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THE SPECIES-AREA RELATIONSHIP IN SPOT-MAP CENSUSING

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ABSTRACT.—To approach an understanding of how plot size affects the results of bird censuses using the spot-mapping method, the species-area effect was studied in two Breeding Bird Censuses (BBCs) and a Winter Bird-Population Study (WBPS). For one BBC (BBC-79) and the WBPS (WBPS-79), a 58.3 ha plot of apparently uniform pine habitat was subdivided into nine subplots. To simulate progressively larger sample areas, all possible combinations of the subplot censuses were made. A study area of 20 to 25 ha contains an estimated 80% of the species observed on the 58.3 ha plot in both winter and the breeding season in this habitat. A BBC (BBC-80) conducted on a 20 ha plot in the same habitat one year later, resulted in 71% of the species observed in BBC-79 on 58.3 ha. Censuses of the subplots were highly variable especially in the winter. A statistical technique, rarefaction, was used to compare the estimated species accumulation curves of the three censuses. The total number of species found in the 20 ha BBC-80 was predicted well by the rarefaction curve of the 58.3 ha BBC-79.

Evaluation of bird populations using the spot-mapping method (Williams 1936) is appropriate when detailed knowledge of the distribution of birds within a habitat is required (Robbins 1978a). This is the method used in the Breeding Bird Census (BBC) and the Winter Bird Population Study (WBPS) sponsored by the National Audubon Society (Anon. 1937, Anon. 1947). In 1979, sixty-four WBPSs were conducted in 22 states and 1 Canadian province and 219 BBCs were conducted in 33 states and 4 Canadian provinces. One of the original goals of the BBC was to permit comparisons between the bird communities of "stable" habitats and those of recently disturbed habitats. Long-term studies were encouraged to provide information about changes in bird communities in relation to plant succession (Anon. 1937).

The BBC and WBPS are based on the premise that careful standardization of methods will produce comparable data. Edge effects, habitat uniformity, and the method of data collection are important variables to be considered before comparing census results (Berthold 1976). Other aspects of data collection that should be considered are time of day (Shields 1977), season (Järvinen et al. 1977b, Slagsvold 1977), between-observer variability (Enemar et al. 1978), map interpretation (Svensson 1974b), grid distance (International Bird Census Committee 1970) and census speed (Robbins 1972). The influence of plot size or sampling area on the results is also an important consideration.

Suggestions have been made for the "minimum" plot size to obtain an adequate representation of a bird community (Table 1). However, the quantitative relationship between plot size and the results of spot-mapping censuses has been approached only recently (Verner 1980a, Engstrom and James 1981).

The species-area effect is simply that species number increases with sampling area (Kilburn 1966). In this study, the species-area effect is discussed in relation to the spot-map censusing method as illustrated by three bird censuses: two BBCs and one WBPS. Two of them, WBPS-79 and BBC-79, were conducted on a 58.3 ha plot which was divided into subplots; the third, BBC-80, was conducted one year later on a 20-ha subset of the 58.3 ha plot. The relationship between plot size and WBPS-79 is investigated in a more detailed paper (Engstrom and James 1981). All three censuses will be used to discuss (1) optimal plot size in this habitat in winter and spring, (2) how plot size affects the comparability of census results, (3) differences between the WBPS and BBC, and (4) how the bird population dynamics of this forest habitat affect census results.

A statistical technique, rarefaction, is used to generate estimated species accumulation curves for the three studies. The rarefaction curves of BBC-79 and BBC-80 are compared as independent descriptions of the same community using different plot sizes. Then rarefaction is used as a means of comparing the results of censuses conducted on plots of different sizes.

METHODS

The WBPS-79 and BBC-79 were conducted on a 58.3 ha plot of apparently homogeneous mature longleaf pine (*Pinus palustris*) forest south of Thomasville, Georgia. The habitat is annually burned and has an open appearance. Some of the trees are 200 to 300 years old. The main plot was divided into nine subplots of 6.5 ha each. The central subplot is surrounded on four sides and the other subplots share either two or three sides each. The accuracy of evaluating territories along a subplot boundary is probably improved if the boundary is shared by another subplot. This nested subplot design may be a source of bias in the

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TABLE 1
RECOMMENDATIONS FOR CENSUS PLOT SIZE

Source	Plot size	
	Open habitat	Closed habitat
IBCC (1970)	40 to 60 ha	10 to 30 ha
Webster (1966)		8 to 12 ha
Anon. (1947)		no smaller than 8 ha (20 ha ideal)
Hall (1964)		not less than 6 ha, 8 ha or more best
Kendeigh (1944)	30 ha	20 ha
Kolb (1965)		plots <8 ha produce biased results
Verner (1980a)		plots <20 ha produce biased results

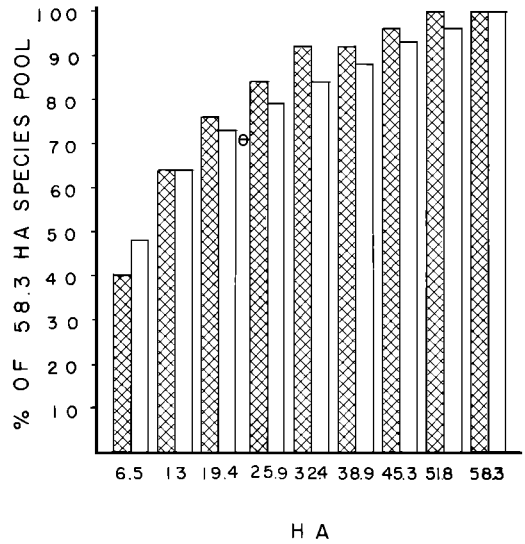

FIGURE 1. Proportional increase in species number with area. The average number of species for progressively larger sample areas can be determined by making all possible combinations of the 6.5-ha subplots. The average number of species for each simulated area as a proportion of the 58.3-ha plot species pool is represented for WBPS-79 (hatched bars) and BBC-79 (open bars). The bar-circle represents the percentage of the BBC-79 species pool observed on 20 ha in BBC-80.

subplot density estimates. However, I don't think that this strongly affected my results.

Independent censuses were made of each subplot according to the guidelines provided for the BBC (Anon. 1937, IBCC 1970) and the WBPS (Anon. 1947, IBCC 1970). Nine complete censuses were made in both the winter and spring. Each census took two days to complete. The effect of time of day on censusing was minimized by rotating the order in which the subplots were censused. Engstrom and James (1981) provide a more detailed description of the general procedure. BBC-80 was conducted on a 20 ha plot with no subplots during eight morning census trips.

All possible combinations of the nine subplot censuses were made to simulate the census results of progressively larger sample areas. For example, the nine 6.5 ha subplots permit 36 pairwise comparisons to make plots of 13 ha, 84 combinations to make 19.4 ha plots and so on. Each combination of subplots has an estimated number of species and individuals (or territories). It is important to recognize that the number of possible combinations varies between the different sized areas.

RESULTS

CENSUS RESULTS

The census results for WBPS-79 (Engstrom 1980b), BBC-79 (Engstrom 1980a) and BBC-80 (Engstrom 1981) are listed in Table 2. WBPS results are expressed in terms of the average number of individuals observed per trip, whereas BBC results are expressed in terms of territories as determined by evaluation of detection clusters and simultaneous records. This difference disallows direct comparison between the WBPS and the BBC.

Fourteen more species were seen during BBC-79 (39 species) than in WBPS-79 (25 species). A breakdown of the residency status of all species in both seasons (Table 2) reveals that 8 species (17%) occurred on the plot in the winter only, and 10 species (21%) were seen in the breeding season only. The remaining 29 species (62%) occur all year in the general vicinity. However, of the permanent resident species, 6 (13%) moved out of the plot during the winter and back again for the breeding season. Some species, such as the Red-headed Woodpecker, shifted habitats. Others occurred in flocks and were only observed flying over the plot in winter (e.g., Common Grackle). Some species might not have been detected because of decreased song and display.

ALL POSSIBLE COMBINATIONS OF SUBPLOTS

The average number of species for progressively larger sample areas can be derived from all possible combinations of the 6.5-ha subplots. The average number of species determined for each simulated sample area can be expressed as a percentage of the 58.3-ha species pool. This can be represented as a proportional increase in the number of species with increasing area for WBPS-79 and BBC-79 (Fig. 1). Within a plot size of 20 to 25 ha, approximately 80% of the species observed on the 58.3 ha plot would have

TABLE 2
THE NUMBER OF INDIVIDUALS IN WBPS-79 (58.3 HA), TERRITORIES IN BBC-79 (58.3 HA) AND BBC-80 (20 HA), AND RESIDENCY STATUS OF EACH SPECIES

Species	WBPS-79	BBC-79	BBC-80	Status[a]
Wood Duck (*Aix sponsa*)	+	2	2	WB
Bobwhite (*Colinus virginianus*)	–	2.5	2.5	BO
Mourning Dove (*Zenaida macroura*)	2	10.5	3	WB
Great Horned Owl (*Bubo virginianus*)	1	1	–	WB
Common Flicker (*Colaptes auratus*)	4	5	1.5	WB
Pileated Woodpecker (*Dryocopus pileatus*)	+	1	+	WB
Red-bellied Woodpecker (*Melanerpes carolinus*)	8	8.5	3.5	WB
Red-headed Woodpecker (*M. erythrocephalus*)	–	13.5	3.5	BO
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	3	–	–	W
Red-cockaded Woodpecker (*Picoides borealis*)	17	5	1.5	WB
Hairy Woodpecker (*Picoides villosus*)	+	1	1	WB
Downy Woodpecker (*Picoides pubescens*)	+	1	+	WB
Eastern Kingbird (*Tyrannus tyrannus*)	–	3	+	B
Great Crested Flycatcher (*Myiarchus crinitus*)	–	13	4	B
Eastern Wood Pewee (*Contopus virens*)	–	8.5	4.5	B
Blue Jay (*Cyanocitta cristata*)	2	8	2	WB
Common Crow (*Corvus brachyrhynchos*)	–	2	–	WB
Tufted Titmouse (*Parus bicolor*)	–	1	–	WB
White-breasted Nuthatch (*Sitta carolinensis*)	7	5	2.5	WB
Brown-headed Nuthatch (*Sitta pusilla*)	7	7	4.5	WB
House Wren (*Troglodytes aedon*)	9	–	–	W
Carolina Wren (*Thryothorus ludovicianus*)	4	4	2.5	WB
Northern Mockingbird (*Mimus polyglottos*)	–	1	–	BO
Brown Thrasher (*Toxostoma rufum*)	–	3	1	BO
American Robin (*Turdus americanus*)	8	–	–	W
Eastern Bluebird (*Sialia sialis*)	3	3	2	WB
Loggerhead Shrike (*Lanius ludovicianus*)	1	1	+	WB
Solitary Vireo (*Vireo solitarius*)	2	–	–	W
Yellow-throated Vireo (*Vireo flavifrons*)	–	1.5	+	B
Yellow-rumped Warbler (*Dendroica coronota*)	2	–	–	W
Pine Warbler (*Dendroica pinus*)	11	10	6.5	WB
Palm Warbler (*Dendroica palmarum*)	2	–	–	W
Common Yellowthroat (*Geothlypis trichas*)	12	14	4.5	WB
Yellow-breasted Chat (*Icteria virens*)	–	11.5	2.5	B
Eastern Meadowlark (*Sturnella magna*)	5	7.5	3	WB
Red-winged Blackbird (*Agelaius phoeniceus*)	60	2	–	WB
Common Grackle (*Quiscalus quicala*)	–	1	–	BO
Brown-headed Cowbird (*Molothrus ater*)	–	5	4	BO
Orchard Oriole (*Icterus spurius*)	–	2	1	B
Summer Tanager (*Piranga rubra*)	–	4	1.5	B
Cardinal (*Cardinalis cardinalis*)	1	4	–	WB
Blue Grosbeak (*Guiraca caerulea*)	–	11	3.5	B
American Goldfinch (*Carduelis tristis*)	1	–	–	W
Indigo Bunting (*Passerina cyanea*)	–	14.5	6.5	B
Rufous-sided Towhee (*Pipilo erythrophthalmus*)	16	30	11	WB
Bachman's Sparrow (*Aimophila aestivalis*)	–	16.5	8	B
Swamp Sparrow (*Melospiza georgiana*)	1	–	–	W
Total species	25	39	27	
Total estimated density	189	245	94.5	

[a] WB = permanent resident, winter and breeding season; BO = permanent resident, breeding season only; W = winter resident only; B = breeding resident only.

been encountered in both winter and spring. Also note that the number of species observed in BBC-80 on 20 ha (27 species) is very close to the average number observed in BBC-79 (28 species) for the simulated 19.4 ha sample area.

RAREFACTION

Rarefaction is a statistical technique that can be used to generate a curve of the expected number of species in smaller random samples

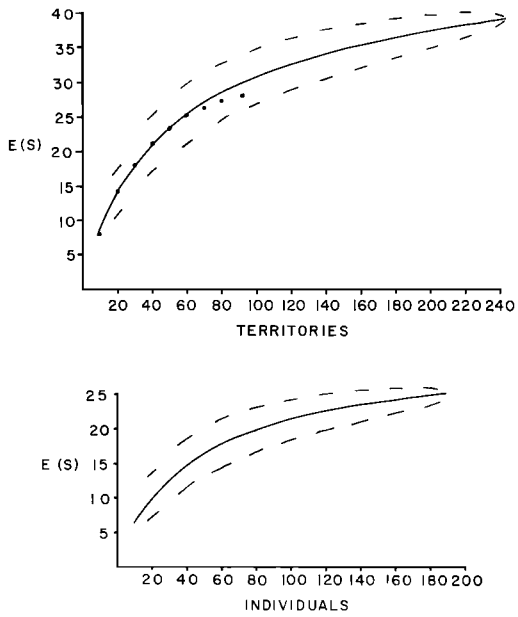

FIGURE 2. Rarefaction curves for BBC-79, BBC-80, and WBPS-79. The estimated number of species for any randomly drawn number of territories or individuals is represented by E(S). FIGURE 2a. These are the rearfaction curves for BBC-79 and BBC-80 combined. The heavy dots represent BBC-80. The solid line is BBC-79. The dashed line represents two standard deviations around BBC-79. The BBC-79 and BBC-80 curves were derived independently of each other. FIGURE 2b. The solid line represents the rarefaction curve for WBPS-79. The dashed line is two standard deviations about the curve.

than the original sample (Sanders 1968, Hurlbert 1971, Fager 1972, Simberloff 1978a). Given N individuals in S species, the expected number of species, $E(S)$, and its standard deviation can be calculated, A Fortran program is available upon request. Rarefaction makes it possible to compare the species richness of different-sized samples using the curves depicting the accumulation of S as a function of N.

Rarefaction curves were prepared for BBC-79 and BBC-80 (Fig. 2a) and WBPS-79 (Fig.2b). Again note that for the BBCs, the abscissa represents territories, but the abscissa of the WBPS curve is the average number of individuals per trip. The data for all three rarefaction curves are given in Table 2. The half-territories of the BBCs were rounded either up or down on a random basis to generate integers; pluses were omitted. The curve representing BBC-80 is well within two standard deviations of BBC-79, indicating that the rarefaction curve did not change much between the study years.

DISCUSSION

The species-area effect is a well-established ecological concept. An increase in species number can be attributable to an increase in habitat diversity with increasing area, by an increase in area per se, or by the "sampling effect," i.e., that larger areas may support more species simply because they contain larger samples of the source fauna (Connor and McCoy 1979). The longleaf pine forest was selected for this study because it appears to be very uniform. The subjective selection of a "representative" portion of a truly uniform habitat should not be difficult, yet all habitats have some degree of patchiness. In contrast to the uniform appearance, quantitative habitat descriptions and bird censuses of the subplots of WBPS-79 (Engstrom and James In press) and BBC-79 revealed substantial variation in habitat structure. This is simular to the results of Kilburn (1966) in a study of the species-area relationship of the plants in a jack pine (*Pinus banksiana*) forest. He found that even though the pine community was selected for its homogeneous appearance, "this apparent similarity was somewhat deceptive."

A large sampling area will reduce the effect of subjectively selecting a census plot in a patchy environment. In this open pine habitat during both WBPS-79 and BBC-79, a plot size of 20 to 25 ha was found to have roughly 80% of the species observed over an area 2 to 3 times larger. Censuses conducted on plots of less than 10 ha can be misleading because they tend to overestimate avian density (Verner 1981) or have more variable results (Engstrom and James In press). The BBC-80 on a 20 ha plot represented 71% of the species seen the year before on the 58.3 ha plot. Determination of sample area should be made on the basis of the amount of habitat available, the grid size, sampling speed and the area needed to obtain an adequate representation of the species pool. A census of 20 to 25 ha could be done effectively in early morning hours, and is the optimal plot size in this habitat.

Rarefaction was originally developed as a means of obtaining an estimate of diversity independent of sample size (Sanders 1968). The estimated species accumulation curves were thought to be habitat specific. James and Rathbun (MS) have generated rarefaction curves from many BBCs made in a wide variety of habitats. The curves are distinctive for each habitat and provide a good means of comparing the communities. The rarefaction curve for BBC-80 falls very close to the BBC-79 curve (Fig. 2a). We can predict the number of species expected for BBC-80 by arithmetically estimating the

number of territories at 84 (245 territories from BBC-79 × 20 ha/58.3 ha) and then estimating the number of species (28 ± 2) by rarefaction. In fact, 27 species with 94 territories were detected on BBC-80.

Long-term studies of bird communities in different habitats over a large area are of great value for both theoretical ecology and resource management, if conducted in a systematic and comparable way. For example, Järvinen and Väisänen (1979a) used long-term censuses to explore the influence of climatic change, habitat alteration, and possible competition in the range dynamics of two pairs of congeners. Lynch and Whitcomb (1977) have used BBCs to look at species turnover rates in habitat islands. Järvinen (1979) made a quantitative test of European bird community stability along a north-south gradient using long-term spot-map censuses.

In conclusion, a number of points related to comparability of spot-map censuses can be made. These points include: (1) censuses conducted on plots of less than 10 ha cannot be reliably compared; (2) in this study, a plot size of 20 to 25 ha represents an optimal balance between minimizing censusing effort and providing an adequate sample of the bird community; (3) more information is needed on grid distances and censusing speeds in different habitats to improve spot-map method guidelines; and (4) rarefaction is a valuable method for comparing species richness of censuses conducted on plots of different size.

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