Testing the importance of patch scale on forest birds

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The relationship between population density and habitat area is of central importance to conservation biology, particularly for species dependent on declining habitat. A recent study by Lee et al. in Oikos in 2002 found that the densities of three forest interior bird species (ovenbirds, wood thrushes, and red-eyed vireos) decline with increasing patch size, contradicting many other studies that demonstrate a positive correlation between area and density for these species. The authors’ argument is based on a misapplied criticism of the prevailing approach based on density, and on an inappropriate statistical methodology, caused by incorrect specification of the null hypothesis after log-transformation. We use three different methods of testing area-dependence: a corrected log–abundance log–area regression; a similar abundance–area regression; and the prevailing density–area approach. For each species, all three methods agree broadly, suggesting the robustness of each approach. For ovenbirds and wood thrushes, we do not find that population density is negatively correlated to patch size. While our analyses of the red-eyed vireo data find a negative correlation between the two factors, the strength of the correlation is far weaker than that of Lee et al. and may derive from landscape factors unconsidered in the original data. Nevertheless, we do not find positive density–area relationships for any of these forest-interior species, further underscoring the site-specificity of the underlying mechanisms of area-sensitivity.

The relationship between population density and habitat area is of central importance to reserve design, landscape management, and conservation biology in general. Lee et al. (2002) examined this crucial question in a fragmented, agriculture-dominated landscape for three forest-dependent bird species, ovenbirds (Seiurus aurocapillus), wood thrushes (Hylocichla mustelina) and red-eyed vireos (Vireo olivaceus). They concluded that density is inversely related to forest patch area for all three species. This conclusion is rather surprising in light of the many studies reporting a positive correlation between density and area for these species (Robbins et al. 1989, Gibbs and Faaborg 1990, Hawrot and Niemi 1996, Porneluzi and Faaborg 1999, Howell et al. 2000). The mechanisms driving this positive correlation are well understood, particularly in agriculture-dominated landscapes: reduced forest area worsens reproductive success due to nest predation and brood parasitism, lowers adult survival, and decreases dispersal (Donovan et al. 1995a, 1995b, Hoover et al. 1995, Trine 1998, Weinberg and Roth 1998, Burke and Nol 2000, Hobson and Bayne 2000, Mancke and Gavín 2000, Bélisle et al. 2001, Bayne and Hobson 2002, Gobeil and Villard 2002).

Our examination of Lee et al.’s (2002) methodology reveals that their surprising results are partly attributable to inappropriate statistical methods. Following Martin (1981), Lee et al. (2002) tested the null hypothesis that the density (abundance, N, over area, A) of each species is independent of patch area through linear regressions of log-abundance on log-area. They compared the slopes of the best-fit lines with 1 (the slope of the line expected under the null hypothesis for log-transformed data) by a t-test on the regression coefficient. However, because Lee et al. (2002) had numerous absences (N = 0) and ln(0) is undefined, they took ln(N + 1) rather than ln(N). Martin (1981) had no abundances of 0, so could test ln(N) without these problems.

Unfortunately, the null hypothesis under a ln(N + 1) transformation is not a slope of 1, which undermines Lee et al.’s (2002) test of the null hypothesis. Given the low densities and small patch sizes in Lee et al.’s (2002) dataset, the predicted ln(N + 1) under constant density is a curved function of ln(A), with slopes considerably less than 1. Any other log-transformation (e.g. ln(N + 0.5)) also yields a curved predicted line with respect to area under the constant-density null hypothesis, defying a simple t-test of the slope. Log-transformations with small additions (e.g. ln(N+0.01)) have little curving effect on the expected slope, but instead cause abundances of 0 to have extreme values and to dominate regressions (e.g. ln(0.01) = −4.61, ln(1.01) = 0.01, ln(2.01) = 0.70, and ln(3.01) = 1.10). Furthermore, the null hypothesis of constant density also specifies an intercept for the best-
fit line of abundance on area (under any transform), but Lee et al.’s (2002) t-test addressed only the slope.

The simplest and most common test of constant density would be to regress density on patch size (Connor et al. 2000). Lee et al. (2002) rejected this approach, referring to statistical problems with ratio variables (since density = N/A), citing Jackson et al. (1990) and Berges (1997). Both papers focus on a problem of spurious correlations that arise when scientists impute causal importance to the relationship between D = B/C and C, where B and C are independent variables. Because of the independence between B and C, large values of C generally result in small values of D, causing a negative (but spurious) correlation between D and C. The problem that Jackson et al. (1990) and Berges (1997) discuss is explicitly one of interpretation, when the negative relationship between D and C is derived entirely from independence of B and C, but this fact is forgotten in the interpretation of a causal mechanism for the relationship between D and C. In the present case we are not vulnerable to such misinterpretation. Negative correlations between density and patch size are easily and correctly interpreted as weak relationships between abundance and area, and nonsignificant or positive correlations between density and area are interpreted just as easily as greater-than-linear relationships between abundance and area. Since concerns of spurious correlations do not apply to the current case, the validity of analyses of density and area depends upon the usual concerns, such as normality and homogenous variance.

We reanalyze Lee et al.’s (2002) data using three simple regression analyses, each testing the null hypothesis that bird density is constant across the forest patches in question.

Analysis 1
Reconsideration of Lee et al.’s (2002) approach, log-transformed abundance vs log-transformed patch size (ln(N+1) on ln(A)). Linear regressions usually test the explanatory power added by allowing the slope of the best-fit line to vary (compared with the null hypothesis of a 0 slope, the global mean value of the dependent variable). In this case, the null hypothesis is not a fixed 0 slope, but a slope equal to the global mean density, which manifests in a curved line upon ln(N+1)-transformation. By calculating null-hypothesized expected values using patch sizes and the mean density, we adopted a regression to test the extent to which the regression adds explanatory power relative to the null hypothesis (the regression allows both slope and intercept to vary, while our null hypothesis allows only the slope to vary; the regular null hypothesis of regressions allows only the intercept to vary).

We tested the additional explanatory power of the alternative hypothesis through the sum of squared deviations of the linear regression from the null hypothesis. This sum of squares replaces the sum of squares in a regular linear regression in calculation of the mean square and F-statistic, as the degrees of freedom and residual error remain the same.

Analysis 2
Abundance vs patch size (N on A), testing the deviation of the best-fit line from the null hypothesis of constant density using the same procedure as analysis 1. While it is possible to test the two components of the null hypothesis (0 intercept, constant slope) separately, it is more appropriate to test the null hypothesis as a whole as explained above. When testing the components separately, it is possible for tests of the two to interfere with each other, since the best-fit intercept is calculated based on the assumption of a straight-line relationship. Accordingly, a curved relationship and non-zero intercept could manifest in a best-fit line with nonsignificant intercept and slope.

Analysis 3
Density vs patch size (N/A on A), testing the best-fit slope vs 0. Though all three approaches agree broadly, each analysis has associated concerns. In analysis 3, one assumption of linear regression – homogeneity of variance – does not hold, as the variance of density is negatively correlated with patch area. The heterogeneous variance of analysis 3 may be biasing the analyses towards non-significance (type II error): all P-values for this analysis are higher than the corresponding P-values from the other analyses. For analysis 2, regressions of abundance on area might over-emphasize the few large patches. On the other hand, analyses of the variables of concern are generally preferable to analyses of transformed variables (analysis 1) unless there are clear biological or statistical reasons supporting the transformation.

For two of the bird species, our results differ qualitatively from those of Lee et al. (2002). All three analyses for ovenbirds and wood thrushes fail to reject the null hypothesis of constant density across forest patch size (Fig. 1, 2. Ovenbird: P1 = 0.126, P2 = 0.466, P3 = 0.610. Wood thrush: P1 = 0.096, P2 = 0.097, P3 = 0.758). Our reanalysis of Lee et al.’s (2002) results complies better with other studies, which report positive relationships between patch area and density of these species, but there is still some disconnect. It is possible that the remaining discrepancy can be explained partly by differences in the ecological context between sites: the literature suggests that there are considerable differences.
between the abilities of small to medium forest fragments (≤ 20 ha – 1000 ha) to support wood thrushes (Hahn and Hatfield 1995, Trine 1998). Perhaps Lee et al.’s (2002) study site is unusually free of factors that elsewhere greatly depress reproductive success in small fragments.

For the red-eyed vireo, all three analyses find significant deviations from the null hypothesis, indicating density decline with increasing patch size (Fig. 3; $P_1 = 0.001, P_2 = 0.001, P_3 = 0.003$). These findings agree qualitatively with Lee et al. (2002), although our results suggest a smaller negative impact of area on density. The apparent negative impact of area conflicts with other studies on this species, which show a non-negative correlation between the two factors (Burke and Nol 2000, Dunford et al. 2002). There is some reason to believe this result is in part a consequence of the small-sized landscape units in Lee et al.’s (2002) original study. Lee et al. (2002) considered their study landscapes (squares 200 ha in area) to be sufficiently large, based on evidence that wood thrushes and ovenbirds seldom venture outside of their 2 ha territories. However, red-eyed vireos are apparently affected by the environment at a much larger scale, as population density increases along with local forest cover within a 2 km radius of bird territories (Dunford et al. 2002). Lee et al. (2002) characterize the entire study region as containing...
3% forest cover. Indeed, our analysis of the map provided in their paper indicates that forest cover comprises 40–45% of the region, with much more in a 2 km radius of many of their landscape units. At such high levels of forest cover, landscape-level factors might play an exceptionally large role in patch-level population dynamics (Andrén 1994, Fahrig 1997), though the strength of the factors would depend heavily on the cover spatial structure and species characteristics (Bender et al. 1998).

We conclude that Lee et al.’s (2002) finding of a negative relationship of forest bird density with patch area stemmed from misrepresentation of the null hypothesis of constant density. Our reanalysis of their data demonstrates that three different approaches – including the prevailing density–area regression – agree broadly with each other, but not the results of Lee et al. (2002). We find non-significant relationships between patch size and the density of ovenbirds and wood thrushes. While this result aligns better with previous findings regarding these species, it still differs from the common finding of a positive density–area relationship. Like Lee et al. (2002), we find a significant decline in the density of red-eyed vireos with increasing size of forest patches. Together, these results suggest that the mechanisms of area-sensitivity are context-dependent in these three species.

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References


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