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SPATIAL OVERLAP AND HABITAT ASSOCIATIONS OF BARRED OWLS AND GREAT HORNED OWLS IN SOUTHERN NEW JERSEY

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ABSTRACT.—Barred owls (*Strix varia*) are closely associated with relatively undisturbed mature forest, in contrast to great horned owls (*Bubo virginianus*) which are characteristically associated with highly fragmented landscapes of forests and fields. The two species are potential competitors, and great horned owls may prey upon barred owls. We assessed the relative abundance and distribution of both species in areas of known barred owl abundance by using taped playback of conspecific vocalizations. Estimated relative abundances of the two owls were virtually identical, and estimated home ranges overlapped extensively between the two species, although our data suggest that temporal partitioning may have reduced actual overlap. Barred owls were associated with cedar swamp-pitch pine lowland habitat and depended on mature hardwood swamp forest for nest sites, but suitable nesting habitat was extremely limited and occurred only in small patches. Forest fragmentation is likely responsible for the extraordinary degree of spatial overlap found between the two species in southern New Jersey and poses a continuing threat to the integrity of the region's barred owl population.

KEY WORDS: *Barred owl*; Bubo virginianus; *great horned owl*; *spatial overlap*; Strix varia; *temporal overlap*; *vocal responsiveness.*

Sobreposición espacial y asociaciones de hábitat de *Strix varia* y *Bubo virginianus* en el sur de New Jersey

RESUMEN.—*Strix varia* está estrechamente asociada a bosques maduros relativamente no perturbados, en contraste a *Bubo virginianus* característicamente asociado a paisajes de bosques y campos altamente fragmentados. Ambas especies son potencialmente competidoras, incluso *B. virginianus* puede predar sobre *S. varia.* Medimos la abundancia relativa y distribución de ambas especies en áreas de conocidas abundancias de *S. varia,* realizando "playbacks" con vocalizaciones conespecíficas. Las abundancias relativas estimadas para los dos búhos fueron virtualmente idénticas. Los rangos de hogar estimados se sobreponían extensamente entre ambas especies, aunque nuestros datos sugieren que la partición temporal puede haber reducido la actual sobreposición. *Strix varia* estaba asociado a hábitat de tierras bajas pantanosas y con pendiente, dependía de bosques leñosos maduros para ubicar sus nidos. Pero este propicio tipo de hábitat era extremadamente escaso y se daba sólo en pequeños parches. Probablemente, el fenómeno de la fragmentación de bosques es el responsable del extraordinario grado de sobreposición espacial entre ambas especies de búhos, en el sur de New Jersey y plantea una continua amenaza a la integridad de la población de *S. varia* de la región.

[Traducción de Ivan Lazo]

The barred owl (*Strix varia*) is widely distributed throughout North America east of the Rockies and across Canada to British Columbia (Clark et al. 1987, Johnsgard 1988). In recent years, the species has expanded its westernmost range into northwestern Montana and northern Idaho, southeastern Alaska, much of western British Columbia, and south through the Cascades of Washington, Oregon, and northern California (Johnsgard 1988, Verner et al. 1992).

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The broad geographic range of barred owls belies a distribution that is often highly localized because of their close association with mature and old-growth forest (Johnsgard 1988), and the owl's relative intolerance of anthropogenic disturbance (Bosakowski et al. 1987, Bosakowski 1989). For example, barred owls in New Jersey have been extirpated from many parts of the state (New Jersey Department of Environmental Protection 1985), and presently occur in substantive numbers only in the extreme northwest (Bosakowski et al. 1987, 1989a) and south (Sutton and Sutton 1985, Sutton 1988)—the only regions that still provide extensive tracts of relatively undisturbed broad-leaved or mixed forest.

Successful management of small, disjunct barred owl populations requires a clear understanding of population distribution and habitat dependency. Although portions of the area inhabited by the southern New Jersey population are protected from development within the Pinelands National Reserve, much of southern New Jersey remains subject to intense development pressure (Collins and Russell 1988). In addition, forest fragmentation as a result of clearcutting, firewood harvest, and deer management (as elsewhere in eastern North America) routinely create openings within contiguous forest. Such forestry practices bring the more disturbance-tolerant great horned owl (*Bubo virginianus*), with its regionally expanding population (Harwood 1988, Bosakowski et al. 1989b), into contact with the more reclusive, forest-dwelling barred owl (Bosakowski et al. 1987, 1989a,b). Great horned owls pose a potential threat to barred owls as predators of both adults and young (Bent 1938, Grant 1966, Fuller 1979, Bosakowski et al. 1989c), and as potential competitors with considerable prey overlap (Johnsgard 1988, Bosakowski and Smith 1992).

The objectives of our study were to (1) assess the relative abundances and distributions of barred owls and great horned owls in southern New Jersey, and (2) examine habitat associations of the two species.

METHODS AND STUDY AREAS

Barred owls and great horned owls were sampled separately during seven survey periods from May 1988 through May 1989, using tape playback of conspecific vocalizations. This technique is particularly efficient for detecting barred owls, which are reliably and highly responsive to tape playback or vocal imitation (McGarigal and Fraser 1984, 1985, Bosakowski 1987).

Six survey routes traversing areas with the greatest potential numbers of barred owls were selected based on previous roadside surveys conducted in southern New Jersey (Sutton and Sutton 1985, Sutton 1988). Survey routes were located in the state's three southernmost counties (Cape May, Cumberland, and Atlantic), and focused on Belleplain State Forest and adjacent state wildlife management areas, Great Cedar Swamp, Bear Swamp, and Mays Landing. Each survey route consisted of 10 broadcast stations at 1-km intervals. Taped territorial vocalizations (Peterson 1983) were broadcast at each station using a Uher 4000 Report Monitor set at full volume. Each broadcast consisted of six repetitions of a 10-sec set of calls followed by 50 sec of silence. The tape recorder speaker was rotated 180 degrees between each 10-sec set of vocalizations to provide broadcast into the forest on both sides of the roadway. Completion of each broadcast was followed by a 10-min response time. Barred owl broadcasts consisted of a single individual followed by a pair of owls emitting the "standard" vocalization. Great horned owl broadcasts consisted of an individual emitting the six- to eight-syllable call that is typical of this species.

Survey periods were separated by 6–8 wk; within each period, surveys for each species on a route were separated by 1–2 wk. Sampling order for each species was alternated between survey periods. Surveys were conducted between sundown and sunrise when wind speed was low and precipitation negligible. At each broadcast station, presence/absence data were collected based on vocal responses or visual contacts. This survey technique assumes that an owl's response indicates intrusion by a conspecific into its breeding territory or home range (Fuller and Mosher 1981).

To simplify habitat quantification, we approximated annual home ranges of owls (Nicholls and Fuller 1987) by circular plots superimposed on U.S. Fish and Wildlife Service National Wetland Inventory (NWI) vegetation maps, with each broadcast station as the center point. Our goal was not to precisely delimit owl home ranges or to determine centers of activity, but rather to characterize conservatively the relative habitat composition within areas likely utilized by owls. To facilitate comparisons, we used circular plots representing a home range of 369 ha for each species, based on radiotelemetry tracking studies conducted in other parts of their ranges (Nicholls and Warner 1972, Fuller 1979, Petersen 1979, Elody and Sloan 1985). Although 369 ha approaches the documented upper limit for barred owl home ranges, we selected this value because (1) it approximated the mid-range of great horned owl home-range sizes, (2) within species, avian home ranges tend to be larger in habitats characterized by low biological productivity (as found on the New Jersey coastal plain [Woodwell 1979]), and (3) roads generally were located in uplands, hence larger plots were necessary to counter underestimation of wetland habitat types. Circular plots of this size spaced at 1-km intervals ensured sampling of habitats at spatial scales appropriate to known movement distances by these species.

As noted by Bosakowski (1987), responses less than 2 km apart should be evaluated cautiously to consider whether owls belong to the same or adjacent territories. We conservatively assessed the spatial and temporal distribution of owl responses to taped vocalizations in combination with mapped estimated home ranges to determine the maximum number and distribution of owl home ranges on each survey route. (Sonagraphic analysis of taped vocal responses for individual identification of barred owls confirmed that at least some individuals responded from adjacent stations [Dobkin and Laidig unpubl. data].) We placed broadcast stations at relatively

Table 1. Number of stations ($N = 10$ per route) yielding barred owl/great horned owl responses on each survey, and estimated total number of home ranges for each species on each survey route in southern New Jersey, May 1988 to May 1989.

Route	Survey Month/Year							Estimated Home Ranges
	5/88	6/88	8/88	11/88	1/89	3/89	5/89	
Belleplain	2/1	0/1	2/3	4/2	2/0	2/1	3/1	3/3
Buckshutem	2/0	1/2	4/1	0/0	0/4	1/2	4/0	3/3
Cedar Swamp	1/0	0/0	1/0	0/1	1/3	0/2	1/0	1/1
Mays Landing	1/0	1/3	1/0	0/1	0/0	0/0	0/0	1/1
Port Elizabeth	3/1	0/4	1/2	0/0	2/1	0/3	2/0	2/2
Steelmantown	[a]	1/0	3/1	3/2	1/1	0/0	3/1	3/2
Total								13/12

[a] Not surveyed.

short, 1-km intervals to increase the probability of owl detections that might otherwise be missed due to (1) variation in owl location within its home range at the time of tape broadcast, and (2) variation in effective transmission distance of broadcasts and detectability of owl vocal responses.

Habitats at each broadcast station were determined from the NWI maps, which delimit 19 habitat types in the vicinity of the survey routes. We condensed these habitat types to five categories: (1) upland oak-pine forest (UP) dominated by relatively short, small-diameter trees, (2) hardwood-mixed hardwood swamp (HMS) usually dominated by large deciduous overstory trees and frequently with dense understories, (3) cedar swamp-pitch pine lowland (CSPP) consisting of Atlantic white cedar (*Chamaecyparis thyoides*) or pitch pine (*Pinus rigida*), respectively; lowland pine understories usually were quite dense, (4) shrub-scrub (SS) of low woody growth that often resulted from clearcut timber harvest, fire, or abandoned cranberry bog succession, and (5) emergent-open water wetlands (EMOW) of shallow ponds or marshes with a notable absence of trees and shrubs. More detailed accounts of floristic composition are provided by McCormick (1979). Coverage by each habitat within the plots was quantified with a Numonics electronic planimeter.

We used nonparametric statistics (Siegel and Castellan 1988) to avoid problems of nonnormality and heteroscedasticity in the data. Owl responses were analyzed by chi-square and binomial tests. Habitat differences between stations with and without owls were examined by Mann-Whitney U-tests. Frequencies of owl occurrence in relation to percent coverage of different habitats were assessed with Spearman rank correlations, but these tests were not performed on the shrub-scrub and emergent-open water habitat types to avoid distortion and possible spurious correlations due to the large number of zeros in the data set (Ludwig and Reynolds 1988).

Results

Relative Abundances and Vocal Responsiveness. We obtained a total of 53 barred owl and 44 great horned owl responses (Table 1). Routes that were most productive for barred owls also were the most productive for great horned owls. Conversely, routes that produced the fewest responses from barred owls also were the least productive for great horned owls (Table 1). Barred owls and great horned owls each responded at 31 of 60 stations surveyed (Table 2), with each species responding exclusively at 16 of 31 stations. Hence, over the duration of the entire study, neither

Table 2. Spatial overlap of barred owls (B) and great horned owls (G) based on responses[a] to playback of tape-recorded conspecific vocalizations along survey routes in southern New Jersey, May 1988 to May 1989.

Route	Broadcast Station Number									
	1	2	3	4	5	6	7	8	9	10
Belleplain	BG	–G	–G	BG	B–	–G	BG	B–	BG	BG
Buckshutem	BG	BG	BG	B–	B–	BG	BG	B–	––	–G
Cedar Swamp	––	–G	––	B–	BG	–G	––	––	––	––
Mays Landing	B–	–G	–G	–G	––	––	––	––	B–	––
Port Elizabeth	–G	B–	BG	B–	––	B–	–G	–G	–G	–G
Steelmantown	B–	B–	BG	BG	B–	B–	B–	–G	BG	–G

[a] B and G indicate at least one response at a station over the course of the entire study period; – indicates no response.

Table 3. Percent coverage of habitat types in 369-ha circular plots centered on owl survey stations (N = 60) in southern New Jersey.

Habitat Type[a]	Mean (SD)	Minimum	Maximum
UP	71.6 (19.0)	16.8	97.6
HMS	22.8 (16.9)	0.9	79.5
CSPP	2.0 (2.1)	0.0	13.1
SS	2.1 (3.2)	0.0	12.9
EMOW	1.5 (4.8)	0.0	32.6

[a] UP = upland oak-pine forest, HMS = deciduous hardwood-mixed hardwood swamp, CSPP = cedar swamp-pitch pine lowland, SS = shrub-scrub, EMOW = emergent-open water.

Table 4. Spearman rank correlation coefficients for barred owl and great horned owl occurrence with percent coverage by habitat type in estimated home ranges centered on each survey station (N = 60) along routes in southern New Jersey, May 1988 to May 1989.

Habitat Type[a]	Barred Owl	Great Horned Owl
UP	−0.14	0.00
HMS	0.21	−0.08
CSPP	0.30[b]	−0.08

[a] UP = upland oak-pine forest, HMS = deciduous hardwood-mixed hardwood swamp, CSPP = cedar swamp-pitch pine lowland
[b] P = 0.05.

positive nor negative interspecific association could be detected among stations. Of the 15 stations where both species responded, however, only four instances occurred in which both species responded from the same station within the same survey period (even though surveys for each species were separated by 1–2 wk). This suggests a possible avoidance or spatiotemporal partitioning of areas between the two species where home ranges overlapped extensively (z = 1.56, P = 0.06).

Viewed over the course of the entire study, adjacent stations frequently yielded responses from single individuals, but most occurred on different survey dates and were evoked in response only to playback at the nearest station. Hence, we view many of these as responses from the same individual. A conservative interpretation of the response data combined with mapping of estimated home ranges results in remarkably similar estimates of home range numbers for each species on each survey route (Table 1), for a total of 13 barred owl and 12 great horned owl home ranges.

Neither species exhibited seasonal differences in responsiveness to taped vocalizations in comparisons between breeding (March to June) and nonbreeding seasons (barred owls, χ^2 = 0.13, df = 1, $P > 0.35$; great horned owls, χ^2 = 0.49, df = 1, $P > 0.20$), or between spring/summer (March to August) and fall/winter (barred owls, χ^2 = 0.42, df = 1, $P > 0.25$; great horned owls, χ^2 = 0.32, df = 1, $P > 0.25$). We recorded the most barred owl responses in May and August, the fewest responses in March and June, and intermediate levels in the winter months (Table 1). Great horned owls responded in relatively uniform numbers across all months surveyed, except for a marked reduction in responsiveness in May surveys (Table 1).

Habitat Associations. Nearly 95% of the total habitat across the 60 stations consisted of upland oak-pine forest and mixed hardwood swamp (Table 3), although the latter comprised less than 25% of the total habitat. However, the percent coverage by each habitat type ranged widely among individual stations (Table 3).

Barred owls were associated positively (r_s = 0.30, P = 0.05, Table 4) with cedar swamp-pitch pine lowland habitat, but no other significant relationships were found in testing either frequency of owl occurrence (Table 4) or absolute owl occurrence (all tests $P > 0.10$) in relation to percent coverage of habitat types.

Discussion

Relative Abundances and Vocal Responsiveness. Our estimate of barred owl home ranges for all of the survey routes combined is considerably smaller than the numbers reported by Sutton (1988) in his survey of some of these same routes. Our estimates represent a more conservative approach based on survey data in combination with mapping of estimated home ranges over time, and supplemented with vocalization analyses. Sutton (1988) viewed responses from adjacent stations at different survey times as distinct individuals. We considered responses clustered around several adjacent broadcast stations as representing a single pair of birds unless vocalization analyses indicated otherwise. Even allowing for differences in estimation between the two surveys, our results indicate that fewer barred owls occur in southern New Jersey than assumed previously (Sutton 1988).

Other studies that examined habitat overlap between barred and great horned owls generally found distinct habitat separation, with overlap occurring only along forest margins or where open fields and woodlands were interspersed (Fuller 1979, McGarigal and Fraser 1984, Bosakowski et al. 1989a). We found virtually complete overlap of occupied areas, with only two of 13 estimated barred owl home ranges not extensively overlapped by estimated great horned owl ranges. We infer that the extraordinary degree of spatial overlap demonstrated in our study (1) results from the small-scale, but pervasive fragmentation created by narrow, forest-dividing corridors (Rich et al. 1994), logging, and deliberate ecotonal development for deer management in southern New Jersey forests, and (2) reflects the patchy distribution of mature hardwood and cedar swamp woodlands relative to the extensive oak-pine forest (Forman 1979).

Although spatial overlap was extensive, our data suggest that temporal partitioning may have reduced actual overlap of the two species, as demonstrated by Fuller (1979) with several instances of radio-tagged barred owls that exhibited apparent spatial avoidance behavior in response to great horned owls. Fuller (1979) found that while some annual home ranges of the two species overlapped considerably, very little home range overlap was evident when examined on a weekly basis. Similarly, although 16 stations yielded both species in our study, few overlaps were noted within individual survey periods.

Other studies have reported distinct seasonal variability in barred owl responsiveness to taped playback of vocalizations (Bosakowski 1987). In northern New Jersey, Bosakowski et al. (1987) found barred owl responsiveness to be greatest in the breeding season from March to June, with relatively few responses outside of these months. Smith (1978) recorded higher barred owl response rates in Connecticut in late spring (May to July), and Elody (1983) found high response rates in northern Michigan in summer months.

Incubation by barred owls in New Jersey occurs in March and early April with most egg dates falling between 17 and 29 March (Johnsgard 1988). Barred owl incubation requires 28–33 d and fledging averages 42 d posthatching (Ehrlich et al. 1988). Hence, we found maximum responsiveness during the nestling and early dispersal periods, and found minimal responsiveness during incubation and early fledgling periods. This pattern is consistent with very low calling rates recorded during incubation in western Maryland (Devereux and Mosher 1984). Overall, the data suggest that maximum responsiveness occurs during specific portions of the annual cycle (which happen progressively later at higher latitudes), a pattern that can be obscured by combining responsiveness data on a seasonal basis.

Marked seasonality in responsiveness to taped playback reportedly also characterizes great horned owls, which were noted as most responsive from December through March (Emlen 1973, Smith et al. 1987), but we found no evidence of seasonality. The only apparent deviation from relative uniformity across all months surveyed was the marked decrease seen in May surveys of both years, which corresponds to the beginning of the fledgling period for great horned owls in New Jersey (Bosakowski et al. 1989c), and is consistent with low responsiveness by barred owls during their early fledgling period.

Habitat Associations. Barred owls usually nest in the interior of contiguous forests with mature and decadent trees of sufficient size to provide cavities for nest sites (Dunstan and Sample 1972, Elody 1983, Allen 1987), preferably in stands with trees >51 cm dbh (Devereux and Mosher 1984). Of the habitats available in our study area, only mature hardwood swamps provided trees that were suitable for nest sites. The only old-growth forests in southern New Jersey are hardwood swamps that escaped logging by virtue of their relative inaccessibility. The high commercial value of Atlantic white cedar resulted in essentially complete (and repeated) harvest of cedar stands over the past 300 yr (Collins et al. 1988).

We believe that the association between barred owls and cedar swamp-pitch pine lowlands (which comprised only 2% of the total mapped area) indicates the importance of this habitat for roosting and foraging. Cedar stands provide camouflage and shelter as roost sites (Applegate 1975, Fuller 1979), especially when deciduous trees are leafless, and likely provide thermal refugia in summer (Havens 1979). Cedar swamps also support substantial populations of voles and shrews (Craig and Dobkin 1993)—the primary prey of barred owls in the region (Rusling 1951, Devereux and Mosher 1984, Bosakowski et al. 1987).

Not surprisingly, great horned owls were not associated with any particular habitat in our study, which is consistent with the view that this species is a habitat generalist (Fuller 1979, Petersen 1979, McGarigal and Fraser 1984, Bosakowski et al. 1989a) across the spectrum of forest habitats found in southern New Jersey.

Increased forest fragmentation as a result of habitat manipulation to increase deer populations (creation of "wildlife openings"), logging operations, and the proliferation of utility rights-of-way (Rich et al. 1994) will continue to create habitat conditions that are likely to benefit great horned owls, but negatively affect barred owls. Thus, the barred owl population in southern New Jersey cannot be considered secure. At the very least, land management activities should not be undertaken that will further diminish suitable barred owl habitat in the region.

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