavidades grandes para nidos, un dosel denso para reglamentación termal y protección de una multitud, y un suelo disperso que puede facilitar detección de presa y captura. Todos estos elementos estructurad mejoran los característicos históricos de la vida del *Tsuga canadensis*.

[Traducción de Raúl De La Garza, Jr.]

Mature and structurally-complex forest is a common feature of breeding habitat in North American *Strix* owls. Affinities for old-growth forest are more widely recognized in the Northern (*S. occidentalis caurina*, Forsman et al. 1984), California (*S. o. occidentalis*, Gutiérrez et al. 1992) and Mexican Spotted Owls (*S. o. lucida*, Ganey and Balda 1994), but Great Gray (*S. nebulosa*) and Barred Owls (*S.*

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varia) have also been linked with late successional forests with large-diameter trees (Elody and Sloan 1985, Allen 1987, Bull et al. 1988). Extensive tracts of old-growth containing eastern hemlock (*Tsuga canadensis*) were identified as important Barred Owl habitat a century ago (Bolles 1890, Eifrig 1907).

Barred Owls have been chosen as a management indicator species in several eastern national forests (USDA 1985, 1986), and are classified as threatened in some states (Bosakowski 1994). Concern for this species has increased because of its sensitivity to anthropogenic disturbance, including forest fragmentation, and because such land-use practices may indirectly erode integrity of its habitat via increasing competition with the more disturbance-tolerant Great Horned Owl (*Bubo virginianus*) (Morrell and Yahner 1994, Laidig and Dobkin 1995).

Generally an uncommon nocturnal predator, the Barred Owl occurs at low densities (one territory per 2.5–6.5 km²; Nicholls and Fuller 1987, Bosakowski et al. 1989). Populations can be monitored by broadcasts of conspecific recordings (McGarigal and Fraser 1985, Mosher et al. 1990), but playback may elicit little response from Barred Owls during incubation and early chick rearing (Devereux and Mosher 1984, Laidig and Dobkin 1995). Objectives of this study were to develop and test statistical models that would evaluate Barred Owl use of breeding sites in old-growth forest using passive sampling at spatial scales less than the size of the home range and to describe structural attributes and habitat configuration in the general vicinity of breeding sites (Hunter et al. 1995).

METHODS

Study Areas. Potential study areas on the Appalachian Plateau physiographic province in western and northcentral Pennsylvania (Fig. 1) were first screened by consulting inventories of locations, forest type, management regime and size of remaining old-growth forests (Mickalitis 1956, Erdman and Wiegman 1975, Smith 1989). Because a major criterion for plot selection was a size sufficient to contain the minimum recommended area for a Breeding Bird Census (BBC) in forested habitat (10 ha, Lowe 1995), the smallest sites (26%, $N = 51$) were excluded from consideration. Two or more study plots were established in each of the three largest consolidated tracts of mixed old-growth forest in Pennsylvania: Cook Forest State Park (>200 ha); Tionesta Scenic and Research natural areas (1675 ha) and Heart's Content, Allegheny National Forest (60 ha).

Aerial photos and detailed maps of stand ages were used visually to establish eleven 10–18 ha plots away from
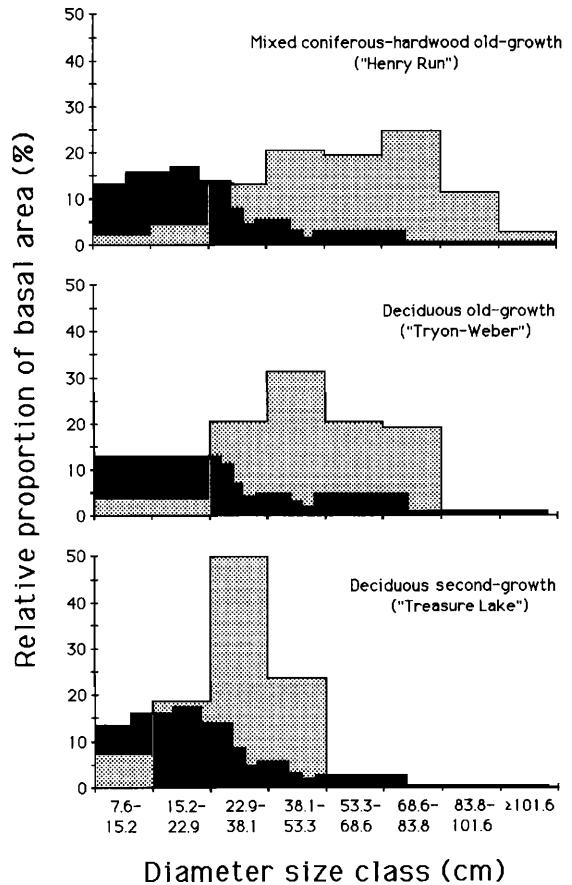

Figure 1. Characteristic diameter size-class distributions of old-growth mixed, old-growth deciduous, and young, previously-harvested deciduous forest. Black histograms represent regional averages for all size classes as calculated with data from the relevant regional unit as summarized in Alerich (1993); different widths to histograms reflect varying size-class intervals for which data were available. Stippled histograms represent the size distributions of trees observed on plots in this study.

roads, rights-of-way, habitat edges and extensive windthrows, and in areas where vegetation age and composition were relatively uniform. Due to limited availability, small size of potential study areas and other logistical constraints, random selection of study plots within sites was not feasible. Nevertheless, all plots were chosen without prior knowledge of the presence of Barred Owls. Variable extent and shape of old-growth forest remnants also necessitated study plots of different sizes; plot shapes were usually square or rectangular. Combined area of all study plots used in this study was approximately 4% of the total old-growth known to remain in Pennsylvania (Haney 1996).

Compared to nearby managed forests, old-growth sites

ın this study possessed stand ages older than the average age at which disturbances interrupt succession (200–300 yr), basal areas 30–73 m²/ha, large (70–100 cm dbh) live and dead trees, canopy cover ≥90% and a primary mode of disturbance by windthrow. Eastern hemlock made up 37–70% of the canopy at mixed forest sites; codominant canopy trees included various hardwoods and occasionally a few eastern white pine (*Pinus strobus*). All three large old-growth study sites were embedded in mostly unfragmented landscapes with extensive forest cover (≥3000 ha, Fig. 1).

Internal structure of mixed old-growth sites has never been altered substantially (Hunter 1989). Each site is dominated by very old forest. No extensive cutting has ever been conducted and stand ages (based on coring) are generally >300 yr. There is some evidence of historical fire in both Cook Forest and Heart's Content, but not in Tionesta (Hough 1936). American chestnut (*Castanea dentata*) was never prevalent (≤10% canopy) or widespread at study sites (Hough and Forbes 1943, Abrams and Ruffner 1995) except for Heart's Content, where it was once the third most common canopy species (Lutz 1930). On the other hand, there has been an eightfold reduction in total area of this forest type on the northern Appalachian Plateau since presettlement times (Abrams and Ruffner 1995).

Due to the regional rarity of deciduous old-growth (Erdman and Wiegman 1975, Smith 1989), only small sites with this forest type were available, and two plots did not meet the minimum preferred size for BBCs. Although possessing large trees, pit-and-mound topography, considerable coarse woody debris (CWD) and other elements of old-growth, the four smaller deciduous old-growth sites were probably cut selectively sometime late ın the 19th or early 20th century. Deciduous plots were located in fragmented landscapes; all were bordered on two or more sides by fields, roads and other open areas. Three sites were in glaciated northwestern Pennsylvania where original forest was beech-maple (*Fagus-Acer*). The fourth deciduous plot was dominated by a mixture of hardwoods, including hickory (*Carya*), oaks (*Quercus*) and maples.

Two 15-ha plots were also established in 40–60-yr-old managed forest on the Appalachian Plateau. Prior to cutting, compositions and basal areas of canopy trees on these plots were similar to the mixed old-growth forest. Further details on the vegetation, exact locations and topographic setting of study plots can be found in *J. Field Ornithol.* 65(Suppl.):73–74, 88–93, and 66(Suppl.):53–54, 56–59, 70–71, 82–88.

Data Collection. Barred Owls and nest sites were detected during repeated (7–10) visits to each study plot while territory mapping for BBCs during the 1993–94 breeding seasons; from one to three additional visits per plot were undertaken to measure vegetation. Each mapping visit, lasting from 1.5–4.0 hr, involved slowly walking established census lines ≤100 m apart and delineating bird territories within gridded plots at 25–50 m resolution. Order of visitation (date and time of day, whether dawn, mid-morning or dusk) was randomized. Two visits at dusk were generally made on each plot. All BBC visits were conducted between 22 April–5 July, a period coin-

ciding with incubation, brooding and prefledging of the Barred Owl (Johnsgard 1988).

Reproduction was determined by beak clapping, hissing and food-begging calls of young from within nest trees, or observations of stationary, prefledging juveniles outside nests begging from or being fed by adults. Adult owls often flushed from daytime roosts and gave nonelicited calls during visits, but adult presence alone was not considered evidence of reproduction.

Data Attributes and Model Construction. Study plots (Table 1) were quite small relative to home ranges recorded for Barred Owls (86–370 ha, Nicholls and Warner 1972); techniques appropriate for other birds, such as the BBC, are usually unsuitable for wide-ranging and secretive raptors (Fuller and Mosher 1981). Over spatial scales at which field work was conducted, occurrence of Barred Owl nests would be unexpected even if plots happened to be fortuitously located within an owl territory. This was not necessarily the case as plots were located solely on the basis of their old-growth chararacterıstics On the other hand, two or more plots that were close together might be situated within a single territory and thus not represent independent sample units.

These elements of the field sampling required developing a statistical approach that addressed explicitly each of the data attributes mentioned above. Thus, I chose a simple probability approach for testing occupancy of habitats by Barred Owls. Binomial models better account for frequency of occurrence in a set of samples (e.g., "incidence," Wright 1991), and similar approaches have been applied to other studies of *Strix* owls (Azuma et al. 1990, Gutiérrez 1994). The general null hypotheses tested were that Barred Owl reproduction and territorial occupancy did not occur in old-growth forest more than expected by chance.

Given a documented upper limit of approximately 370 ha for the home range (Nicholls and Warner 1972), only distances ≥1.0 km (the approximate radius of a circle having area 370 ha) could certainly be supposed to contain biologically-independent territories. Plots separated by distances less than 1000 m were therefore combined into a single unit, ultimately reducing sample size from 15 to 11 (Table 1). This interval to independence was of the same order used in other studies where the survey scale matched movement distances by the species (Bosakowski et al. 1987, Laidig and Dobkin 1995).

Modeling was approached as follows: if owl nests are located randomly within a hypothetical home range of area B, and plot A represents some fraction of this area, then let $p = A/B$. The variable p is the binomial for the likelihood that reproductive effort will be localized in area A (= positive incidence), and is expected to be quite small, except for plots of moderately large size (e.g., $p = 0.10$ if $A = 10$ ha and $B = 100$ ha). Values for A were derived from plot sizes used in the study, including plots combined due to spatial proximity (Table 1). Parameter values for B were obtained from the literature: minimum, mean and maximum home range (Nicholls and Warner 1972), and mean annual and mean summer home range (Elody and Sloan 1985).

Probabilities of owl reproduction on a particular plot were estimated by dividing its area, A, by each of the parameter values available for B. For plots studied both

Table 1. Cumulative (observed) probabilities ($\hat{p}$, $\hat{q}$, or $2\hat{p}\hat{q}$) of the likelihood of Barred Owl reproduction in sample plots during a 2-yr period in eastern old-growth forests. The subsample ($N = 11$ plots) includes four pairs of plots that were combined due to spatial proximity (see Methods). Final probabilities indicate the likelihood of obtaining as many instances of owl reproduction as were actually observed across all plots. Seven different estimates of Barred Owl home range size or density were used to develop probabilities.

| | PLOT | | | | | | |
| | MIXED CONIFEROUS-DECIDUOUS | | | | | | |
PARAMETER	SWAMP[a] 15 ha	SENECA[a] 15 ha	CATHE- DRAL/HILL- SIDE[a] 33.2 ha	HENRY RUN 15 ha	TIONESTA I,II[a] 24 ha	TIONESTA III,IV 24 ha	HC I,II 22 ha
BBC area (0.0095/ha)	0.2451[b]	0.2451	0.4326	0.1430	0.3529	0.7712	0.2097
BBC incidence (0.1413)	0.2532	0.2532	0.4417	0.1487	0.3627	0.7620	0.2182
Mean home range (229 ha)[c]	0.1207	0.1207	0.2448	0.0645	0.1851	0.8968	0.0946
Min. home range (86 ha)[c]	0.2880	0.2880	0.4740	0.1744	0.4024	0.7209	0.2558
Max. home range (369 ha)[c]	0.0778	0.0778	0.1634	0.0405	0.1213	0.9351	0.0595
Mean annual home range (282 ha)[e]	0.1007	0.1007	0.2077	0.0532	0.1557	0.9149	0.0780
Mean summer home range (118 ha)[e]	0.2219	0.2219	0.4044	0.1271	0.3240	0.7966	0.1864

[a] Plot studied during both breeding seasons (1993, 1994).
[b] Final probability based on multiplication rule, i.e., the product of all cumulative probabilities of owl reproduction across all plots.
[c] Nicholls and Warner (1972).
[d] Exact probabilities are 1.6 and 7.4 × 10^{-7} for maximum and mean annual home range parameters, respectively.
[e] Elody and Sloan (1985).

years, the probability of finding reproduction in one, neither or both study years is given by the binomial expansion: p^2, $\hat{q}^2$, or $2\hat{p}\hat{q}$, where $\hat{q} = 1 - \hat{p}$ (e.g., the probability that a plot will not have owl breeding; = negative incidence). Because in no plot was reproduction detected in both years, nor did any plot studied for two years fail to have reproduction in one of the years, in practice only $\hat{p}$, $\hat{q}$, or $2\hat{p}\hat{q}$ gave cumulative plot probabilities. The fact that no plot had nests or fledglings in both years, and plots studied for two years had a nest or fledglings in at least one year, mitigated against violating the independence assumption for binomial trials (Snedecor and Cochran 1980).

In addition to home range size, two other estimates of $\hat{p}$ based on published BBCs were available. The first ($\hat{p} = 0.0095$/ha) was calculated by dividing the total number of owl territories by the total area of all study plots in a sample of 92 BBCs (J. Field Ornithol. 64[Suppl.] and 65[Suppl.]). These 92 BBCs originated solely from within the species' range and consisted of all available plots from potential habitat (completely vegetated plots in upland forest). The second estimate ($\hat{p} = 0.1413$) was derived by taking the proportion of the 92 BBCs on which entire or partial Barred Owl territories were registered. Note that neither BBC estimate for $\hat{p}$ necessarily implies that reproduction occurred; rather, it is a measure of territorial occupancy.

Statistical Analyses. Each of five home range- and two BBC-based parameter values for $\hat{p}$ was used to calculate a plot-specific probability of reproduction for either one or two years; that is, the product of plot area with $\hat{p}$, $\hat{q}$, or $2\hat{p}\hat{q}$. Each of the seven parameter values was subsequently used to compute a final cumulative probability of reproduction using the binomial multiplication rule (e.g., the product of probabilities in a specified series of events such as owl reproduction in independent plots). Use of different parameter values for $\hat{p}$ acted as a sensitivity analysis in executions of the binomial model to allow examining whether results were solely the consequence of parameter outliers.

In a second approach, I used a two-sample test of proportions (Snedecor and Cochran 1980) to evaluate the probability of obtaining the observed number of Barred Owl territories in old-growth. If $\hat{p}_1$ is the probability of territorial occupancy in the sample of old-growth plot-years (where $N_1 = 15$), and $\hat{p}_2$ is the probability of territorial occupancy in a sample of BBCs ($N_2 = 92$ plot-years), then the test statistic for differences between two sample proportions is given by the normal deviate, Z, where:

$$Z = \hat{p}_1 - \hat{p}_2/\sqrt{\hat{p}\cdot\hat{q}(1/N_1 + 1/N_2)},$$

and $\hat{p}$ and $\hat{q}$ are the joint probabilities across all BBCs ($N = 107$) of finding and not finding owls, respectively.

Reproduction by Barred Owls at spatial scales employed in this study should be rare, a condition for which the Poisson distribution is well-suited. I calculated the expected number of reproductive events (nests or owl fledgings) in $r = 11$ trials (number of combined plots) using the highest, most conservative parameter value

Table 1. Extended.

		PLOT		
		DECIDUOUS		
PRINCE GALLITZIN 10.3 ha	ERIE I 6 ha	ERIE II 7.5 ha	TRYON-WEBER 9.8 ha	FINAL P
0.9023	0.9428	0.9285	0.0929	0.000109[b]
0.8984	0.9405	0.9256	0.0967	0.000129
0.9559	0.9742	0.9678	0.0419	0.000002
0.8808	0.9302	0.9128	0.1134	0.000247
0.9723	0.9838	0.9797	0.0264	<0.000001[d]
0.9637	0.9787	0.9734	0.0346	<0.000001[d]
0.9131	0.9492	0.9364	0.0826	<0.000064

available ($\hat{p}$ = 0.1413, Table 1). If owl reproductive events are distributed randomly with average incidence, $\hat{p}$, the number of events expected in a sample of size C is a Poisson variable with mean $\hat{p}C$ (Snedecor and Cochran 1980). If there are more incidences of owl reproduction than expected, the Poisson model will be a poor fit and the null hypothesis of randomness will be rejected. Expected values for the number of reproductive events ≥ 1 were figured with the Poisson expression:

$$\Sigma\, P(r) = (\hat{p}^r / r!)\, e^{-\hat{p}}, \quad \text{for all } r > 0,$$

and where e = 2.71828, the base of natural logarithms (Snedecor and Cochran 1980). Expected values were then compared to those actually observed using a χ^2 test for goodness-of-fit.

Although I provide exact probability values (P) for model runs, these estimates are biased (albeit conservatively so). For example, if any plot was actually outside an owl home range, values of $\hat{p}$ based on area would be inflated, increasing the likelihood of falsely accepting the null hypothesis of no effect of old-growth on owl reproduction. Such bias acts to increase the final absolute value of P. Although this increases risk of Type II error, I was more concerned in these analyses with making false conclusions regarding Barred Owl use of old-growth. Thus, P values should be considered as upper limits on the real chance of committing a Type I error. To guard against Type II error resulting from small sample sizes, inferences were considered significant at α = 0.10. When available, I provide observed significance levels (Forbes 1990).

Vegetation Measurement. On the basis of breeding, I poststratified plots to compare vegetation characteristics of forest stands used and not used by owls. Canopy composition and shrub stem density on all plots were estimated at randomly-drawn points with 0.04 ha circular subplots (James and Shugart 1970); sample size for circular subplots was set uniformly at one per ha of total plot size (4%). Canopy height was measured at each subplot with a clinometer. Canopy foliage (leaf) cover was

estimated with a concave spherical densiometer (Lemmon 1957) based on the average of measurements from four cardinal directions. Systematic transects were used to estimate size, total elliptical area and frequency of treefall gaps (Runkle 1985); 10 m × 50 m randomly-chosen rectangular plots were used to measure snag type and density, and type, volume and biomass of downed CWD (Tyrrell and Crow 1994).

RESULTS

Incidence of Reproduction. During both years, Barred Owls nested on 7 of 15 (47%) original plots, or 7 of 11 (64%) combined plots (those ≤ 1000 m apart). Nests (N = 1) or prefledging juveniles (N = 6 instances) were recorded on "Seneca" and "Tionesta I/II" in 1993, and "Swamp," "Hillside/Cathedral," "Henry Run," "Heart's Content I/II" (HC I) and "Tryon-Weber" in 1994 (Table 1). The single nest detected was in a live eastern hemlock with a broken top. Five of 6 sets of juveniles (1–3 individuals per brood) were also being fed in large, old hemlocks. Reproduction occurred on more of the combined plots dominated by mixed conifer-hardwood old-growth (86%) than plots dominated by deciduous old-growth (25%; Z = 2.033, P = 0.05).

Adult owls were recorded as visitors, or had partially-overlapping territories, on other plots and/or during other years: "Hillside/Cathedral" in 1993, and "Seneca," "Tionesta I/II" and "Erie II" in 1994. In none of these instances was reproduction confirmed, although it could have occurred nearby in similar forest surrounding most plots.

Model Results. With the first model, some parameter values for $\hat{p}$ gave significant incidences of reproduction on single plots within a single year. Reproductive incidence on the "Tryon-Weber" plot alone was significant for all but the minimum home range parameter ($\hat{p}$ > 0.10). Greater than expected reproduction in a single year also occurred when the model was executed with parameter maximum home range (5 plots), mean home range and mean annual home range (3 plots), BBC area, BBC incidence, and mean summer home range (1 plot). No plot had a significantly greater than expected incidence of reproduction within a single year when the model was executed with the minimum home range parameter.

Observed number of reproductive events in old-growth was highly unlikely due to chance alone (Table 1). No final cumulative probability with the binomial model exceeded P = 0.000247, and one cumulative probability (using the model parameter

Table 2. Comparison of observed and expected number of breeding incidences by Barred Owls in some eastern old-growth forest. Expected numbers were generated with a Poisson model of rare events in 11 trials (plots).

BREEDING INCIDENCES	EXPECTED	OBSERVED
0	9.551	4
≥1	1.449	7
Total	11.000	11

maximum home range) fell to $P = 1.6 \times 10^{-7}$. When all plots were analyzed jointly, each parameter value for $\hat{p}$ gave a highly significant final result, giving no indication that results came from outliers (extreme values) in model parameters.

Other statistical models gave similar results. There were more incidences of reproduction than expected under the Poisson model ($\chi^2 = 24.47$, $P < 0.0001$; Table 2). Based on a two-sample test of proportions, there were also more occurrences of territory occupancy in plots located in old-growth (80%) compared to younger, managed forests (14%; $Z = 5.63$, $P < 0.0001$).

Vegetation Characteristics. Relative to the entire regional landscape, diameter size distributions of canopy trees were different in old-growth plots used for breeding (Fig. 1). Both mixed and deciduous old-growth plots had more diverse diameter size classes in canopy trees, and were skewed toward trees in larger size classes. Most plots used by owls had at least some very large trees (70–100 cm dbh). No evidence of owl reproduction or of territorial occupancy was found in younger forest. Power to detect avoidance of this habitat type was very low, however. Analyses indicated that with the binomial model $N \geq 12$ 15-ha plots would be required to detect whether owls used younger forest less than expected.

Canopy complexity created by tree-fall gaps distinguished old-growth sites used and not used for breeding (Table 3). Owls bred where on average such canopy gaps opened up 8% of the stand; no breeding was observed where less than 5% of the stand was in tree-fall gaps. No significant differences were detected in the size class distributions of canopy gaps (Kolmogorov-Smirnov $\chi^2 = 3.34$, maximum difference 0.133, $P = 0.361$; Fig. 2).

Table 3. Comparison of forest structure at old-growth sites used and not used for breeding by Barred Owls.

STRUCTURAL CHARACTERISTIC	BREEDING ($N = 7$)			NOT BREEDING ($N = 9$[a] OR 10)			COMPARISON			
	$\bar{x}$	SE	RANGE	$\bar{x}$	SE	RANGE	Z[b]	U	U'	P[b]
Tree stems (per ha)	499	50.4	348–644	473	41.6	317–697	−0.342	31.5	38.5	0.732
Basal area (m²/ha)	38	2.7	30–49	42	4.1	31–73	−0.441	30.5	39.5	0.659
Hemlock basal area (m²/ha)	17	3.2	<1–25	12	4.1	0–30	−0.587	29	41	0.557
Canopy height (m)	30	2.0	21–34	29	1.8	20–37	−0.532	26.5	36.5	0.595
Range canopy height (m)	14	1.5	10–20	11	1.9	6–24	−1.865	14	49	0.062
Variation canopy height (CV)	16	1.9	11–25	12	1.2	8–19	−1.747	15	48	0.081
Canopy gaps (%)	8	1.0	5–13	4	0.8	0–9	−2.733	7	63	0.006
Mean canopy gap size (m²)	116	34.7	37–301	159	71.5	0–728	−0.489	30	40	0.625
Largest canopy gap (m²)	430	107	133–915	658	253	0–2261	−0.195	33	37	0.845
Foliage cover (%)[c]	96	1.1	92–99	97	0.7	93–99	−0.401	31	39	0.689
Snag stems (per ha)	32	5.6	12–54	42	6.0	20–73	−0.977	25	45	0.329
Snag basal area (m²/ha)	4	1.2	1–9	4	0.9	1–8	−0.683	28	42	0.495
Snag volume[d] (m³/ha)	48	13.5	3–100	51	21.8	4–222	−0.586	29	41	0.558
Volume CWD[e] (m³/ha)	152	47.8	20–408	142	57.9	8–612	−0.586	29	41	0.558
Biomass CWD (10³ kg/ha)	27.5	6.6	2.8–58.4	28.2	12.1	1.3–124.6	−0.781	27	43	0.435
Shrub stems (10³/ha)	4.8	2.7	0.2–20.7	5.9	2.5	1.2–24.6	−0.688	25	38	0.491

[a] Some missing data for one plot.
[b] Mann-Whitney U-test corrected for ties.
[c] Relative cover; high canopy cover in this study mitigated against potential positive biases found in some forest stands measured with densiometers (see Cook et al. 1995).
[d] Volume estimates based on decay classes defined in Cline et al. (1980), Tyrrell and Crow (1994).
[e] CWD = coarse woody debris; biomass of downed tree boles estimated as a function of decay class (Tyrrell and Crow 1994).

Table 4. Number of samples[a] (as a function of plot size, in ha) required to detect significantly more incidences (= positive incidence) of breeding by Barred Owls than expected by chance.

| | | ALPHA LEVEL | | | | | | | | | |
| | | $\alpha = 0.10$ | | | | | $\alpha = 0.05$ | | | | |
PARAMETER	PLOT SIZE =	5	10	15	20	25	5	10	15	20	25
BBC area		1	1	2	2	2	1	2	2	2	3
BBC incidence[b]		2	2	2	2	2	2	2	2	2	2
$\bar{x}$ home range		1	1	1	1	2	1	1	2	2	2
Min. home range		1	2	2	2	2	2	2	2	3	3
Max. home range		1	1	1	1	1	1	1	1	1	2
$\bar{x}$ ann. home range		1	1	1	1	1	1	1	1	2	2
$\bar{x}$ summer home range		1	1	2	2	2	1	2	2	2	2

[a] Number of samples in a binomial model based on differences in spatial scales between plot size and owl activity (see text).
[b] Number of samples is derived from a frequency-based parameter rather than a scale difference (see text).
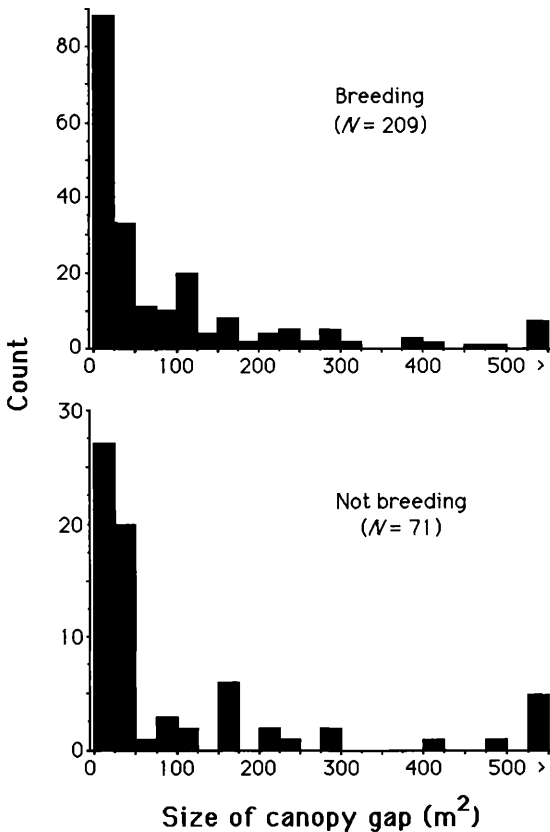

Figure 2. Canopy gap size-distributions in areas used and not used for breeding by Barred Owls (*Strix varia*).

Rather it was spatial arrangement of the canopy gaps (e.g., interspersion throughout the stand) that characterized breeding areas. Breeding sites on average also had an increase of approximately 25% in variability of canopy height (Table 3).

Plots with breeding owls were more likely to contain large (≥ 45 cm dbh) hemlock snags than plots not used for breeding (Fig. 3). Some plots on which owls bred had snags >100 cm dbh. Breeding owls were also more likely to use stands with higher densities of large snags (all tree species) and greater total snag basal area (all tree species).

Understory at breeding sites was generally sparse. Most plots on which Barred Owls bred had fewer shrubs and sapling trees (stems ≤ 7.6 cm dbh). Out of 15 original old-growth study plots, nine were used by owls for either breeding, roosting or foraging, and seven of these (78%) had shrub densities <3000 stems/ha. Conversely, 67% of old-growth plots where neither breeding, roosting or foraging was detected had shrub densities >3000 stems/ha.

Most other vegetation measurements exhibited little difference between old-growth areas used and not used by breeding owls (Table 3). For example, average tree diameter in all plots used for breeding ($\bar{x} = 31.7$ cm dbh, SD = 5.1, range = 24.4–38.5, $N = 7$) was not different than average tree diameter in plots not used ($\bar{x} = 33.9$ cm, SD = 6.9, range = 23.9–44.5, $N = 10$; Mann-Whitney U-test, Z corrected for ties = -0.684, $P = 0.4943$).
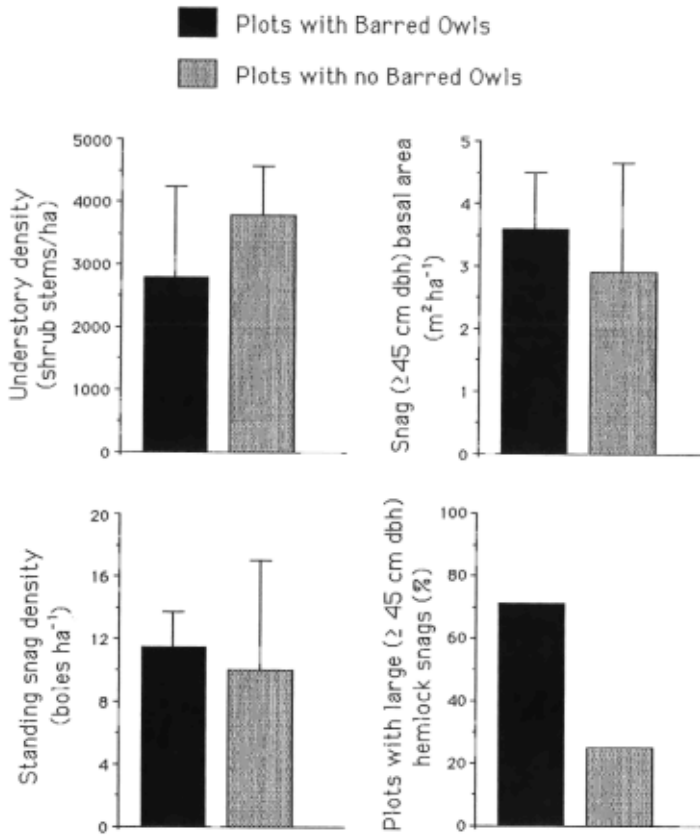
■ Plots with Barred Owls

▓ Plots with no Barred Owls

Figure 3.   Vegetation of forested plots with Barred Owl reproduction compared to plots without reproduction. Bars indicate +1 SE.

DISCUSSION

Scale and Type of Habitat Use. Barred Owl breeding was strongly linked to patches of old-growth hemlock-hardwood forest on the northern Appalachian Plateau. Given this owl's low density, such a large number of breeding events in a relatively small sample was not expected. At plot sizes ranging from 5–25 ha, however, and regardless of the home range parameter chosen, no more than 3 plots are required to detect greater-than-expected incidence of reproduction if all plots are used for nesting (Table 4).

Except at Tionesta, breeding territories of the size typically recorded for the species (Nicholls and Warner 1972, Elody and Sloan 1985) were unlikely to have been situated entirely within late successional forest; remnant patches of old-growth in this region are usually smaller than Barred Owl territories (Haney 1996). In silvicultural terms, the spa-

tial scale of habitat use observed in this study corresponds to the stand level. Specifically, Barred Owl use of breeding habitat was detected over scales on the order of 1–10s ha and horizontal distances of 10s–100s m.

These scales correspond to an activity center within the home range. Because habitat use of *Strix* owls is quite scale-sensitive (Carey et al. 1992, Hunter et al. 1995), use or selection at the level of nests or territories may differ. Further study might reveal whether microhabitat at nest sites used by Barred Owls is similar to their North American congeners (Seamans and Gutiérrez 1995) via comparison of nest to random sites (Buchanan et al. 1993), whether at landscape levels Barred Owl territories are smaller in or adjacent to old-growth (Carey et al. 1990) and whether territorial occupancy occurs in proportion to the availability of different seral stages. Habitat use is likely to vary also as a func-

tion of demography (sex, age), social organization (population, pair, individual; Carey et al. 1992) and activity type (foraging, roosting, or nesting; Ganey and Balda 1994).

Barred Owls and Old-growth. Forest contiguity and age both influence habitat use by Barred Owls (Bosakowski 1994, Laidig and Dobkin 1995). Hunter et al. (1995) found that fragmentation adjacent to nest sites influenced habitat selection of Spotted Owls. In contrast, several other studies cited by Hunter et al. (1995) found seral stage heterogeneity to be similar between random sites and areas used by Strix owls. Barred Owls prefer mature to young forest in patches of similar size (McGarigal and Fraser 1984). The preference for old-growth is not a regional artifact. In a follow-up study >800 km away, territorial occupancy and breeding by Barred Owls occurred in old-growth (≥200 yr) hemlock-hardwood forest more than expected by chance ($P \leq 0.017$ in all model executions; $N = 3$ plots [12–27 ha each] dispersed across three Southern Appalachian national forests).

Seeming inconsistencies in owl use of forested habitats may arise if all areas studied happen to meet a threshold of suitability. For example, although I did not find average tree diameter to differ between sites used and not used for breeding, my comparisons were restricted largely to old-growth, and thus all sites may have contained adequate features. Barred Owls avoid forests with average tree diameters ≤15 cm (Bosakowski et al. 1987). Average diameter for all forests in my study region was 20 cm (weighted mean, based on Alerich 1993); all sites where I detected breeding owls had average tree diameters ≥30 cm. Despite trees ≥50 cm dbh making up <2% of all stems on the northern Appalachian Plateau (Alerich 1993), some trees in this size class characterized each site used by Barred Owls in this study (Devereux and Mosher 1984).

Barred Owls are thought to prefer mature forest, including old-growth, due to greater availability of nest sites, because lower stem densities in the understory facilitate unimpeded visibility and travelways for foraging, or because dense canopies provide protection from mobbing (Nicholls and Warner 1972, McGarigal and Fraser 1984, Bosakowski 1994). Dense canopies also foster thermally-neutral microclimates for some Strix owls (Barrows 1981). Since all of these structural characteristics were evident on sites studied here, and I did not measure availability, it was not possible to identify which fac-

tor(s) were actually selected. Compared to younger forest, older forest provides other Strix owls with their preferred prey type, size, or abundance (Thrailkill and Bias 1989, Waters and Zabel 1995, Zabel et al. 1995). Barred owls usually have diverse diets (Bosakowski and Smith 1992), but the prey base in eastern old-growth would be worthy of detailed study.

Breeding sites were located where the canopy was more complex. These areas had more vertical variation in tree heights and greater horizontal patchiness and internal edge created by tree-fall gaps. Small openings that are interspersed throughout the stand yet still near breeding sites may facilitate foraging by adults who must satisfy both their own dietary needs as well as provision chicks. Thus, spatial juxtaposition of diverse ecological characteristics may enhance suitability of old-growth habitat for Barred Owls.

Any use of older forest by Barred Owls could have implications for conservation of the Northern Spotted Owl. Barred Owls have displaced (Sharp 1989) and interbred (Hamer et al. 1994) with Northern Spotted Owls during the past few decades in the Pacific Northwest. Although the former species has been implicated as more adaptable, throughout much of eastern North America the Barred Owl is the more specialized large owl (Laidig and Dobkin 1995), and its populations are impacted negatively by forest alterations detrimental to Northern Spotted Owls, such as fragmentation and seral truncation (Bosakowski 1994). I suggest that recent overlap in the ranges of Strix owls stems at least in part from their broadly-similar habitat requirements.

Management Considerations. As a codominant canopy tree (Rogers 1978), eastern hemlock plays a key role in providing habitat for Barred Owls. The "eastern hemlock" or "hemlock-white pine-hardwood" region (Nichols 1935) once stretched from the Great Lakes, St. Lawrence River Valley and New England south through the Southern Appalachians. Apparent antibiotic properties of hemlock litter (Rogers 1978) and canopy shading both tend to suppress understory vegetation, maintaining a rather open ground layer that may benefit foraging owls. After acheiving old-growth conditions at 275–300 yr (Tyrrell and Crow 1994), hemlocks tend to have snapped tops, broken limbs, cavity inclusions and other signs of decadence that furnish ample sites for nests as well as perches suitable for sit-and-wait foraging. Dense groves of hem-

lock also attract certain hawks, corvids and squir-rels, all of which construct bulky nests occasionally appropriated by Barred Owls (Johnsgard 1988). Hemlock decomposes more slowly than most hard-woods (Harmon et al. 1986), so snags suitable as nest sites tend to persist for long periods.

Because hemlock tends to grow well in shade (Rogers 1978), it ensures a continuous supply of replacement canopy dominants, thereby exploiting low-intensity disturbances typical of late-seral com-munities (Runkle 1982, Ward and Parker 1989). Hemlock's longevity ($\approx$800 yr; Loehle 1988) and low frequency of catastrophic stand disturbance ($\approx$1200 yr; Canham and Loucks 1984, Frelich and Lorimer 1991) would, historically, have tended to provide large areas of owl habitat. On the northern Appalachian Plateau alone, presettlement beech-hemlock forest covered 2.4 million ha (Bjorkblom and Larson 1977). Management practices that pro-mote stand development or allow expanded cov-erage of large hemlock (Farr and Tyndall 1992) are thus likely to benefit Barred Owls.

The Barred Owl's utility as a management indi-cator species is predicated on an affinity for older forest (USDA 1985, 1986). High breeding inci-dence in the very old stands studied here suggests that merely extending the rotation ages of timber harvests to $\approx$110 yr (the criterion for "old-growth" in many eastern forests) may not in itself provide optimal habitat for Barred Owls. Further research is needed on Barred Owl abundance, habitat use and reproduction across the full spectrum of stand ages representative of eastern forests.

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