

Detecting Area Sensitivity: A Comment on Previous Studies

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ABSTRACT.—Several studies have reported that some grassland birds are area sensitive; they exhibit a nonrandom avoidance of small fields. The methods used to test for area sensitivity, however, differed among studies. Some investigators sampled fields with sampling effort proportional to field size, whereas others used equal sampling effort in all fields. We created a simulation model with the same number of fields and field sizes as those examined in earlier studies to determine if birds that select habitat randomly would display area sensitivity if fields were sampled in proportion to their size. The three species that we modeled to settle randomly, upland sandpiper (*Bartramia longicauda*), Henslow's sparrow (*Ammodramus henslowii*) and eastern meadowlark (*Sturnella magna*), had positive relationships between occurrence and field size when a complete census or proportional sampling was used, and therefore, would have been considered area sensitive by the methods used by some previous authors. When equal-effort sampling was used, these species showed no relationship between occurrence and field size. Future studies on area sensitivity that use proportional sampling should compare results to a null model. Otherwise, conclusions made about area sensitivity may be erroneous because the response is a sampling artifact.

INTRODUCTION

One proposed reason for the population declines of grassland birds is habitat loss and fragmentation of their breeding ground (Herkert, 1994; Vickery *et al.*, 1994; Warner, 1994; Igl and Johnson, 1997). Habitat fragmentation may result in a landscape of small habitat patches within a matrix of unusable habitat (Meffe and Carroll, 1994; Primack, 1995). Small habitat patches may be unsuitable for many species of grassland birds. Thus, larger patches may contain a greater number of individuals and species (Samson, 1980; Herkert, 1994; Vickery *et al.*, 1994). Species that are found more often in larger patches than smaller patches are termed "area sensitive" (Robbins *et al.*, 1989; Herkert, 1994; Vickery *et al.*, 1994). Although not always explicitly stated in area sensitivity definitions, it is generally assumed that the reason a species is not found in small patches is biological, not because of a sampling bias (Askins *et al.*, 1990).

Area sensitivity of grassland birds has been studied in several regions including Missouri (Samson, 1980), Nebraska (Helzer and Jelinski, 1999), Illinois (Herkert, 1994; Walk and Warner, 1999) and Maine (Vickery *et al.*, 1994). However, methods used to study area sensitivity differed. For example, Samson (1980), Helzer and Jelinski (1999) and Walk and Warner (1999) sampled fields proportionately with field size. Vickery *et al.* (1994) used equal sampling effort in all fields.

Several of the previous studies that sampled fields in proportion to their size did not correct for differences in sampling effort, but concluded that species they studied were area sensitive. We asked whether sampling fields in proportion to each field's size, without correcting for differences in sampling effort, is a valid way to determine whether a species is

area sensitive. To do this, we simulated the random settlement of three grassland bird species in a landscape that had the same number of fields and field sizes used in the study by Walk and Warner (1999) to see if birds that settled in fields randomly would exhibit a relationship between probability of occurrence and field size. Furthermore, we examined how varying densities and using different sampling techniques would influence relationships we observed between occurrence and field size.

METHODS

We developed a simulation model to determine if positive occurrence-area patterns could be derived from random settlement, and how different population densities and types of sampling may affect these patterns. The model we used simulated the landscape investigated by Walk and Warner (1999), an agricultural landscape with nine grassland fields that were 7, 17, 32, 40, 44, 64, 72, 93 and 120 ha (collectively referred to as the landscape). We simulated three species: upland sandpiper (*Bartramia longicauda*), Henslow's sparrow (*Ammodramus henslowii*) and eastern meadowlark (*Sturnella magna*). These species were chosen because each occurred in the Walk and Warner study and these species have a wide range of breeding territory requirements. We used a 10.0 ha territory size for upland sandpiper, 3.0 for eastern meadowlark and 0.6 for Henslow's sparrow (Wiens, 1969; Lanyon, 1995).

We determined the maximum number of potential breeding territories available in the landscape (T_{max}) by dividing each field size by the average territory size for each species and rounding to the nearest whole number. Although some species may use matrix habitat for foraging and display, we assumed that individuals required an amount of grassland equal to the average territory size of the species. The species considered nest primarily in grassland habitat and not in rowcrop fields (Best *et al.*, 1997). For simulations, we assumed that habitat quality within and among fields was similar. This is a biologically unlikely assumption; however, it is conservative and makes it harder to detect differences.

To simulate random settlement we seeded the landscape with individuals that randomly chose territories from unoccupied habitat (T_{max}) in the landscape. Individuals were seeded into the landscape sequentially. After a territory was occupied it was no longer available to other individuals. Each individual had an equal probability of selecting any unoccupied territory on any field in the landscape. Each species was investigated independently; we assumed no interspecific territorial exclusion. For each species we ran the model at three population densities: low density (5% of T_{max}), moderate density (10% of T_{max}) and high density (20% of T_{max}). These densities correspond to 0.04, 0.10 and 0.20 birds per 10 ha for upland sandpiper at low, moderate and high densities, respectively; 0.84, 1.68 and 3.33 for Henslow's sparrow; and 0.16, 0.32 and 0.67 for eastern meadowlark. The densities we selected are similar to the ones reported by Koford (1999) for small-bodied grassland birds in Minnesota and North Dakota. Moreover, habitat selection is generally detected only at lower densities, and the densities selected will indicate how changes in population size affect occurrence-area patterns.

Because sampling may potentially affect results from occurrence-area studies, for each species at each density we sampled the landscape using three techniques: a complete census, an equal-effort sample and a proportional sample. The complete census considered the total number of individuals entered into the landscape and the occurrence of these individuals in each field. For equal-effort sampling and proportional sampling we simulated 3 ha sampling units, a size equivalent to a 100 m radius point count. For equal-effort sampling we randomly picked one 3 ha unit in each field during each simulation. For proportional sampling we used a stratified random sampling technique where approximately 50% of the patch was sampled using 3 ha sampling units. For each patch we stratified the habitat based

on the total number of sampling units for that patch. In order to cover the field each stratum was 5–7 ha and one 3 ha sampling unit was randomly picked to sample in each stratum during each simulation. For example, the largest field in the landscape, 120 ha, contained 20 strata each containing 6 ha of habitat. In each simulation one 3 ha sampling unit was randomly picked to sample in each of the 20 strata covering a total of 60 ha. When all or part of an occupied territory fell within a sampling unit, we considered the individual to be detected.

We ran 100 simulations for each species at each density in the landscape. Using logistic regression, we determined whether the occurrence of the three species under varying densities and sampling techniques was influenced by field size. Data were analyzed using the Logistic Procedure of the SAS Statistical Package (Stokes *et al.*, 1995). We used a Bonferroni correction to account for multiple tests of the same hypothesis (Snedecor and Cochran, 1989), and results were considered significant if $\alpha < 0.0019$. We plotted incidence functions using the upper and lower 99% confidence limits for each field to examine if species that settled randomly showed positive occurrence-area patterns and if these patterns differed using different sampling techniques and at different densities.

RESULTS

For all three species our simulations revealed a positive relationship between probability of occurrence in a field and field size when individual birds randomly selected territories in a landscape and a complete census was used (Table 1, Figs. 1–3). The one exception to this pattern was the Henslow's sparrow at high density. In this case we detected no relationship and the 99% upper confidence limit reached 100% probability of occurrence at the smallest field size (Table 1, Fig. 2). In all cases we found positive relationships between occurrence and field size when fields were sampled in proportion to their size (Table 1, Figs. 1–3). Conversely, we found no relationship between occurrence and field size when equal-effort sampling was used (Table 1, Figs. 1–3).

DISCUSSION

We demonstrated a positive relationship between probability of occurrence and field size if birds select fields randomly and fields are sampled in proportion to field size or with a complete census. Thus, studies that use proportional sampling and find a positive relationship between a species' probability of occurrence and field size do not necessarily indicate that the species is area sensitive. Results of Samson (1980), Helzer and Jelinski (1999) and Walk and Warner (1999) are difficult to interpret because the observed patterns could be a sampling artifact or could indeed be due to sensitivity to area.

Although Samson (1980), Helzer and Jelinski (1999) and Walk and Warner (1999) do not demonstrate that grassland birds are area sensitive, they do confirm that there is a higher probability of detecting a grassland bird in larger fields. Thus, given a 25 ha field and a 50 ha field, proportional sampling of both fields would have a greater probability of detecting birds in the 50 ha field than in the 25 ha field. However, future studies on the area sensitivity of grassland birds should assess whether the same number and species of grassland birds would be found in five 10 ha fields as compared to one 50 ha field. For example, Robbins *et al.* (1989) compared the number of 1 ha, 10 ha and 50 ha forests that would have to be sampled in order to have the same probability of occurrence as a single point count in a large forest tract where probability of occurrence is at a maximum. If the species was not area sensitive, the number of smaller tracts that needed to be sampled should be one, whereas for area sensitive species the result should be greater than one—a result found by Robbins *et al.* (1989).

TABLE 1.—Logistic regression summary statistics for an analysis of the effects of field size on the probability of occurrence of three grassland bird species that randomly choose unoccupied territories in a landscape under varying densities and using different sampling techniques

Species/sampling technique/density	Parameter estimate	Wald's χ^2	P	Concordance (%)
Upland sandpiper				
Census				
Low density	0.019	58.12	0.0001	63.3
Moderate density	0.029	142.29	0.0001	70.3
High density	0.040	155.75	0.0001	75.3
Proportional sampling				
Low density	0.026	89.50	0.0001	68.2
Moderate density	0.021	89.48	0.0001	63.3
High density	0.024	104.58	0.0001	65.6
Equal-effort sampling				
Low density	-0.009	2.70	0.1003	52.5
Moderate density	-0.003	0.99	0.3188	45.6
High density	-0.002	0.63	0.4255	45.0
Henslow's sparrow				
Census				
Low density	0.133	87.15	0.0001	89.7
Moderate density	0.160	26.80	0.0001	88.9
High density	0.807	0.13	0.7183	89.5
Proportional sampling				
Low density	0.057	142.50	0.0001	80.4
Moderate density	0.112	97.19	0.0001	88.6
High density	0.170	26.80	0.0001	87.4
Equal-effort sampling				
Low density	-0.003	1.30	0.2538	47.6
Moderate density	-0.001	0.13	0.7913	44.3
High density	0.001	0.24	0.6259	45.5
Eastern meadowlark				
Census				
Low density	0.040	178.05	0.0001	75.9
Moderate density	0.056	157.20	0.0001	80.8
High density	0.105	104.70	0.0001	88.0
Proportional sampling				
Low density	0.024	106.83	0.0001	67.0
Moderate density	0.036	164.49	0.0001	74.5
High density	0.053	140.42	0.0001	79.2
Equal-effort sampling				
Low density	0.001	0.06	0.8007	36.4
Moderate density	0.006	4.36	0.0368	50.1
High density	0.002	0.62	0.4322	46.1

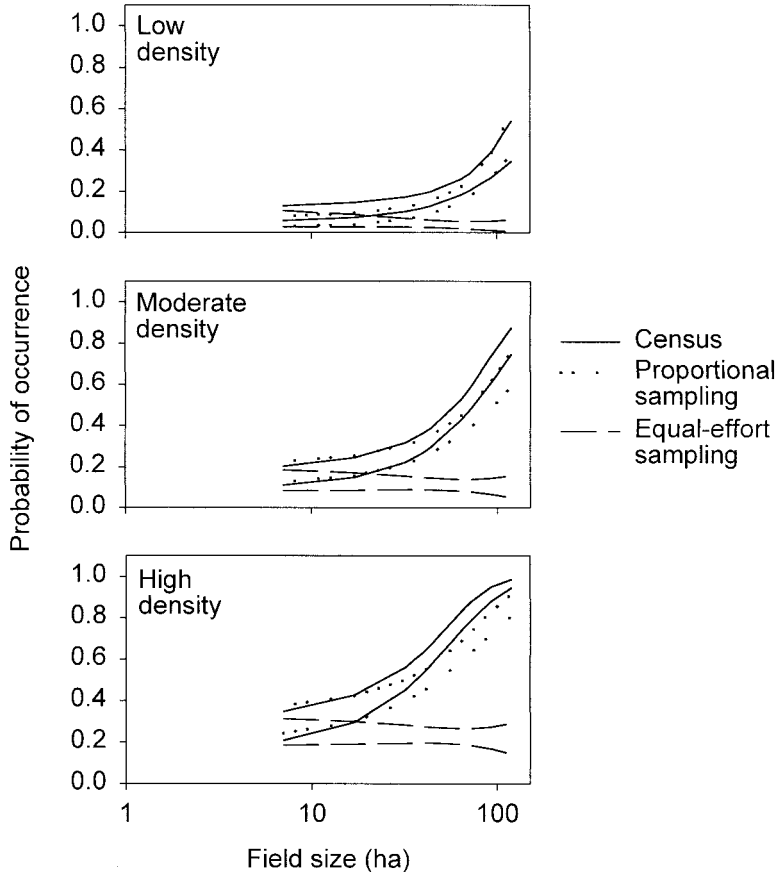


FIG. 1.—Relationships between probability of occurrence of randomly settling upland sandpipers in a field and field size under varying densities using different sampling techniques. Plotted incidence functions are the 99% confidence limits for each field

Future studies using proportional sampling should also use a null model to determine whether a species is area sensitive (e.g., Hinsley *et al.*, 1996). One possible null model would be the expected relationship between probability of occurrence and field size given the relative abundance of the species. In order to account for proportional sampling, Hinsley *et al.* (1996) compared the expected number of pairs of birds in a patch [(population size observed in all patches/total area of all patches) \times size of given patch] to the observed number of pairs in a patch. They then used linear regression to determine if there was a residual relationship between the difference in observed and expected pairs of birds in a patch and patch size. A significant difference indicated that the relationship between occurrence and patch size was more than just a function of sampling.

Results from our model simulations demonstrate that, when birds settle randomly and fields are sampled with equal effort, no relationship between probability of occurrence and field size is detected. Thus, using equal sampling effort in fields will also lead to an accurate assessment of a species' area sensitivity (e.g., Askins *et al.*, 1990; Vickery *et al.*, 1994). For

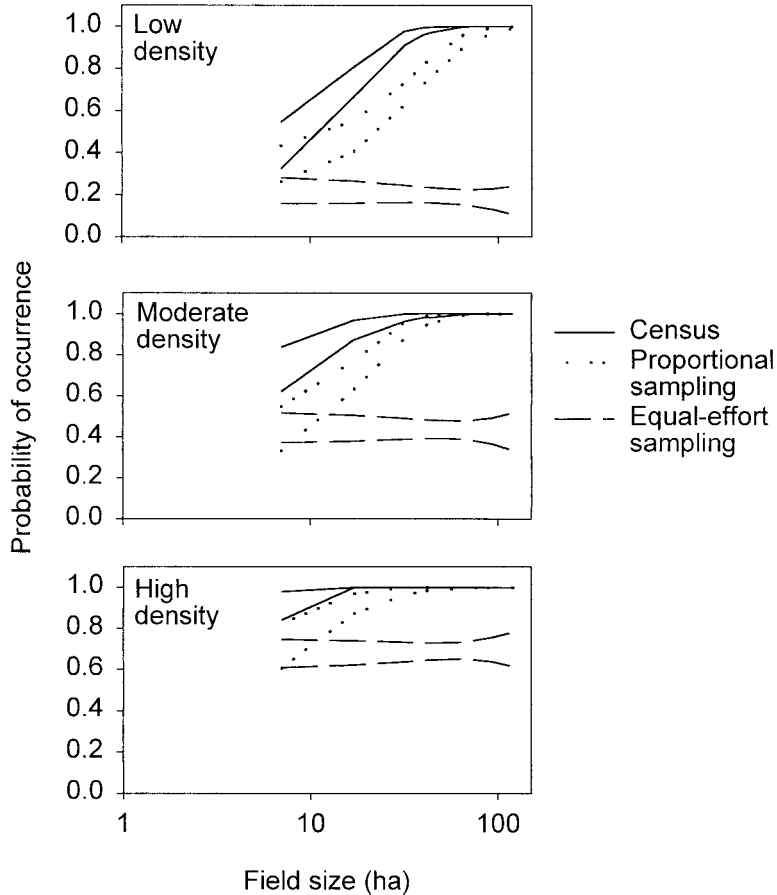


FIG. 2.—Relationships between probability of occurrence of randomly settling Henslow's sparrows in a field and field size under varying densities using different sampling techniques. Plotted incidence functions are the 99% confidence limits for each field

example, Vickery *et al.* (1994) used only one randomly selected census plot at each of their fields to determine occurrence-field size relationships. Using null models and equal sampling effort have previously been advocated for addressing species-area relationships (*e.g.*, Connor and McCoy, 1979; Haila, 1986).

One scenario where fields are sampled in proportion to field size and a null model may not be necessary is for small-bodied birds found at high densities. In our model, when the density of Henslow's sparrow was high, we found no relationship between probability of occurrence and field size when a complete census was used. Thus, if a species had a high density, a positive relationship between probability of occurrence and field size would most likely be an indication of area sensitivity and not a sampling artifact.

The relationship between probability of occurrence and field size will be influenced by variation in density, regardless of the sampling method used to detect area sensitivity (Vickery *et al.*, 1994). If a species' density is high, birds may occupy all territories in all fields.

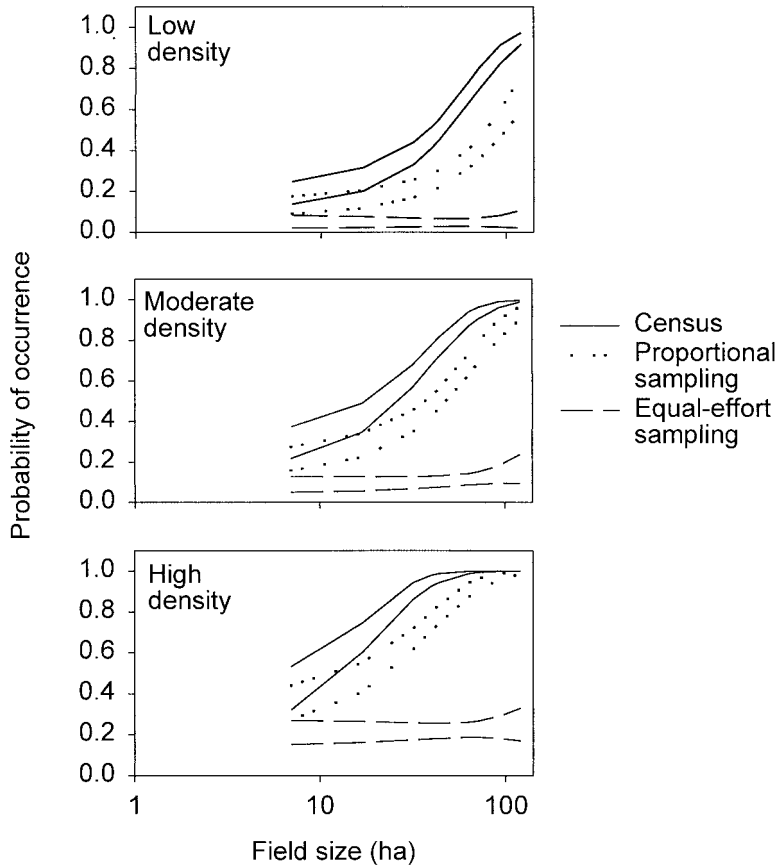


FIG. 3.—Relationships between probability of occurrence of randomly settling eastern meadowlarks in a field and field size under varying densities using different sampling techniques. Plotted incidence functions are the 99% confidence limits for each field

Thus, investigators would not detect a relationship between occurrence and field size. If a species' density was low, investigators may not detect birds on any fields and a relationship between occurrence and field size would not be found simply because the species' probability of detection was low. This is illustrated in our model when comparing large and small-bodied birds at density extremes. Using equal-effort sampling, the occurrence of Henslow's sparrow at high density was already 0.65 at the smallest field we modeled, whereas the occurrence of upland sandpiper at low density using equal-effort sampling was <0.10 at the largest field we modeled.

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