



Body mass, habitat generality, and avian community composition in forest remnants

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ABSTRACT

Aim Many theories of biodiversity and biogeography assume that species respond equally to variability in habitat area and isolation. This assumption does not allow for differential responses due to interspecific competition or other mechanisms, and therefore does not allow community composition to be predicted. As body size is relevant to area requirements and interspecific dominance, a natural experiment was conducted to quantify the differential responses of avian species abundance to variability in remnant area, isolation and forest cover based on average species body mass.

Location Deciduous forest remnants of varying area and isolation throughout the State of Delaware, USA.

Methods Forest remnants within stratified area and isolation classes were randomly selected for breeding bird surveys; total forest cover (ha) within 2 km of each survey point was subsequently determined as a covariate. Surveys were conducted within 100–150 m from the edge of each remnant and detected bird species were divided into five classes based on a \log_2 -transformation of body mass (very small, small, medium, large and very large). Assuming a negative binomial distribution, the abundance of detected individuals in each mass class was analysed using generalized linear models with remnant area, isolation, local forest cover and two-way interactions specified as independent variables. The same analyses were conducted for individual species where sample size allowed.

Results Very small, small and very large bodied species decreased in abundance with decreasing local forest cover and remnant area and with increasing remnant isolation, while large species increased in abundance. Medium-sized species decreased in abundance with increasing forest cover, did not respond to remnant isolation and showed a concave, curvilinear response to increasing remnant area. Large and medium-sized species were the most abundant birds in small, isolated remnants despite occurring in the largest remnants with the more abundant very small and small species, suggesting that communities are not randomly organized.

Main conclusions Regardless of presumed habitat associations, large and medium-sized species are of the appropriate size to be dominant competitors when forest resources are limiting, and thus may be considered 'generalists'. The smallest species may be excluded entirely from small, isolated remnants even though such remnants meet their ecological needs; the needs of very large species are not met in small remnants. The applicability of biodiversity theories to community composition, species abundance and, by extension, to conservation, can be improved by incorporating differential responses based on body mass into their assumptions.

Keywords

Biogeography, community assembly, conservation biology, deforestation, Delaware forest fragmentation, interspecific competition, USA.

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INTRODUCTION

Despite extensive evidence that body mass and interspecific competition influence community composition and dynamics (e.g. Schoener, 1983; Martin & Martin, 2001; Luck & Daily, 2003; Brown & Sullivan, 2005; Mac Nally & Timewell, 2005; Parsons *et al.*, 2006), biotic variables or interactions are poorly integrated into theories of biodiversity and biogeography. Many classical and current theories treat the response of individual species to given area and isolation conditions of uniform habitat equally and anonymously (MacArthur & Wilson, 1967; Hubbell, 2001), yet species differentially respond to these factors (MacArthur & Wilson, 1967; Whittaker, 1998; Trzcinski *et al.*, 1999; Brown & Sullivan, 2005). While these assumptions, such as random species turnover, have allowed some success at predicting species richness among true islands and habitat islands, theoretical and basic applications related to community composition and the abundance of individual species are much more limited.

Predicting community composition in forest remnants is a continuing challenge because the response of individual species may depend on the degree of forest removal and the scale at which the response is measured (Fahrig, 2003). Unlike the universally negative effect that landscape-scale deforestation has on populations of forest species (Drapeau *et al.*, 2000; Fahrig, 2003), local fragmentation effects are not consistent (Fahrig, 2003). For example, some avian species increase in local abundance in small, isolated remnants while other species are rarely present, even if the remnant meets their home range or territorial area requirements (Brown & Sullivan, 2005). The negative effects of deforestation may be correlated with, or confounded by, the secondary effects of forest fragmentation, defined as 'the breaking apart of habitat, independent of habitat loss' (Fahrig, 2003). Fragmentation effects may include those due to increased amounts of edge, greater isolation and loss of connectivity among forest remnants, remnant shape and interspecific competition (Robinson *et al.*, 1995; Schmiegelow & Mönkkönen, 2002; Fahrig, 2003; Henle *et al.*, 2004; Brown & Sullivan, 2005). Except for interspecific competition, including nest predation and nest parasitism ('encounter competition'; Schoener, 1983), these commonly described fragmentation effects indicate the degree to which forest resources (e.g. food, nest sites, mates) may be limiting. Interspecific competition, of various forms (see Schoener, 1983), may be a response to such limitation and influence the composition of avian communities in forest remnants (Grey *et al.*, 1997; Brown & Sullivan, 2005; Parsons *et al.*, 2006).

Predicting the effects of forest cover, remnant area, remnant isolation (see review by Fahrig, 2003) and average species body mass, a surrogate for competitive ability, on community composition is of theoretical interest and of practical concern because a substantial amount of forested habitat has been removed and degraded at continental (Noss & Cooperrider, 1994; Foster *et al.*, 2002), regional and local scales (Environmental Law Institute, 1999; Radeloff *et al.*, 2005). From a resource-based perspective, deforestation and the subsequent

isolation and degradation of resultant forest remnants lead to three general predictions regarding the effects of body mass on community composition: (1) very large species will not occur in small remnants because insufficient resources are available to meet their basal metabolic or ecological requirements; (2) the smallest species will not occur in small remnants because they will be out-competed by any larger species whose needs are met in those remnants; (3) medium- and large-sized species are more likely to occur in small remnants and may even increase in local abundance because of reduced interference from other species (Terborgh, 1974; Brown & Sullivan, 2005). Other medium- and large-sized species not commonly considered as forest birds (e.g. European starling, mourning dove, common grackle; see Appendix S1 in Supplementary Material for scientific names), yet which use forest remnants during some aspect of their life cycle, may successfully compete for forest resources too, especially if resources become limiting. These body mass patterns also are expected to be nested within guilds, such as feeding and nesting guilds, which may extend across taxonomic boundaries.

Interactions among remnant area, isolation and degree of local forest cover complicate these predictions. Individuals that occur in remnants within a forest-dominated landscape may experience effects different from those of individuals in similar sized remnants in a landscape otherwise devoid of forest (Trzcinski *et al.*, 1999; Fahrig, 2003). It is expected that any community structuring effects of limiting forest resources will be prominent in the smallest and most isolated remnants and less distinct as local forest cover and remnant area increase and as remnant isolation decreases (Watson *et al.*, 2005).

Data were collected on breeding bird abundances from 296 forest remnants in the State of Delaware to test the prediction that species differentially respond to limited forest resources based on their body mass. Body mass patterns within the insectivorous and cup-nesting guilds of forest birds also were explored.

METHODS

As it was logistically impossible to create forest remnants of controlled area and isolation within landscapes of specified composition, a natural experiment was conducted (Cody, 1974) to test the above predictions. Delaware was suitable for such an experiment because most of the state lies within one physiographic province, the coastal plain, elevation is nearly constant statewide, many forests have been fragmented and isolated for more than 30 years (Fleming, 1978; Environmental Law Institute, 1999) and wide ranges of remnant area and isolation existed.

Land-use classification

The independently derived classification of the 2002 State of Delaware land-use/land-cover (LULC; http://stateplanning.delaware.gov/info/lulcdata/2002_lulc.shtml) map was accepted for determining forest remnant composition. LULC polygon

boundaries were first digitized from 1-m resolution ortho-photos before they were classified into land-cover types. Additional polygons classified as deciduous forest by the Delaware Natural Heritage Program from the same data were merged with the LULC map to create a statewide digital forest coverage. Only deciduous and mixed deciduous–coniferous (hereafter ‘mixed’) forest remnants were of concern in this study; mixed forests may meet some of the breeding requirements of birds that use deciduous forest remnants. Coniferous forest remnants or plantations were not included in any surveys, analyses or statistics presented here.

As forest birds may be unwilling to cross even short distances between remnants during the breeding season (Bélisle & Desrochers, 2002), the forest coverage was overlaid with a digital statewide road system (<http://datamil.delaware.gov/>) used to split forest polygons into separate, smaller polygons. Remnant statistics and the sampling design (below) were determined from these modified polygons.

Avian mass classes

Detected bird species ($n = 54$) were divided into five classes based on a \log_2 -transformation of body mass (mass followed Sibley, 2000). The \log_2 -transformation was used to increase the number of mass categories available for analyses, and therefore resolution of results (Hubbell, 2001), as compared with a \log_{10} -transformation of mass where only three broad categories were possible. ‘Very small’ species ranged in mass from 3 to 11 g ($\log_2 = 2-3$, $n = 7$ species), ‘small’ species ranged from 12 to 22 g ($\log_2 = 4$, $n = 16$), ‘medium’ species ranged from 27 to 47 g ($\log_2 = 5$, $n = 11$), ‘large’ species ranged from 49 to 135 g ($\log_2 = 6-7$, $n = 12$) and ‘very large’ species ranged in mass from 290 to 7400 g ($\log_2 > 7$, $n = 8$; Appendix S1). These classifications are for the convenience of grouping and describing patterns among similar-sized species in this study; it is not suggested that these designations are necessarily useful in other systems. All detected species (see Appendix S1) were used in analyses involving mass classes.

Remnant area, isolation and forest cover

The area, isolation and surrounding local forest cover of deciduous and mixed forest polygons statewide were determined using ArcView 3.2 (ESRI, Inc., 1999) and Fragstats 3.3 (McGarigal & Marks, 2002) on a rasterized, resampled statewide forest coverage with a pixel size of 20 m. Except for very large birds, home ranges for nearly all other species were 1–2 ha (see <http://www.oikos.ekol.lu.se/app.html>, appendix O13725 for home range values of North American forest birds; Brown & Sullivan, 2005). Other ‘non-forest’ species such as the European starling, blue jay, northern flicker, brown-headed cowbird and cedar waxwing have variable, yet similar, home range or territorial area requirements (1–2 ha; Tarvin *et al.*, 1998; Moore, 1995; Elchuk & Wiebe, 2003; Hansen & Urban, 1992). These species were detected during surveys of Delaware forest remnants (see Appendix S1) and were similarly

detected in other studies of forest birds in eastern North America (Robbins *et al.*, 1989; Austen *et al.*, 2001). Starting with this common home range size, 10 classes of forest remnant areas were determined on a \log_2 -scale to establish an inclusive sampling scheme: 1–2, 2–4, 4–8, 8–16, 16–32, 32–64, 64–128, 128–256, 256–512 and remnants > 512 ha.

The isolation of a given forest remnant was the shortest straight-line distance (m) to the next nearest deciduous or mixed forest remnant (Robbins *et al.*, 1989). As there was no ecological basis for establishing isolation classes of forest remnants known to elicit general responses from forest birds, isolation categories were established based on existing statewide variability in this measure. Of the 5051 forest remnants in Delaware larger than 1 ha, mean isolation was 94.8 m (SD = 127.5). Three categories of remnant isolation were defined based on this average, the standard deviation and the 20-m pixel size of the digital forest coverage: 20–100, 100–240 and > 240 m isolation classes. Isolation defined in this manner reflects anthropogenic habitat conditions in Delaware and it is useful to know if birds respond at this scale of disturbance.

Deciduous forest remnants within each stratified area and isolation class combination were randomly selected statewide for breeding bird surveys, thereby incorporating variability in habitat quality among remnants. Nonetheless, surveys were not conducted if the selected remnant was inaccessible, was generally < 15 m tall, or did not have a shrub layer (a condition found in very wet or heavily browsed remnants). After sampling the abundance of breeding birds, remnant area and isolation were subsequently treated as continuous variables in analyses. Except for the largest forests (those > 512 ha, $n = 4$), from 20 to 47 remnants within each of the nine other area classes were surveyed. Isolation was more difficult to control, especially for the larger area classes. Effects of isolation were probably less relevant for the largest forest remnants, however (Fahrig, 2003). Within the three isolation classes, 218, 44 and 34 remnants were surveyed, respectively; few forests > 128 ha isolated by > 100 m from any other remnant were available for surveys. Local forest cover was defined as the amount of deciduous and mixed forest (ha) within a 2-km radius of each survey point (Robbins *et al.*, 1989; Hinsley *et al.*, 1995; Austen *et al.*, 2001) and was included as a covariate in the study design.

Breeding bird surveys

Breeding bird surveys were conducted from mid May to late June, for 2003 to 2005. One circular, fixed-radius (100 m) point-count survey (Ralph *et al.*, 1995) of 10 min in duration was conducted in each forest remnant, totalling 296 surveys in 296 forest remnants. This method standardized effort and survey area among remnants; any differences in species abundance (the number of individuals detected per survey) cannot be attributed to differential effort among remnants of varying area (Robbins *et al.*, 1989; Mac Nally & Horrocks, 2002). Further, all surveys were conducted within 100–150 m from the edge of each remnant, regardless of remnant area;

surveys were conducted near the centre of the smallest remnants. Conducting surveys near the edge of large forests may provide a conservative abundance estimate for some species in these forests. The methodology employed here, however, reduced the error of comparing avian abundance collected from the 'edge' habitat of small remnants to the 'interior' portions of larger forests. To some extent, habitat differences among remnants also were controlled with this design.

Detection probabilities may have differed among species because of observer bias (only the author conducted surveys), species behaviours or detection differences due to area, isolation and forest cover variability among remnants (McShea & Rappole, 1997). As birds may sing more if they are unmated, and they are more likely to be unmated in the smallest, most isolated remnants (Van Horn *et al.*, 1995), results and conclusions related to differences in abundance in the smallest and largest remnants are particularly conservative given that all surveys were conducted near edges. Note that abundance, defined here as the number of individuals detected per survey, is also referred to as density or relative abundance in other survey studies.

Statistical analyses

All species ($n = 54$) were used in abundance analyses of the five avian mass classes ($n \geq 7$ species in each class) with respect to local forest cover, remnant area and remnant isolation. As only a fraction of all species were detected at any given survey point, the survey data were zero inflated (Barry & Welsh, 2002), or composed mostly of zeros. Zero inflated data are commonly encountered in ecological survey data, resulting in a form of overdispersion, in which the variance is greater than expected under a given model (McCullagh & Nelder, 1989). Another feature of abundance data is that the variance may change with treatment (White & Bennetts, 1996), such as remnant area. Because of its flexibility in handling these issues, the negative binomial distribution is preferred when analysing abundance data (White & Bennetts, 1996; Young & Young, 1998) and was the distribution specified here. Abundance analyses of individual species, conducted separately from those of mass classes, were completed only if a species was present in at least nine remnants, which reduced the number of available species to 41 (see Appendix S2 in Supplementary Material). Regarding analyses of abundance patterns within guilds, only mass classes within the open-cup nesting and insectivorous guilds (Ehrlich *et al.*, 1988) were examined, as sample sizes were insufficient for analyses of other guilds.

Generalized linear models (PROC GENMOD, SAS version 9.1; SAS Institute, Inc., 2004, Cary, NC, USA) were used to model the abundance of each mass class, each mass class within each guild and each species (those with appropriate sample size, see Appendix S2). Local forest cover, remnant area, remnant isolation and two-way interactions of these variables were specified as independent variables and \log_2 -transformed before analyses. Linear and quadratic forms of each independent variable, as well as two-way interactions of variables, were

modelled. The linear model was presented if the linear and quadratic models were significant ($P \leq 0.05$) and of adequate fit. Goodness of fit was determined by checking the model deviance divided by the degrees of freedom. The closer this value is to 1.0 (values can be less than or greater than 1.0), the more appropriate the model (McCullagh & Nelder, 1989). Goodness-of-fit measures between 0.5 and 2.0 indicated an acceptable model.

Generalized linear models use maximum-likelihood estimation to produce coefficients. This iterative process may require several passes through the data to estimate stable coefficients. In some cases, no convergence on stable estimates is possible even after a large number of iterations. While poor model specification may cause lack of convergence, misspecification is often associated with trying to estimate coefficients that are close to or equal to zero, which in turn leads to lack of convergence. This is another difficulty of analysing zero-inflated data. For analyses presented here, specified models did not always converge for those mass classes or species with no or few detections in the smallest or largest forest remnants; these results were indicated where appropriate.

RESULTS

The total area of extant (as of 2002) deciduous and mixed forest remnants at least 1 ha in size was 122,273 ha, or approximately 23% of the area of Delaware. The average area of forest remnants at least 1 ha in size was 24.2 ha ($n = 5051$, $SD = 69.8$). Modal remnant size was < 4 ha (46% of remnants); very few forests greater than 500 ha existed in the state (0.003%). Mean isolation of patches statewide was 94.8 m ($n = 5051$, $SD = 127.5$, range = 20–1217). Average local forest cover within 2 km of the survey point was 359.6 ha ($n = 287$, $SD = 220.6$, range = 18.0–960.9).

Nearly 5500 individuals of 54 bird species were detected during this study. Eight species were detected on $\geq 50\%$ of survey points, including the red-eyed vireo, wood thrush and northern cardinal, the most commonly detected species, respectively, whereas 13 species were detected on eight or fewer surveys.

Local forest cover

As forest cover within 2 km of the survey point increased, the abundance of species in the very small, small and very large mass classes increased while the abundance of medium- and large-sized species decreased (Table 1, Fig. 1). These results may be correlated with those of remnant area and isolation: as the area of the remnant in which surveys were conducted increased, forest cover within 2 km of the survey point increased. Likewise, as remnant isolation decreased, forest cover increased (Table 2).

Of the 41 species with adequate sample size for analyses, abundance of 32% ($n = 13$ species) responded positively to increasing forest cover, 7% ($n = 3$) responded negatively, 10% ($n = 4$) responded in a concave, curvilinear fashion and 44%

Table 1 The effect of local forest cover (ha), remnant area (ha), and remnant isolation (m) on the abundance of five mass classes of birds detected in 296 forest remnants in Delaware, 2003–2005. Abundance (individuals per mass class detected per survey) was regressed on log₂-transformed independent variables, assuming a negative binomial distribution of abundance data. Goodness of fit was determined by dividing model deviance by degrees of freedom; values close to 1.0 indicate a good fit. Medium species (see text) showed a curvilinear response to remnant area, increasing and then decreasing in abundance as area increased; medium species did not respond to isolation. All other mass classes responded linearly (either positively or negatively) to forest cover, remnant area and remnant isolation.

Mass class	Variable	Parameter estimate	SE	Wald 95% confidence interval		Chi-square	P	Goodness of fit
Very small	Cover	0.30	0.07	0.17	0.44	20.1	< 0.0001	0.94
Small	Cover	0.39	0.03	0.32	0.46	123.5	< 0.0001	0.94
Medium	Cover	-0.10	0.03	-0.16	-0.05	12.4	0.0004	0.94
Large	Cover	-0.17	0.03	-0.23	-0.11	29.6	< 0.0001	1.03
Very large	Cover	0.58	0.15	0.30	0.87	16.1	< 0.0001	0.98
Very small	Area	0.17	0.03	0.12	0.22	43.1	< 0.0001	0.96
Small	Area	0.18	0.01	0.15	0.20	177.9	< 0.0001	0.93
Medium	Area	0.17	0.05	0.08	0.25	13.5	0.0002	0.95
	Area ²	-0.02	0.01	-0.03	-0.01	16.8	< 0.0001	
Large	Area	-0.08	0.01	-0.11	-0.06	40.9	< 0.0001	1.00
Very large	Area	0.41	0.06	0.29	0.53	47.0	< 0.0001	0.95
Very small	Isolation	-0.18	0.05	-0.28	-0.10	14.8	0.0001	0.97
Small	Isolation	-0.18	0.02	-0.22	-0.13	56.4	< 0.0001	0.91
Medium	Isolation	0.02	0.02	-0.01	0.06	1.5	0.22	0.94
Large	Isolation	0.09	0.02	0.05	0.13	21.9	< 0.0001	1.03
Very large	Isolation	-0.40	0.11	-0.62	-0.18	12.2	0.0005	0.92

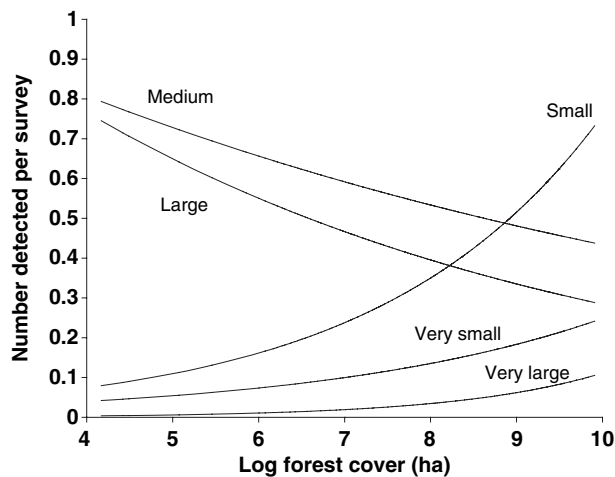


Figure 1 Generalized responses of each mass class of forest birds to forest cover (ha) within 2 km of each survey point. Abundance (number detected per survey) was modelled using generalized linear models assuming a negative binomial distribution of abundance data and log₂-transformed forest cover. Very small, small and very large species increased in abundance with increasing local forest cover, while the abundance of medium and large species decreased. All relationships were significant at the $P \leq 0.05$ level (Table 1). See Supplementary Material for membership of mass classes.

($n = 18$) were not affected by local forest cover (models for three species did not converge; Appendix S2). Three of the four species that showed a curvilinear pattern were medium-sized species; the other was of large size.

Table 2 Pearson correlation matrix for forest cover (ha), area (ha) and isolation (m) among 296 forest remnants in which bird surveys were conducted in Delaware, 2003–2005. All variables were log₂-transformed. Correlations are listed on the first row, significance of the relationship on the second. Forest cover could not be determined for all survey points due to proximity to the State of Maryland, where compatible land-use data were not available ($n = 287$).

	Isolation	Cover
Area	-0.49 < 0.0001	0.61 < 0.0001
Isolation	-	-0.45 < 0.0001

Remnant area

Species in the very small, small and very large body mass classes increased in abundance as remnant area increased. Medium-sized species initially increased in abundance with increasing area until remnants were approximately 22 ha in size and then decreased in abundance. Large species decreased in abundance as remnant area increased (Table 1, Fig. 2).

The abundance of 37% ($n = 15$) of Delaware forest birds with adequate sample size, which does not represent all species of regional or historical relevance, did not respond to an increase in remnant area. Twenty-nine per cent ($n = 12$) increased in abundance with increasing area, 12% ($n = 5$) decreased in abundance, while 15% ($n = 6$) responded in a

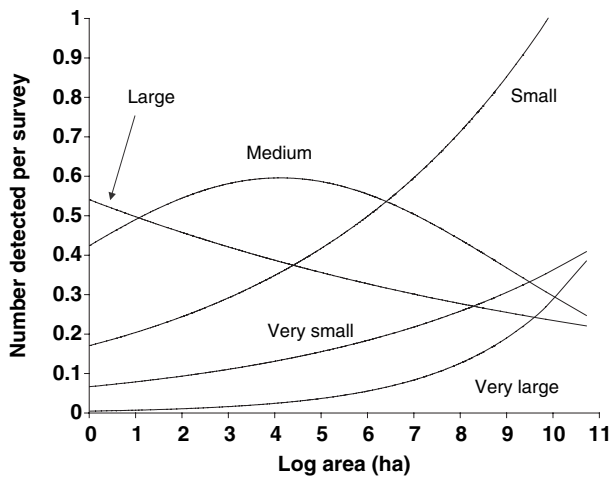


Figure 2 Generalized responses of each mass class of forest birds to increasing remnant area (ha; log₂-transformed). See Fig. 1 for the model description. Very small, small and very large species increased in abundance (number detected per survey) with increasing remnant area, large species decreased in abundance, while medium species initially increased and then decreased in abundance with increasing remnant area. All relationships were significant at the $P \leq 0.05$ level (Table 1).

concave, curvilinear manner (models for three species did not converge; see Appendix S3 in Supplementary Material).

As the effect of remnant area may be confounded with that of forest cover (Table 2), area was examined after controlling for local forest cover. Based on simulations, Andr en (1994) determined that forest birds were negatively affected after 80% of forest in the landscape was removed. Due to inadequate

sample sizes, the local abundance in forest remnants with 80% loss of surrounding forest cover could not be examined. Instead, two categories of forest cover were determined based on the mean (359.6 ha) and standard deviation (220) of forest cover within 2 km of all survey points: points that had < 580 ha of forest cover (mean forest cover + 1 SD, or < 46% forest coverage) and those that had ≥ 580 ha of forest cover ($\geq 46\%$ forest coverage) within 2 km. Results of these analyses indicate whether birds in remnants of varying area respond to anthropogenic patterns of surrounding forest cover. Relative to existing variability in this measure, the abundance in remnants with a high percentage of surrounding forest cover and those with a low percentage of forest cover were examined.

Restricting analyses of the effect of remnant area on the abundance of mass classes to survey points that had < 46% surrounding forest cover reduced the sample of very large species to the point where model convergence was not possible or was questionable (goodness of fit < 0.5). Abundance patterns in the other mass classes did not differ qualitatively from results when all remnants were considered together (see Fig. 2): very small and small birds increased in abundance as remnant area increased, medium birds showed a curvilinear relationship with remnant area and large birds decreased in abundance as remnant area increased (Table 3).

Including only survey points that had $\geq 46\%$ surrounding forest cover produced different results. Very small, small and very large species increased in abundance as remnant area increased, while the abundance of medium and large birds did not respond to remnant area, counter to the above findings (Table 3).

Table 3 The effect of remnant area (ha) on the abundance of avian mass classes within two categories of local forest cover. When local forest cover was < 46% (see text) medium species increased and then decreased in abundance with increasing remnant area, while large species decreased in abundance. When local forest cover was $\geq 46\%$ medium and large species did not respond to remnant area. Goodness of fit is described in Table 1; convergence is described in Methods.

Mass class	Model term	Parameter estimate	SE	Wald 95% confidence interval		Chi-square	P	Goodness of fit
<i>< 46% forest cover (n = 227)</i>								
Very small		0.15	0	0.08	0.22	17.6	< 0.0001	0.96
Small		0.18	0	0.14	0.22	91.5	< 0.0001	0.93
Medium	Linear	0.12	0.1	0.00	0.24	4.1	0.04	0.99
	Quadratic	-0.02	0	-0.03	0.00	5.1	0.02	
Large		-0.04	0	-0.07	-0.01	6.8	0.01	1.00
Very large				Model did not converge				
Mass class		Parameter estimate	SE	Wald 95% confidence interval		Chi-square	P	Goodness of fit
<i>$\geq 46\%$ forest cover (n = 60)</i>								
Very small		0.11	0.07	-0.01	0.25	3.3	0.06	0.92
Small		0.09	0.03	0.02	0.15	6.7	0.01	0.87
Medium		0.01	0.04	-0.07	0.10	0.1	0.79	0.89
Large		0.01	0.03	-0.05	0.08	0.1	0.76	0.99
Very large		0.29	0.2	0.00	0.57	4.7	0.03	0.88

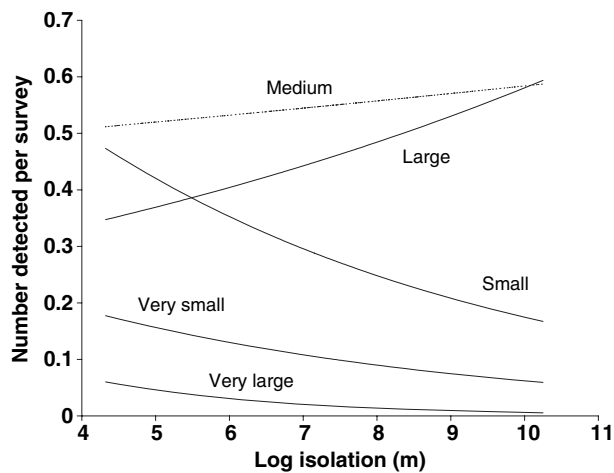


Figure 3 Generalized responses of each mass class of forest birds to increasing remnant isolation (m; log₂-transformed). See Fig. 1 for the model description. Very small, small and very large species decreased in abundance (number detected per survey) with increasing isolation, while the abundance of large species increased. The abundance of medium species (dotted line) was not influenced by remnant isolation. Except for medium species, all other relationships were significant at the $P \leq 0.05$ level (Table 1).

Remnant isolation

As remnant isolation increased, the abundance of very small, small and very large species decreased, while the abundance of large species increased. The abundance of medium-sized species was not affected by isolation (Table 1, Fig. 3).

Fifteen per cent ($n = 6$) of Delaware forest bird species with appropriate sample size responded positively to increasing isolation, 34% ($n = 14$) responded negatively and 44% ($n = 18$) were not affected by isolation alone (models for three species did not converge; see Appendix S4 in Supplementary Material).

Cup-nesting and insectivorous guilds

In general, forest cover, area and isolation models for very small cup-nesting species were of questionable fit, probably due to the insufficient sample size of very small species in this guild. Models for very large insectivores did not converge for similar reasons. Otherwise, qualitative results for these two guilds (Table 4) were similar to those observed for all forest birds considered together (see Table 1).

Interactions

All two-way interactions, positive or negative, between local forest cover, remnant area and remnant isolation on the abundance of mass classes of forest birds were explored. Because of correlations among all independent variables (Table 2) and therefore the lack of interpretability, the three-way model was not considered. As surrounding forest cover and remnant area increased, abundances of small and medium-sized species were

less than predicted by each variable separately (interaction term estimates: small species = -0.06 , $SE = 0.02$, $\chi^2 = 8.9$, $P = 0.003$; medium species = -0.04 , $SE = 0.01$, $\chi^2 = 9.2$, $P = 0.002$). Compared with each variable considered separately, large species tended to increase in abundance as forest cover and remnant isolation increased (interaction term estimate = 0.03 , $SE = 0.02$, $\chi^2 = 3.1$, $P = 0.08$).

No significant interactions between remnant area and remnant isolation were observed for any mass class, although medium-sized birds tended to increase in local abundance as remnant area and isolation increased (interaction term estimate = 0.02 , $SE = 0.01$, $\chi^2 = 2.7$, $P = 0.10$). No models approached significance ($P \geq 0.15$) for any other interaction of independent variables.

DISCUSSION

Deforestation directly removes breeding habitat and, independently, is the overwhelmingly most important factor related to forest bird population declines (McGarigal & McComb, 1995; Trzcinski *et al.*, 1999; Fahrig, 2003). The isolation, connectivity, area and habitat quality of remaining remnants exert further, secondary, effects on forest species. Increased isolation may result in greater mortality when moving or dispersing among remnants (Woodroffe & Ginsberg, 1998) and there may be lower rates of recolonization in the most isolated, least connected remnants (Uezu *et al.*, 2005). Area effects include changes in microhabitat, habitat composition and structure, food availability, nest predation and brown-headed cowbird nest parasitism, at least in North America, which may negatively affect birds in the smallest, most isolated remnants (see reviews by Fahrig, 2003; Henle *et al.*, 2004).

Species respond differentially to area and isolation effects, however. In this study, large and medium species were the most abundant birds in small, isolated forest remnants. Owing to their common occurrence in such 'edge' habitat, many of these species are referred to as 'edge specialists', 'generalists' or 'interior/edge' species, including the blue jay, wood thrush, common grackle, American robin, European starling, northern flicker and red-bellied woodpecker, among others (Whitcomb *et al.*, 1981; Freemark & Collins, 1992; Drapeau *et al.*, 2000; Howell *et al.*, 2000; Moorman & Guynn, 2001). These classifications are not useful (Villard, 1998) because they are often wrong (Imbeau *et al.*, 2003), are not consistently applied, and may change over a species' geographical range or with landscape conditions. Very few species are true forest interior specialists (Villard, 1998) or true edge specialists (Imbeau *et al.*, 2003). Further, these classifications are confounded by their lack of independence from 'area sensitivity' (Villard, 1998), another problematic term.

Because edge effects, such as nest predation and parasitism, are presumed to diminish towards the forest interior (Henle *et al.*, 2004), the differential responses of the avian mass classes presented here are not directly explained by edge effects *per se*: remnant area, isolation and surrounding forest cover

Table 4 The effect of forest cover (ha), remnant area (ha) and remnant isolation (m) on the abundance of five mass classes of cup-nesting (a) and insectivorous (b) birds detected in 296 forest remnants in Delaware, 2003–2005. Abundance (individuals per mass class detected per survey) was regressed on \log_2 -transformed independent variables, assuming a negative binomial distribution of abundance data. Goodness of fit is described in Table 1; models for very small cup-nesting species were of questionable fit. Inadequate sample size caused a lack of model convergence (see Methods) for very large insectivores.

Mass class	Variable	Parameter estimate	SE	Wald 95% confidence interval		Chi-square	P	Goodness of fit
(a)								
Very small	Cover	0.05	0.04	-0.03	-0.13	1.5	0.22	0.52
Small	Cover	0.38	0.05	0.29	0.48	60.8	< 0.0001	0.90
Medium	Cover	-0.11	0.03	-0.19	-0.05	11.3	0.0008	0.88
Large	Cover	-0.37	0.05	-0.46	-0.27	59.6	< 0.0001	1.00
Very large	Cover	0.60	0.17	0.27	0.94	12.3	0.0005	0.94
Very small	Area	0.04	0.02	0.01	0.07	5.9	0.02	0.51
Small	Area	0.19	0.02	0.15	0.23	98.2	< 0.0001	0.91
Medium	Area	0.13	0.05	0.03	0.23	6.2	0.01	0.89
	Area ²	-0.02	0.01	-0.03	-0.01	9.1	0.003	
Large	Area	-0.21	0.02	-0.25	-0.17	105.0	< 0.0001	0.96
Very large	Area	0.41	0.07	0.27	0.55	33.3	< 0.0001	0.92
Very small	Isolation	-0.03	0.03	-0.08	0.02	1.3	0.25	0.52
Small	Isolation	-0.20	0.03	-0.27	-0.13	35.4	< 0.0001	0.87
Medium	Isolation	0.04	0.02	-0.01	0.08	2.8	0.09	0.89
Large	Isolation	0.19	0.03	0.13	0.24	44.0	< 0.0001	1.00
Very large	Isolation	-0.34	0.13	-0.60	-0.09	7.2	0.007	0.86
(b)								
Very small	Cover	0.34	0.07	0.19	0.48	20.6	< 0.0001	0.94
Small	Cover	0.39	0.03	0.32	0.46	123.5	< 0.0001	0.94
Medium	Cover	-0.11	0.03	-0.17	-0.05	14.0	0.0002	0.95
Large	Cover	-0.07	0.04	-0.14	0.00	3.4	0.07	1.01
Very large	Cover			Model did not converge				
Very small	Area	0.16	0.03	0.11	0.22	35.0	< 0.0001	0.95
Small	Area	0.18	0.01	0.15	0.21	177.9	< 0.0001	0.93
Medium	Area	0.16	0.05	0.07	0.25	12.2	0.0005	0.96
	Area ²	-0.02	0.01	-0.03	-0.01	15.7	< 0.0001	
Large	Area	-0.03	0.02	-0.06	0.00	2.8	0.09	1.00
Very large	Area			Model did not converge				
Very small	Isolation	-0.19	0.05	-0.30	-0.09	13.9	0.0002	0.96
Small	Isolation	-0.18	0.02	-0.22	-0.13	56.4	< 0.0001	0.91
Medium	Isolation	0.02	0.02	-0.01	0.06	1.4	0.24	0.96
Large	Isolation	0.03	0.02	-0.02	0.08	1.7	0.19	1.01
Very large	Isolation			Model did not converge				

independently influenced avian abundance and differences in community composition among remnants. Otherwise, no difference in community composition or abundance is expected as all surveys were conducted near the edge of all remnants. Only the edge habitat of large forests held the smallest and largest birds. The greater abundance of medium and large species in small remnants also is not explained by edge effects or presumed habitat associations. For example, so-called edge species such as the northern cardinal, common grackle, and American robin were often detected in close proximity to 'interior' species, such as the ovenbird, black-and-white warbler, and scarlet tanager, in the largest forests. Most large species and some medium species, including the scarlet tanager, occurred in some of the smallest

remnants surveyed, presumably composed entirely of edge habitat, while most small species did not. In other words, small species dropped out of the community as remnant area decreased, even though they were detected side by side with larger species in the edge habitat of the largest forests. Medium and large species were less likely to disappear from the community in small remnants despite being less numerous than smaller species in the largest forests (see Fig. 2).

Interspecific competition

That the smallest species were not detected in the smallest remnants complements findings that subordinate, usually

smaller, species may be relegated to sub-optimal habitats by more competitive species, as evidenced by results of removal studies (e.g. Robinson & Terborgh, 1995; Martin & Martin, 2001). Perhaps they are completely absent in the smallest forest remnants due to similar forms of interference competition. For example, when the dominant competitor, the noisy miner (*Manorina melanocephala*), was removed from eucalypt woodland in Australia, small birds rapidly recolonized the area (Grey *et al.*, 1997). But, if resources are not limiting, as may be the case if a small remnant is in close proximity to a contiguous forest, some species may not experience area effects (Robbins *et al.*, 1989; Trzcinski *et al.*, 1999; Fahrig, 2003). In this study, negative effects were more prevalent as forest cover decreased, and were more pronounced for extremes of body sizes.

Other possible explanations for the reduced abundance, or absence, of some species in small, isolated remnants are that resources are limited or depredation is greater in those remnants. While resources are probably limited for the largest species (Turner, 1996; Henle *et al.*, 2004), the smallest forests surveyed met the home range or territorial area requirements of nearly all other species detected in this study (Brown & Sullivan, 2005). Some authors have suggested that the abundance of small species should increase in the smallest forests because predators or dominant competitors will be absent (see Henle *et al.*, 2004). All empirical results examined refute the suggestion of an increase in small species in small remnants, however (e.g. Martin, 1981; Robbins *et al.*, 1989; Austen *et al.*, 2001; Mac Nally & Horrocks, 2002; Lindenmayer *et al.*, 2002; Parsons *et al.*, 2006; this study; see also Brown & Sullivan, 2005). Further, dominant competitors – those capable of usurping nest sites, depredating nests and controlling access to food sources – may be common in the smallest remnants. In fact, outcomes of competitive interactions, generally indicated by body mass, among species capable of utilizing the resources of a given remnant may determine the community composition and the relative abundance of species in the remnant (Grey *et al.*, 1997; Luck & Daily, 2003; Piper & Catterall, 2003; Brown & Sullivan, 2005; Mac Nally & Timewell, 2005).

Observations of intra- and interspecific interactions and removal experiments support the hypothesis that competition is a community-structuring mechanism. In intraspecific encounters, individuals with greater body mass were generally dominant to smaller individuals and had preferential access to food (Dhondt, 1989; Tarvin & Woolfenden, 1997), nest sites (Krüger, 2002) and mates (Garcia & Arroyo, 2002). Observations of interspecific interactions signify that dominant competitors, again indicated by body mass, had preferential access to nest sites (Ingold, 1994; Piper & Catterall, 2003) and food resources (Luck & Daily, 2003; Mac Nally & Timewell, 2005). Removal experiments nearly always indicated body mass as the major factor in dominance determinations and in access to food or nest sites (Alatalo *et al.*, 1987; Sherry & Holmes, 1988; Tiebout, 1993; Robinson & Terborgh, 1995; Grey *et al.*, 1997; Martin & Martin, 2001), the most important resources relevant to interspecific competition (Newton, 1998).

The structuring properties of interspecific competition may be of various forms (e.g. Schoener, 1983) and includes direct competition (Garcia & Arroyo, 2002; Piper & Catterall, 2003), diffuse competition (Terborgh & Weske, 1975; Mountain-spring & Scott, 1986) and especially interference competition (Grey *et al.*, 1997; Martin & Martin, 2001; Mac Nally & Timewell, 2005; Parsons *et al.*, 2006).

Nest predation and brown-headed cowbird nest parasitism are forms of interspecific competition referred to as encounter competition, defined as '...a result of an interaction between mobile, nonspatially attached individuals, in which some harm comes to one or more; such harm can include time or energy losses, theft of food, injury, or death by predation, fighting, or mere accident' (Schoener, 1983, p. 258). Aggressive nest defence is one method of reducing rates of parasitism (Neudorf & Sealy, 1992), perhaps accounting for the lack of parasitism in the two largest species in a community-wide study of parasitism (common grackle and mourning dove; Strausberger & Ashley, 1997); both species are over twice as large as cowbirds. The common assumption of universal population declines driven by parasitism in the smallest remnants may not hold if there is a reduced selection of hosts to choose from and, following results of this study, many of the species present are larger than the cowbirds themselves. Even if active nest defence is not practised, the relatively larger egg size of larger potential hosts may provide for inadequate brood patch contact with cowbird eggs (Strausberger & Ashley, 1997). It may be trivial to point out that predators are commonly larger than their prey, but the advantage of size also extends to nest predators (common grackle, blue jay, American crow) that, like cowbirds, need to overcome any active defence by nest owners. No studies could be identified that described greater rates of predation on adult birds in small remnants, only greater depredation of nests. Even so, given the greater probability of occurrence and abundance of medium and large species in small forests (Brown & Sullivan, 2005; this study), nest predation may also have a mass bias, with the smallest species disproportionately depredated.

Habitat generality

Habitat generalists are presumed to be the only species found in small, isolated remnants (Henle *et al.*, 2004). Habitat generality may be determined more by body mass, however, and less by the ability to use resources in several habitats *per se*. Those species large enough to secure resources, regardless of resource location, may do so at the expense of less competitive, usually smaller, species that also may be able to use the resources (Luck & Daily, 2003; Mac Nally & Timewell, 2005; Parsons *et al.*, 2006). If resources are limiting, small species may be excluded entirely, as in the removal experiments previously listed (see also Mac Nally & Horrocks, 2002). Given that ecological requirements are met, which may preclude the presence of very large species in small remnants, large species are of the appropriate size to be dominant competitors and thus be considered 'generalists'. Several

medium-sized species also may be large enough, or aggressive enough, to successfully compete for limiting resources, such as those in small, isolated forest remnants. Small species cannot be generalists except in the absence of dominant competitors. There will always be exceptions in variable ecological systems and no generality will capture the range of responses among all species. For example, some small or social species are notoriously aggressive and attack other species much larger than themselves (Murphy, 1983; Piper & Catterall, 2003). Those small species that did occur in the smallest remnants tended to be cavity-nesting species, perhaps avoiding some effects of interspecific competition, such as nest depredation, with this nesting behaviour (Brown & Sullivan, 2005). Dominance also may depend on the age, social status and sex of the individual, as well as the time of year and life-history stage in which dominance was assessed (Arcese & Smith, 1985; Dhondt, 1989).

Community composition

Although interspecific competition among very large species restricts access to common resources (Thiollay, 1998; Garcia & Arroyo, 2002), inadequate resources in the absence of competition may be a sufficient explanation for declines or absences in small areas (Turner, 1996; Cooper & Walters, 2002; Marsden & Pilgrim, 2003). Abundance patterns exhibited by the other mass classes of birds are difficult to interpret based solely on resource availability or habitat specificity because, again, many of the forest remnants in which they were absent either met or exceeded their all-purpose home range or territorial area requirements.

Large species were at their greatest abundance in small, isolated remnants. Several Australian species in the large size classification used here also increased in abundance in small forests (Lindenmayer *et al.*, 2002; Parsons *et al.*, 2006). The mechanism for this pattern may be similar to that of 'mesopredator release' in tropical systems (Terborgh, 1974), where the lack of large predators in small forests leads to an increase in 'medium-sized' predators. In this study, where there were no formal avian 'mesopredators', lack of very large species may nonetheless benefit the next largest size class of birds, the large species. As with the species in the very large size classification used here, there is direct evidence that birds in the large classification compete for limiting resources (Schoener, 1983; Ingold, 1994; Picman & Schriml, 1994; Saracco & Colazzo, 1999). Another attribute of large species nesting in forest remnants, including those not commonly considered as forest species, is that some resources necessary for survival or breeding may be gathered outside of the remnant (Møller, 1987; Sallabanks & James, 1999). For example, many large species visit bird feeders and are often the most behaviourally dominant birds present (e.g. mourning dove, common grackle, blue jay). Further reflecting the competitive ability and generality of this mass class, large species are among the most widespread and numerous in North America (Cabe, 1993; Sallabanks & James, 1999) and

have successfully invaded new regions worldwide (Cassey, 2001).

As a class, medium-sized species were most abundant in forest remnants of approximately 22 ha and least abundant in the smallest and largest remnants. A greater probability of occurrence in 'medium-sized' remnants was reported for some species in at least two other studies (Robbins *et al.*, 1989; Lindenmayer *et al.*, 2002); many of those species fall into the medium size classification defined here. Potential mechanisms for this pattern are not well described. Several studies have noted that avian abundance, or density, decreased linearly as remnant area increased (Beer *et al.*, 1956; Martin, 1981; Austen *et al.*, 2001; Lee *et al.*, 2002; Loman, 2003), in contrast to the many fragmentation studies that indicated abundance increased linearly with habitat area (e.g. Chan & Ranganathan, 2005 and studies therein). Part of this discrepancy may be due to the rarity of sampling large forests in fragmentation studies (see review by Debinski & Holt, 2000), with 15–25 ha fragments considered as 'large' remnants in some studies (Galli *et al.*, 1976; Weinberg & Roth, 1998). Likewise, Whitcomb *et al.* (1981) did not find an effect of body mass on sensitivity to several measures of fragmentation, but none of the 25 remnants examined in their study was between 14 and 70 ha, the range of remnant area that elicited a response among medium-sized birds in this study.

Deforestation may cause birds to pack into remaining habitat remnants or atypical habitat, perhaps for a short time only (Bierregaard & Lovejoy, 1989), although this study suggests a more permanent situation. For methodological reasons, even a small increase in population size in a small area can inflate abundance estimates when compared to larger areas. This is, perhaps, yet another underappreciated area effect and is probably sensitive to the survey methodology employed, and how it was practiced. Other reasons for a decrease in abundance with increasing remnant area are less apparent and refining our understanding of this effect requires further work. Nonetheless, the abundance of some species may either decrease with increasing area or increase with decreasing area (or both), an effect potentially due to limiting forest resources and body mass.

As with patterns for the other mass classes, the curvilinear response of medium-sized birds to remnant area may be driven by interspecific competition (Lindenmayer *et al.*, 2002). Abundances may be suppressed in the smallest forests by the heightened presence of large species, which include those recognized as nest predators and aggressive cavity nesters. Abundances then increase in somewhat larger forests as large species decrease, and therefore competition decreases (see Fig. 2). The abundance of medium species may be reduced in the largest forests for two non-exclusive reasons: (1) the needs of very large species, including avian predators, are now met and their presence either directly or indirectly suppresses the abundance of medium species (Lima, 1998) – species in the medium size class defined here are a preferred prey size for some predators (Forsman *et al.*, 2001); (2) the abundance of medium species is reduced in the largest forests because of an

inherent tendency of abundance or density to decrease as area increases (references above).

These conclusions must be tempered by acknowledging the potential for differences in habitat quality among forest remnants, as well as differences in habitat composition and remnant placement in the landscape. In this study, however, nearly all fragments were surrounded by agriculture or suburban developments; none were surrounded by old fields or brushy growth that may have confounded results by providing marginally suitable habitat for some species. The incidence of pine (*Pinus taeda* and *Pinus palustris*) tended to increase near coastal Delaware and even the presence of a few pines positively influenced the detection of pine warblers and chipping sparrows, both in the small size classification. It is doubtful that the composition of small fragments substantially differed from larger forests in that both were probably in existence because they tended to be wet, at least in some years, and unsuitable for agriculture (Fleming, 1978). Remnants of all sizes have been high-graded and degraded (Environmental Law Institute, 1999).

The same mechanisms that structure forest bird communities by body mass, and that operate within avian guilds, also may hold for mammalian predators in small, isolated remnants: insufficient resources exist for the largest potential predator species and the smallest species are out-competed by increased abundances of mammalian mesopredators. High populations of mesopredators occur in small forest remnants (Hoover & Brittingham, 1998; Crooks & Soulé, 1999). As with avian nest predators, there may be a mass bias to birds susceptible to mammalian mesopredators, with the smallest species most susceptible.

Interspecific competition, as indicated by body mass, may drive the assembly and maintenance of avian communities (Grey *et al.*, 1997; Lindenmayer *et al.*, 2002; Mac Nally & Horrocks, 2002; Brown & Sullivan, 2005; Mac Nally & Timewell, 2005; Parsons *et al.*, 2006). Removal experiments show a clear pattern of interspecific dominance based on size and aggressiveness (Grey *et al.*, 1997; Martin & Martin, 2001). The presence of predators (Lima, 1998), dominant competitors (Grey *et al.*, 1997) and brown-headed cowbirds (Strausberger & Ashley, 1997) differentially affect species of varying body mass, with the strongest negative effects exerted on the smallest, subordinate species. The general effects of deforestation are clear: populations of forest birds decrease with substantial habitat loss and degradation (Andrén, 1994; Fahrig, 2003), as has occurred in Delaware (Fleming, 1978; Environmental Law Institute, 1999). Species exhibit differential responses to the secondary effects of forest cover, remnant isolation and area, however (Robbins *et al.*, 1989; Trzcinski *et al.*, 1999; Lindenmayer *et al.*, 2002; Fahrig, 2003; Luck & Daily, 2003; Brown & Sullivan, 2005; this study), most of which can be predicted from average species body mass. The generality and applicability of theories of biodiversity and biogeography to community composition, species abundance and conservation can be improved by incorporating these differential responses into their assumptions.

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REFERENCES

- Alatalo, R.V., Gottlander, K. & Lundberg, A. (1987) Extra-pair copulations and mate guarding in the polyterritorial pied flycatcher, *Ficedula hypoleuca*. *Behaviour*, **101**, 139–155.
- American Ornithologists' Union (1998) *Check-list of North American birds*, 7th edn. American Ornithologists' Union, Washington, DC.
- Andrén, H. (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos*, **71**, 355–366.
- Arcese, P. & Smith, J.N.M. (1985) Phenotypic correlates and ecological consequences of dominance in song sparrows. *Journal of Animal Ecology*, **54**, 817–830.
- Austen, M.J.W., Francis, C.M., Burke, D.M. & Bradstreet, M.S. (2001) Landscape context and fragmentation effects on forest birds in southern Ontario. *Condor*, **103**, 701–714.
- Barry, S.C. & Welsh, A.H. (2002) Generalized additive modelling and zero inflated count data. *Ecological Modelling*, **157**, 179–188.
- Beer, J.R., Frenzel, L.D. & Hansen, N. (1956) Minimum space requirements of some nesting passerines. *Wilson Bulletin*, **68**, 200–209.
- Bélisle, M. & Desrochers, A. (2002) Gap-crossing decisions by forest birds: an empirical basis for parameterizing spatially-explicit, individual-based models. *Landscape Ecology*, **17**, 219–231.
- Bierregaard, R.O., Jr & Lovejoy, T.E. (1989) Effects of forest fragmentation on Amazonian understory bird communities. *Acta Amazonia*, **19**, 215–241.
- Brown, W.P. & Sullivan, P. (2005) Avian community composition in isolated forest fragments: a conceptual revision. *Oikos*, **111**, 1–8.
- Cabe, P.R. (1993) European starling (*Sturnus vulgaris*). *The birds of North America*, no. 48 (ed. by A. Poole and F. Gill), pp. 1–24. The Academy of Natural Sciences, Philadelphia, PA, and the American Ornithologists' Union, Washington, DC.
- Cassey, P. (2001) Are there body size implications for the success of globally introduced land birds? *Ecography*, **24**, 413–420.
- Chan, M.A. & Ranganathan, J. (2005) Testing the importance of remnant scale on forest birds. *Oikos*, **111**, 606–610.
- Cody, M.L. (1974) *Competition and the structure of bird communities*. Princeton University Press, Princeton, NJ.
- Cooper, C.B. & Walters, J.R. (2002) Experimental evidence of disrupted dispersal causing decline of an Australian passerine in fragmented habitat. *Conservation Biology*, **16**, 471–478.

- Crooks, K.R. & Soulé, M.E. (1999) Mesopredator release and avifaunal extinctions in a fragmented system. *Nature*, **400**, 563–566.
- Debinski, D.D. & Holt, R.D. (2000) A survey and overview of habitat fragmentation experiments. *Conservation Biology*, **14**, 342–355.
- Dhondt, A.A. (1989) Ecological and evolutionary effects of interspecific competition in tits. *Wilson Bulletin*, **101**, 198–216.
- Drapeau, P., Leduc, A., Giroux, J.-F., Savard, J.-P.L., Bergeron, Y. & Vickery, W.L. (2000) Landscape-scale disturbances and changes in bird communities of boreal mixed-woods forests. *Ecological Monographs*, **70**, 423–444.
- Ehrlich, P.R., Dobkin, D.S. & Wheye, D. (1988) *The birder's handbook: a field guide to the natural history of North American birds*. Simon and Schuster, New York.
- Elchuk, C.L. & Wiebe, K.L. (2003) Home-range size of northern flickers (*Colaptes auratus*) in relation to habitat and parental attributes. *Canadian Journal of Zoology*, **81**, 954–961.
- Environmental Law Institute (1999) *Protecting Delaware's natural heritage*. Delaware Department of Natural Resources and Environmental Control, Dover, DE.
- Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology and Systematics*, **34**, 487–515.
- Fleming, L.M. (1978) *Delaware's outstanding natural areas and their preservation*. Delaware Nature Education Society, Hockessin, DE.
- Forsman, J.T., Mönkkönen, M. & Hukkanen, M. (2001) Effects of predation on community assembly and spatial dispersion of breeding forest birds. *Ecology*, **82**, 232–244.
- Foster, D.R., Motzkin, G., Bernardos, D. & Cardoza, J. (2002) Wildlife dynamics in the changing New England landscape. *Journal of Biogeography*, **29**, 1337–1357.
- Freemark, K.E. & Collins, B. (1992) Landscape ecology of birds breeding in temperate forest fragments. *Ecology and conservation of Neotropical migrant landbirds* (ed. by J.M. Hagan III and D.W. Johnston), pp. 443–454. Smithsonian Institution Press, Washington, DC.
- Galli, A.E., Leck, C.F. & Forman, R.T.T. (1976) Avian distribution patterns in forest islands of different sizes in New Jersey. *The Auk*, **93**, 356–364.
- Garcia, J.T. & Arroyo, E. (2002) Intra- and interspecific agonistic behaviour in sympatric harriers during the breeding season. *Animal Behavior*, **64**, 77–84.
- Grey, M., Clarke, M.F. & Loyn, R.H. (1997) Initial changes in the avian communities of remnant Eucalyptus woodlands following a reduction in the abundance of noisy miners, *Manorina melanocephala*. *Wildlife Research*, **24**, 631–648.
- Hansen, A.J. & Urban, D.L. (1992) Avian response to landscape pattern: the role of species' life histories. *Landscape Ecology*, **7**, 163–180.
- Henle, K., Davies, K.F., Kleyer, M., Margules, C. & Settele, J. (2004) Predictors of sensitivity to fragmentation. *Biodiversity and Conservation*, **13**, 207–251.
- Hinsley, S.A., Bellamy, P.E., Newton, I. & Sparks, T.H. (1995) Habitat and landscape factors influencing the presence of individual breeding birds species in woodland fragments. *Journal of Avian Biology*, **26**, 94–104.
- Hoover, J.P. & Brittingham, M.C. (1998) Nest-site selection and nesting success of wood thrushes. *Wilson Bulletin*, **110**, 375–383.
- Howell, C.A., Latta, S.C., Donovan, T.M., Porneluzi, P.A., Parks, G.R. & Faaborg, J. (2000) Landscape effects mediate breeding bird abundance in midwestern forests. *Landscape Ecology*, **15**, 547–562.
- Hubbell, S.P. (2001) *The unified neutral theory of biodiversity and biogeography*. Monographs in population biology, 32. Princeton University Press, Princeton, NJ.
- Imbeau, L., Drapeau, P. & Mönkkönen, M. (2003) Are forest birds categorised as 'edge species' strictly associated with edges? *Ecography*, **26**, 514–520.
- Ingold, D.J. (1994) Influence of nest-site competition between European starlings and woodpeckers. *Wilson Bulletin*, **106**, 227–241.
- Krüger, O. (2002) Analysis of nest occupancy and nest reproduction in two sympatric raptors: common buzzard *Buteo buteo* and goshawk *Accipiter gentiles*. *Ecography*, **25**, 523–532.
- Lee, M., Fahrig, L., Freemark, K. & Currie, D.J. (2002) Importance of remnant scale vs landscape scale on selected forest birds. *Oikos*, **96**, 110–118.
- Lima, S.L. (1998) Nonlethal effects in the ecology of predator-prey interactions. *Bioscience*, **48**, 25–34.
- Lindenmayer, D.B., Cunningham, R.B., Donnelly, C.F., Nix, H. & Lindenmayer, B.D. (2002) Effects of forest fragmentation on bird assemblages in a novel landscape context. *Ecological Monographs*, **72**, 1–18.
- Loman, J. (2003) Small habitat islands are inferior breeding habitats but are used by some great tits – competition or ignorance? *Biodiversity and Conservation*, **12**, 1467–1479.
- Luck, G.W. & Daily, G.C. (2003) Tropical countryside bird assemblages: richness, composition, and foraging differ by landscape context. *Ecological Applications*, **13**, 235–247.
- Mac Nally, R.C. & Horrocks, G. (2002) Relative influences of patch, landscape and historical factors on birds in an Australian fragmented landscape. *Journal of Biogeography*, **29**, 395–410.
- Mac Nally, R. & Timewell, C.A.R. (2005) Resource availability controls bird-assemblage composition through interspecific aggression. *The Auk*, **122**, 1097–1111.
- MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Monographs in population biology, 1. Princeton University Press, Princeton, NJ.
- Marsden, S.J. & Pilgrim, J.D. (2003) Factors influencing the abundance of parrots and hornbills in pristine and disturbed forests on New Britain, PNG. *Ibis*, **145**, 45–53.
- Martin, T.E. (1981) Limitation in small habitat islands: chance or competition? *The Auk*, **98**, 715–734.

- Martin, P.R. & Martin, T.E. (2001) Ecological and fitness consequences of species coexistence: a removal experiment with wood warblers. *Ecology*, **82**, 189–206.
- McCullagh, P. & Nelder, J.A. (1989) *Generalized linear models*, 2nd edn. Chapman & Hall, London.
- McGarigal, K. & Marks, B. (2002) *Fragstats 3.3*. USDA Forest Service General Technical Report (PNW-GTR-351). United States Department of Agriculture.
- McGarigal, K. & McComb, W.C. (1995) Relationships between landscape structure and breeding birds in the Oregon coast range. *Ecological Monographs*, **65**, 235–260.
- McShea, W.J. & Rappole, J.H. (1997) Variable song rates in three species of passerines and implications for estimating bird populations. *Journal of Field Ornithology*, **68**, 367–375.
- Møller, A.P. (1987) Breeding birds in habitat remnants: random distribution of species and individuals? *Journal of Biogeography*, **14**, 225–236.
- Moore, W.S. (1995) Northern Flicker (*Colaptes auratus*). *The birds of North America*, no. 166 (ed. by A. Poole and F. Gill) pp. 1–28. The Academy of Natural Sciences, Philadelphia, PA, and the American Ornithologists' Union, Washington, DC.
- Moorman, C.E. & Guynn, D.C. (2001) Effects of group-selection opening size on breeding bird habitat use in a bottomland forest. *Ecological Applications*, **11**, 1680–1691.
- Mountainspring, S. & Scott, J.M. (1986) Interspecific competition among Hawaiian forest birds. *Ecological Monographs*, **55**, 219–239.
- Murphy, M. (1983) Nest success and nesting habits of Eastern kingbirds and other flycatchers. *Condor*, **85**, 208–219.
- Neudorf, D.L. & Sealy, S.G. (1992) Reactions of four passerine species to threats of predation and cowbird parasitism: enemy recognition or generalized response? *Behaviour*, **123**, 84–105.
- Newton, I. (1998) *Population limitation in birds*. Academic Press, London.
- Noss, R.F. & Cooperrider, A.Y. (1994) *Saving nature's legacy*. Island Press, Washington, DC.
- Parsons, H., Major, R.E. & French, K. (2006) Species interactions and habitat associations of birds inhabiting urban areas of Sydney, Australia. *Austral Ecology*, **31**, 217–227.
- Picman, J. & Schriml, L.M. (1994) A camera study of temporal patterns of nest predation in different habitats. *Wilson Bulletin*, **106**, 456–465.
- Piper, S.D. & Catterall, C.P. (2003) A particular case and a general pattern: hyperaggressive behaviour by one species mediate avifaunal decreases in fragmented Australian forests. *Oikos*, **101**, 602–614.
- Radeloff, V.C., Hammer, R.B. & Stewart, S.I. (2005) Sprawl and forest fragmentation in the U.S. Midwest from 1940 to 2000. *Conservation Biology*, **19**, 793–805.
- Ralph, C.J., Droege, S. & Sauer, J.R. (1995) Managing and monitoring birds using point counts: standards and applications. *Monitoring bird populations by point counts* (ed. by C.J. Ralph, J.R. Sauer and S. Droege), pp. 161–169. USDA Forest Service, Pacific Southwest Research Station, General Technical Report (PSW-GTR-149). USDA Forest Service, Albany, CA.
- Robbins, C.S., Dawson, D.K. & Dowell, B.A. (1989) Habitat area requirements of breeding forest birds of the Middle Atlantic States. *Wildlife Monographs*, **103**, 1–34.
- Robinson, S.K. & Terborgh, J. (1995) Interspecific aggression and habitat selection by Amazonian birds. *Journal of Animal Ecology*, **64**, 1–11.
- Robinson, S.K., Thompson, F.R., Donovan, T.M., Whitehead, D.R. & Faaborg, J. (1995) Regional forest fragmentation and the nesting success of migratory birds. *Science*, **267**, 1987–1990.
- Sallabanks, R. & James, F.C. (1999) American Robin (*Turdus migratorius*). *The birds of North America*, no. 462 (ed. by A. Poole and F. Gill) pp. 1–28. The Birds of North America, Inc., Philadelphia, PA.
- Saracco, J.F. & Colazzo, J.A. (1999) Predation on artificial nests along three edge types in a North Carolina bottomland hardwood forest. *Wilson Bulletin*, **11**, 541–549.
- Schmiegelow, F.K.A. & Mönkkönen, M. (2002) Habitat loss and fragmentation in dynamic landscapes: avian perspectives from the boreal forest. *Ecological Applications*, **12**, 375–389.
- Schoener, T.W. (1983) Field experiments on interspecific competition. *The American Naturalist*, **122**, 240–285.
- Sherry, T.W. & Holmes, R.T. (1988) Habitat selection by breeding American redstarts in response to a dominant competitor, the least flycatcher. *The Auk*, **105**, 350–364.
- Sibley, D.A. (2000) *The Sibley guide to birds*. Alfred A Knopf Inc., New York.
- Strausberger, B.M. & Ashley, M.V. (1997) Community-wide patterns of parasitism of a host 'generalist' brood-parasitic cowbird. *Oecologia*, **112**, 254–262.
- Tarvin, K.A. & Woolfenden, G.E. (1997) Patterns of dominance and aggressive behavior in blue jays at a feeder. *Condor*, **99**, 434–444.
- Tarvin, K.A., Garvin, M.C., Jawor, J.M. & Dayer, K.A. (1998) A field evaluation of techniques used to estimate density of blue jays. *Journal of Field Ornithology*, **69**, 209–222.
- Terborgh, J. (1974) Preservation of natural diversity: the problem of extinction prone species. *Bioscience*, **24**, 715–722.
- Terborgh, J. & Weske, J.S. (1975) The role of competition in the distribution of Andean birds. *Ecology*, **56**, 562–576.
- Thiollay, J.-M. (1998) Distribution patterns and insular biogeography of south Asian raptor communities. *Journal of Biogeography*, **25**, 57–72.
- Tiebout, H.M. (1993) Mechanisms of competition in tropical hummingbirds: metabolic costs for losers and winners. *Ecology*, **74**, 405–418.
- Trzcinski, M.K., Fahrig, L. & Merriam, G. (1999) Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. *Ecological Applications*, **9**, 586–593.
- Turner, I.M. (1996) Species loss in fragments of tropical rain forest: a review of the evidence. *Journal of Applied Ecology*, **33**, 200–209.

- Uezu, A., Metzger, J.P. & Vielliard, J.M.E. (2005) Effects of structural and functional connectivity and patch size on the abundance of seven Atlantic Forest bird species. *Biological Conservation*, **123**, 507–519.
- Van Horn, M.A., Gentry, R.M. & Faaborg, J. (1995) Patterns of ovenbird (*Seiurus aurocapillus*) pairing success in Missouri forest tracts. *The Auk*, **112**, 98–106.
- Villard, M.-A. (1998) On forest-interior species, edge avoidance, area sensitivity, and dogmas in avian conservation. *The Auk*, **115**, 801–805.
- Watson, J.E.M., Whittaker, R.J. & Freudenberger, D. (2005) Bird community responses to habitat fragmentation: how consistent are they across landscapes? *Journal of Biogeography*, **32**, 1353–1370.
- Weinberg, H.J. & Roth, R.R. (1998) Forest area and habitat quality for nesting wood thrushes. *The Auk*, **115**, 879–889.
- Whitcomb, R.F., Robbins, C.S., Lynch, J.F., Whitcomb, B.L., Klimkiewicz, M.K. & Bystrak, D. (1981) Effects of forest fragmentation on the avifauna of the Eastern deciduous forest. *Forest island dynamics in man-dominated landscapes* (ed. by R. Burgess and D. Sharpe), pp. 125–205. Springer-Verlag, New York.
- White, G.C. & Bennetts, R.E. (1996) Analysis of frequency count data using the negative binomial distribution. *Ecology*, **77**, 2549–2557.
- Whittaker, R.J. (1998) *Island biogeography: ecology, evolution, and conservation*. Oxford University Press, Oxford.
- Woodroffe, R. & Ginsberg, J.R. (1998) Edge effects and the extinction of populations inside protected areas. *Science*, **280**, 2126–2128.
- Young, L.J. & Young, G.H. (1998) *Statistical ecology: a population perspective*. Kluwer Academic, Boston, MA.

SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online:

Appendix S1 Species detected during point-count bird surveys in 296 forest remnants in the State of Delaware, 2003–2005.

Appendix S2 The effect of forest cover (ha) within 2 km of the survey point on the abundance of individual species of Delaware forest birds.

Appendix S3 The effect of remnant area (ha) on the abundance of individual species of Delaware forest birds.

Appendix S4 The effect of remnant isolation (m) on the abundance of individual species of Delaware forest birds.

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BIOSKETCH

Bill Brown has over 15 years of experience conducting bird surveys throughout North America. He is interested in understanding the mechanisms that determine and maintain avian community composition.

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