EFFECTS OF FOREST FRAGMENTATION ON TANAGER AND THRUSH SPECIES IN EASTERN AND WESTERN NORTH AMERICA

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Abstract. It is likely that selective forces on forest-specialist birds differ by region across the North American continent, and closely related species that evolved under presumably differing selective regimes may show markedly different responses to human-caused habitat fragmentation. We report the results of research by the Cornell Laboratory of Ornithology that used volunteers to gather data on the effects of habitat fragmentation on forest tanager and thrush species across their ranges and the continent. This large-scale approach permits the comparison of effects between regions within species as well as between species. Although forested landscapes in western North America are often naturally fragmented compared to historically contiguous forests in eastern North America, an identical set of principal components described forest fragmentation in both regions. Response by the Western Tanager (*Piranga ludoviciana*) to overall fragmentation was very similar to that of the Scarlet Tanager (*P. olivacea*) in eastern regions; probability of breeding dropped significantly for both species in highly fragmented landscapes. The Hermit Thrush (*Catharus guttatus*), with both eastern and western populations, is highly affected by fragmentation, with no geographic variation. Additionally, both the Swainson's Thrush (*C. ustulatus*) in the West and the Veery (*C. fuscescens*) in the East showed similar strong effects of fragmentation. Predation and parasitism pressures as estimated by detections of mammalian and avian predators or of Brown-headed Cowbirds (*Molothrus ater*) differed between eastern and western study sites, as did the response by cowbirds to fragmentation gradients in different regions. Overall, however, we found that closely related species and populations showed similar responses to habitat fragmentation, regardless of the historic configuration of the forests in which they occurred.

Key Words: Catharus fuscescens; Catharus guttatus; Catharus ustulatus; geographic variation; *Hylocichla mustelina; Molothrus ater; Piranga ludoviciana; Piranga olivacea*; predators; principal components analysis.

Selective forces on forest-specialist birds differ by region across the North American continent, with differing levels of disturbance, nest parasitism, and of predation by a variable suite of predators. Further, closely related species, or populations within widely distributed species, that have evolved under differing selective regimes may show markedly different responses to human-caused habitat fragmentation. However, testing whether presumably different selective regimes have indeed led to different responses to fragmentation in western and eastern North America is not a trivial matter. It requires several things that, heretofore, have not been combined in one research project (or even in a series of research projects); these include a large geographic extent, a large sample size, standardized data collection, and a widely applicable measure of fragmentation. Further, the species to be studied must have continent-wide distributions, or comparisons must be made between closely related species with primarily eastern or western geographic ranges. We report the results to date from the Cornell Lab of Ornithology's Birds in Forested Landscapes (BFL) project, which used volunteers to gather data on the effects of habitat fragmentation on forest tanager and thrush species across their ranges and across North America.

Several authors have pointed out the differences between western, often coniferous, forest and eastern deciduous forest landscapes as selective environments for obligate forest-nesting birds (Hejl 1992, Freemark et al. 1995, Tewksbury et al. 1998). For example, western and eastern forests differ both in their original configuration and in their subsequent use by humans (Hejl 1992). Western forests are naturally patchy, and in many areas are confined by moisture regimes to riparian zones or to topographic "islands" (Tewksbury et al. 1998). Further, human-caused fragmentation in western North America has often been due to logging (Hejl 1992), and is of fairly recent origin. In contrast, the formerly contiguous eastern hardwood forests have been cleared for agriculture as long as 200 years before present (Smith et al. 1993, Yahner 1997), and are now increasing from historical lows as abandoned farms revert to forest.

In addition to disturbances caused by humans, naturally occurring disturbances also play a large role in shaping the selective environment in which forest bird species evolve, and it is clear that the type, scale, and frequency of disturbance are different in the two regions. In

western North America, the rainiest months occur in winter and spring, with relatively little rain occurring during the summer and fall (Perry 1994). There are also extensive stands of early-successional, serotinous tree species (lodgepole pine, *Pinus contorta*; jack pine, *P. banksiana*; and black spruce, *Picea mariana*) in boreal and temperate montane forest (Perry 1994). Further, dryer forests throughout the West are dominated by the equally fire-adapted ponderosa pine (*Pinus ponderosa*; Perry 1994). This combination of seasonal droughts and fire-adapted vegetation is reflected in frequent disturbance by fire (Freemark et al. 1995). In contrast, eastern deciduous forests are relatively free of fire because of frequent rains during the summer and fall, and because the combination of warmth and high moisture levels leads to rapid decomposition of fallen trees and other potential fuels (Perry 1994).

Other selective forces such as predation and rates of nest parasitism also appear to differ between western and eastern North America. Both the suites of predator species present, nest parasites, and their abundance (Donovan et al. 1995a), appear to combine to alter the selection regimes in the two regions (Tewksbury et al. 1998, Rosenberg et al. 1999). For example, red squirrels (*Tamiasciurus hudsonicus*), which are the most common nest predator in some western landscapes (Bayne and Hobson 1997, Darveau et al. 1997, Tewksbury et al. 1998), are relatively rare in the East where avian predators such as corvid species are much more common (Hogrefe et al. 1998). Moreover, rates of nest parasitism by the Brown-headed Cowbird (*Molothrus ater*) also vary with region, with highest rates in the Midwest region (42.1% of Wood Thrush, *Hylocichla mustelina*, nests) and lower rates in the Mid-Atlantic (26.5%) and Northeast (14.7%) (Hoover and Brittingham 1993). Finally, the responses of both nest predators and parasites to fragmentation has also been shown to vary across physiographic regions (Robinson et al. 1995b, Trine 1998, Rosenberg et al. 1999).

These large differences between eastern and western forest vegetation, historical land uses, disturbance, and between parasitism and predation regimes provide ample grounds to suspect differences in responses to fragmentation between eastern and western landscapes (Freemark et al. 1995). The question becomes how to test for these hypothesized differences. The first requirement is for a measure of fragmentation that is applicable across the continent, and in landscapes with differing conformations of habitat.

Habitat fragmentation implies loss of habitat, a reduction in mean habitat patch size, increases in the mean isolation of patches, and increases in the mean amount of forest/non-forest edge

(Andrén 1994). Most workers agree that loss of habitat is one of the primary mechanisms by which human-caused habitat fragmentation affects populations of birds; some even suggest that habitat loss is the primary (Trzcinski et al. 1999) or only (Fahrig 1997, 1998) mechanism. Others have cited the effects of increased edge (Paton 1994, Hoover et al. 1995, Donovan et al. 1997) and isolation (Robbins et al. 1989a, Villard and Taylor 1994, Villard et al. 1995, Desrochers and Hannon 1997), or of decreased patch size (Schieck et al. 1995, Bellamy et al. 1996a, Keyser et al. 1998, Trine 1998) as also playing an important role. However, it seems most likely that both habitat abundance and configuration (McGarigal and McComb 1995, Villard et al. 1999) play important roles, with the effect of configuration increasing in importance below a critical threshold in abundance (Turner 1989, Andrén 1994, Andrén et al. 1997, With et al. 1997, Andrén 1999). What is needed is a composite measure of habitat fragmentation that captures a large proportion of the information contained within these variables. Such a composite measure should include information captured at the level of the surrounding landscape, as well as at the patch (Freemark et al. 1995), to afford a more complete understanding of the factors affecting the distribution of sensitive species (Hinsley et al. 1995). The Cornell Laboratory of Ornithology's BFL project provides both the fragmentation data needed to calculate such a composite measure, as well as data on species occurrence from across the continent that are necessary to test the hypothesis of different responses to fragmentation in eastern and western landscapes.

BFL is a natural continuation of the Cornell Lab of Ornithology's Project Tanager, which began as a National Science Foundation (NSF) National Science Experiment. Project Tanager used volunteers across North America (north of Mexico) to study the effects of forest fragmentation on four species of tanagers (Rosenberg et al. 1999). BFL uses the same methodology to study the effects of fragmentation on seven species of forest thrushes and two species of *Accipiter* hawks. BFL was undertaken during the 1997 and 1998 breeding season in cooperation with Partners in Flight, an umbrella organization of government agencies, conservation organizations, and industry working together to promote the conservation of birds in the Americas. Birds in Forested Landscapes was continued during the 1999 and 2000 field seasons in cooperation with the United States Department of Agriculture (USDA) Forest Service. For simplicity's sake, we will refer to both Project Tanager and

Birds in Forested Landscapes as BFL hereinafter.

METHODS

DATA COLLECTION

The data-collection protocol for both Project Tanager (Rosenberg et al. 1999) and BFL were essentially identical. Each protocol consisted of four stages: the unbiased selection of one or more study sites; repeated visits to the study sites with the playback of conspecific vocalizations to elicit responses from territorial birds so that they could be counted; the estimation of a number of patch- and landscape-scale measures of fragmentation; and the coding of data onto computer-readable bubble-forms, which were returned to the Lab of Ornithology for collation and analysis.

In both studies, the volunteer participants selected study sites in suitable wooded habitat (e.g., trees >6 m tall, canopy coverage >30%). The instructions stressed that almost any patch of relatively mature forest or woodland was acceptable, and participants were urged to find a range of patch sizes in similar habitat. To avoid bias, participants were cautioned to select their study sites based only on apparent habitat suitability and to not select sites where the species of interest was known to nest (Rosenberg et al. 1999). Each study site was defined as a circle of 150-m radius; point-counts and playbacks were conducted at the center of each study site. Participants made two visits to each site to census for territorial males of the focal species. During a ten-minute point count on each visit, participants looked and listened for territorial individuals of the species of interest within the study site. Participants also recorded the presence of avian and mammalian predators, as well as any detections of Brown-headed Cowbirds during the two point-counts. The two required visits were timed to coincide with pair bonding or nest building, and with the nestling/fledgling stages of the breeding cycle. If no individuals of the species of interest were detected within the point count period, participants used playback of conspecific territorial vocalizations to elicit a response from any previously silent birds in order to verify that no territorial males were present (Villard et al. 1995, Rosenberg et al. 1999). Based on the behavior of birds that were detected, each site was scored as missing, present, possible, probable, or confirmed breeding using breeding atlas codes (Anonymous 1986, Butcher and Smith 1986, Rosenberg et al. 1999). To avoid counting birds passing through on migration, we scored study sites as "possible" breeding sites only if a singing male of the focal species was detected on both visits.

While in the field, participants also used simple techniques to estimate canopy height and amount of canopy closure and noted other site characteristics such as the forest type (coniferous, deciduous or mixed), three most common tree species, and presence or absence of surface water (streams or ponds) at each site. After completion of the fieldwork, participants used USGS topographic maps in conjunction with a clear acetate grid overlay to estimate a number of measures of fragmentation for each site. (The grid was intended for use with 1:24000 maps or aerial photos, and was divided into 1 ha squares at that scale.) Estimated fragmentation measures included the size of the forest patch surrounding the study site, the isolation of that patch from other patches, and the proportion of forest and edge density (amount of forest/non-forest edge corrected for the amount of forest) in the surrounding 1000 ha block. The site's elevation above mean sea level (MSL) was also recorded, as was an estimate of the canopy height. A number of other data were also collected at each site, but were not used in this analysis. For further details on the development of this protocol see Rosenberg et al. (1999). Participants then coded these data onto computer-readable forms and returned the forms to the Lab of Ornithology. At the Lab, we edited each form by hand to ensure it had been correctly completed; simple checks were also performed when the SAS (SAS Institute 1989) dataset was constructed to ensure that each datum was within possible ranges. We excluded all sites with missing data from subsequent analyses.

ANALYSES

At each site participants collected a number of data, including measures of forest fragmentation. We checked the distributions of all fragmentation variables on normal probability plots and transformed variables as needed before analysis began. Many of the measures of fragmentation are highly significantly intercorrelated (Hames et al. 2001). To avoid multicollinearity and the fitting of complicated models with difficult-to-interpret interaction terms, we used principal component analysis (PCA) on the transformed data to simplify the dataset by yielding fewer uncorrelated factors (principal components), which explained a high proportion of the variance in the original dataset (Johnson and Wichern 1982, Villard et al. 1995, Rosenberg et al. 1999). We then used multiple logistic regression to model the probability that territorial birds would be found, based on the principal component values at each site. We also used logistic regression to model the probability of occurrence of the Brown-headed Cowbird. To test the hypothesis that the effects of fragmentation varied between eastern and western landscapes, we compared the magnitude of the fragmentation coefficients derived from logistic regression for each region.

Principal components analysis

To conduct the PCA we combined all unique study points from the 1995, 1996, 1997, and 1998 field seasons of BFL into one dataset. We then used PROC FACTOR (SAS Institute 1989) with the orthogonal varimax rotation option to ensure that there was maximal separation (Johnson and Wichern 1982) and no intercorrelation between the resulting principal components. These rotated factors were then standardized to a mean of zero and a standard deviation of one (SAS Institute 1989) to facilitate comparison of estimated coefficients, before they were used as predictor variables in the logistic regression.

We included a number of transformed variables from each study site in the PCA. These variables were the natural log of the forest patch size (Ln Size), edge density (Ln Edge Density), elevation above msl (Ln Elevation) and canopy height (Ln Canopy Height), as well as the arcsine square-root transformed proportion of forest (Asqrt %Forest; Table 1). The natural log of

TABLE 1. CORRELATION MATRIX FOR VARIABLES INCLUDED IN PRINCIPAL COMPONENTS ANALYSIS

	Ln(size)	Asqrt(%forest)	Ln(edge density)	Ln(elevation)	Ln(canopy height)
Ln(Size)	1.000	0.556**	−0.386**	0.114**	0.064**
Asqrt(%Forest)		1.000	−0.740**	0.151**	0.029
Ln(Edge Density)			1.000	−0.156**	−0.033
Ln(Elevation)				1.000	−0.031
Ln(Canopy Height)					1.000

Notes: Ln(Size) is the natural log of the patch size; Asqrt(% Forest) is the arcsine square-root transformed % forest in the surrounding 1000 ha; Ln(Edge Density) is the linear measure of forest/non-forest in m/ha; Ln(Elevation) is the natural log of distance above Mean Sea Level, in m; Ln(Canopy Height) is the natural log of canopy height, in m. * $P \leq 0.01$, ** $P \leq 0.001$.

isolation, measured as distance to the nearest forest patch of 40 or 200 ha, was not included in the PCA because these data were missing from a substantial number of records. As this variable was highly significantly correlated with Ln Size ($r = -0.228$, $P \leq 0.001$), Ln Edge Density ($r = 0.413$, $P \leq 0.001$), and Asqrt %Forest ($r = -0.567$, $P \leq 0.001$), we felt that the increase in sample size gained by omitting this variable more than compensated for any loss of explanatory power caused by its omission.

Logistic regression analysis

We used PROC LOGISTIC (SAS Institute 1996) to model the probability that a singing male of the species of interest would be detected on the two required visits, either vocalizing spontaneously or in response to playback of conspecific territorial calls, based on the level of fragmentation at each site. We fit multiple logistic regressions using all of the calculated predictor variables (Principal Components), and used manual backward elimination of non-significant (Wald chi-square $P > 0.1$) variables to fit the best model. Models were compared using the G^2 statistic (difference in -2 log-likelihood between two nested models; Agresti 1996) and Akaike Information Criterion (AIC; Agresti 1996). The model chosen in each case was the most parsimonious one that minimized the AIC and had a G^2 that was not significant at the $P \leq 0.05$ level.

Comparison of fragmentation effects

To compare the effects of fragmentation in eastern and western landscapes, we first subset our data into two parts at the 98th meridian, a natural break in the dataset that coincides roughly with the Great Plains. We focused our analyses on widespread species that had both eastern and western populations (e.g., Hermit and Swainson's, *Catharus ustulatus*, thrushes and Veery, *C. fuscescens*) or congeneric species pairs (e.g., Western, *Piranga ludoviciana*, and Scarlet, *P. olivacea*, tanagers) with one eastern and one western member. In addition to these focal species, we compared the effects of fragmentation on the presence of Brown-headed Cowbird across North America. Additionally, we used contingency table analysis to test for differences in the frequency of occurrence of several species of predators in eastern and western landscapes.

We fit separate regression models for each member of species pairs, and tested for differences in the strength of regression coefficients between the pair using a large sample t-test. We rejected the null hypothesis of no differences if $P \leq 0.05$. However, because we had very large sample sizes for several species, we also compared 95% confidence intervals for the fragmentation coefficient in each model, to avoid rejecting the null hypothesis based on differences that were statistically, but not biologically, significant. We accepted the null hypothesis of no difference in the effects of fragmentation between species pairs if the 95% confidence intervals for the mean estimated effect of fragmentation overlapped substantially. For single species, we fit regression models that included an east/west dummy or indicator variable, and region by factor interaction terms. We rejected the null hypothesis of no difference in effects of fragmentation for widespread species if $P \leq 0.05$ (Wald chi-square) for the region by fragmentation interaction term.

Comparison of predator and nest parasite pressure

To characterize differences in predation and nest parasitism pressures between eastern and western landscapes, we used contingency table analysis to test for differences in frequency of occurrence for the Brown-headed Cowbird and for several species of predator. Predator species included nest predators such as squirrels, chipmunks, and corvid species, as well as predators of fledglings and adult birds such as *Accipiter* hawks.

RESULTS

DATA COLLECTION

Volunteers collected data at a total of 1840 sites during the 1995 and 1996 field seasons (tanager species) and at an additional 1298 sites during the 1997 and 1998 field seasons (thrush species), for a total of 3138 sites (Fig. 1). These sites spanned North America, covering 50 states and provinces, and 55 physiographic regions (Robbins et al. 1986). However, many sites were missing required data, and we based subsequent analyses only on sites for which complete data were available. The proportion of sites which contained a territorial male of the focal species on both visits varied from 0.15 for the Swainson's Thrush to 0.325 for the Scarlet Tanager.

ANALYSES

Principal component analysis

Our principal component analysis was based on 2515 unique study sites. These sites included 1933 sites with complete data east of the 98th meridian (East), and 582 west of the 98th me-
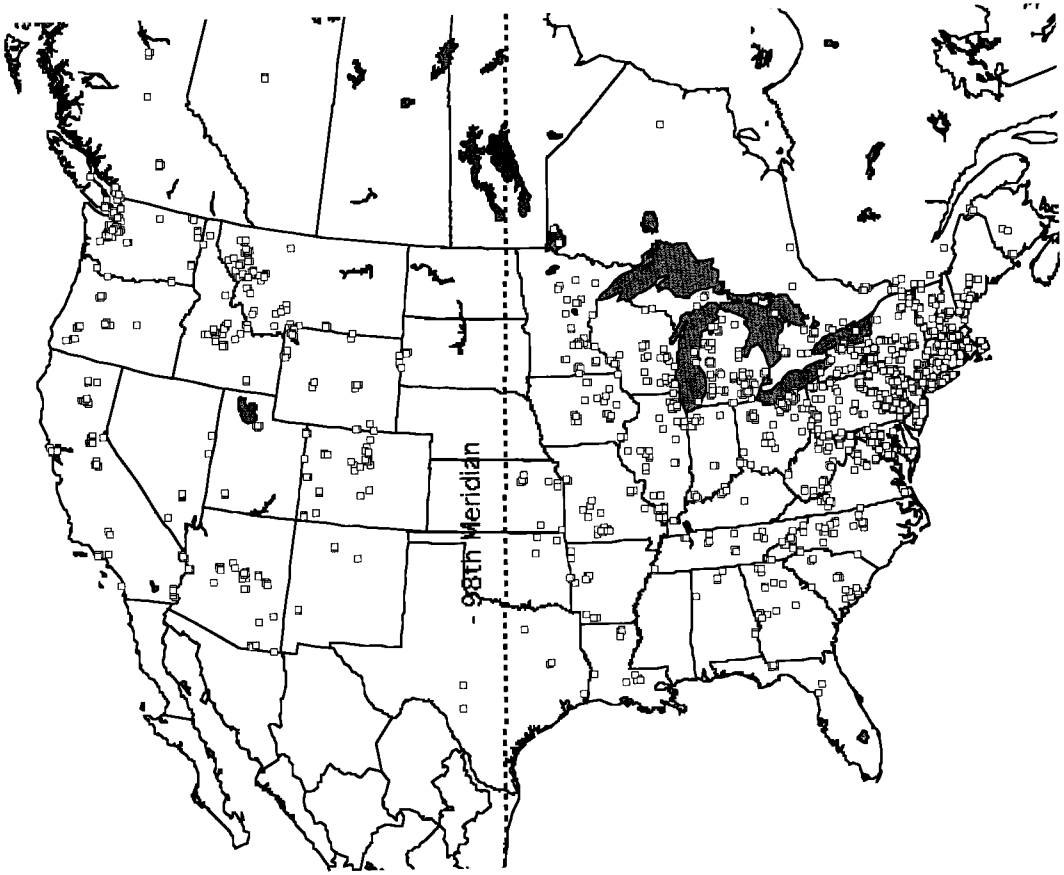
FIGURE 1. Locations of the approximately 2500 study sites on which this analysis is based. Because of the large size of the symbols representing study sites relative to distances on the map, one study site may cover several others.

ridian (West). The correlation matrix for the included variables showed highly significant correlations between patch size, proportion of forest, and edge density (Table 1), which was removed by the orthogonal varimax rotation, thus yielding uncorrelated and easily interpretable principal components (Table 2).

The first three principal components explained 83% of the variance in the data set (Ta-

ble 2). The first principal component (PC1) had high positive loadings (coefficients >0.5) for patch size and proportion of forest, and high negative loading for edge density in the surrounding landscape; we interpreted this principal component as an overall measure of fragmentation. PC1 varies from negative values for small patches in a landscape with little forest and a large amount of forest/non-forest edge, to posi-

TABLE 2. FACTOR LOADINGS DERIVED FROM PRINCIPAL COMPONENTS ANALYSIS OF 2515 FORESTED SITES

Variable	PC1	PC2	PC3
Ln(Size)	0.742	0.029	0.082
Asqrt(%Forest)	0.921	0.067	−0.041
Ln(Edge Density)	−0.850	−0.090	0.178
Ln(Elevation)	0.093	0.995	−0.016
Ln(Canopy Height)	0.032	−0.016	0.997
Eigenvalue	2.187	1.027	0.923
Cumulative variance explained	0.437	0.643	0.827

TABLE 3. COMPARISONS OF FRAGMENTATION VALUES (PC1) AT SITES SAMPLED IN EASTERN AND WESTERN NORTH AMERICA FOR BIRDS IN FORESTED LANDSCAPES PROJECT

Geographic region	N	Mean	SD	Minimum	Maximum	Range
East	1933	0.036	1.0069	−2.440	2.819	5.259
West	582	−0.127	0.9820	−2.591	2.393	4.984

Notes: Data were included from both the 1997 and 1998 field season of BFL. The mean fragmentation values from eastern and western landscapes were not significantly different (pooled test of H_0: $\mu_1 - \mu_2 = 0$, z = 0.366, df = 2513, P = 0.373).

tive values for large patches in a landscape with high proportions of forest and little edge. Interpretations of the second and third principal components were straightforward: PC2 had a high loading only for elevation and PC3 had a high loading only for canopy height. PC3 was retained in the PCA despite an eigenvalue (0.92), which was less than the commonly accepted cutoff of 1.0, because other studies have suggested that the height of the canopy plays an important role in habitat selection by forest-obligate birds (Cody 1985, Hames 2001). Hereinafter PC1, PC2, and PC3 will be referred to by their interpretations as overall fragmentation, elevation, and canopy height, respectively.

Overall, there was little difference between western and eastern sites in the PCA-derived overall fragmentation values (PC1). The mean overall fragmentation values were not significantly different for western and eastern sites (z = −0.158, df = 2347, P = 0.874) and the minima, maxima, and ranges were very similar (Table 3).

Logistic regression analysis

The effect of fragmentation was a very similar decrease in the probability of detection with increasing habitat fragmentation for both tanager species. Both the Scarlet Tanager in the East,

and the Western Tanager in the West, showed a strong, highly significant increase in probability of "possible" breeding as the fragmentation measure PC1 increased (Table 4). This resulted in an approximately five-fold decrease in the estimated probability of occurrence from the least to the most fragmented site. The probability of detection also increased with increasing elevation in the Scarlet (Fig. 2), but not the Western, tanager (Fig. 3).

Sample sizes for the eastern populations of the Swainson's Thrush, and for western populations of the Veery, were insufficient to make within-species comparisons for these species. We therefore treated these as a species pair and restricted the regression analyses to eastern sites for the Veery and to western sites for the Swainson's Thrush. Both of these thrushes displayed similar highly significant increases in the probability of "possible" breeding as PC1 increased, and fragmentation decreased (Table 4). As in the tanager species, this resulted in an approximately five-fold decrease in probability from the least to most fragmented sites. In both species the probability of detection also decreased with increasing elevation (Figs. 4, 5). The Hermit Thrush (Table 5) also showed a highly significant negative response to fragmentation of approximately the same magnitude as that dis-

TABLE 4. STRENGTH OF THE EFFECTS OF FRAGMENTATION (PC1), ELEVATION (PC2), AND CANOPY HEIGHT (PC3) ON THE PROBABILITY OF DETECTING TERRITORIAL BIRDS, SHOWN AS ESTIMATED COEFFICIENTS DERIVED FROM MULTIPLE LOGISTIC REGRESSION

	Scarlet Tanager	Western Tanager	Veery	Swainson's Thrush	Wood Thrush
Intercept	−0.6174***	−1.4866***	−1.5899***	−0.8660***	−0.7545***
PC1/east	0.3648[a]***	—	0.5755[b]**	—	−0.1668**
PC1/west	—	0.5954[a]***	—	0.7315[b]**	—
95% CI low	0.2304	0.2765	0.3747	0.3054	−0.3089
95% CI high	0.5016	0.9299	0.7835	1.1902	−0.0453
PC2/east	0.3148**	—	−0.2061*	—	ns
PC2/west	—	ns	—	−0.3184*	—
PC3/east	ns	—	ns	—	0.3245***
PC3/west	—	ns	—	ns	—

Notes: The PCA was calculated using all data from across North America; the notations "east" and "west" refer to the region in which each species was studied; — denotes that the corresponding coefficient was not calculated; ns indicates that the coefficient was not significant at the P ≤ 0.05 level.
[a] Test of H_0: no difference between coefficients, z = −1.2812, P = 0.176, ns.
[b] Test of H_0: no difference between coefficients, z = 0.5968, P = 0.334, ns.
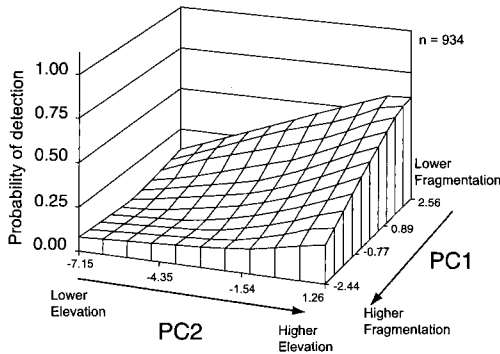* P ≤ 0.10, ** P ≤ 0.01, *** P ≤ 0.001.

FIGURE 2. The effects of fragmentation (PC1) and elevation (PC2) on the probability of detecting a singing or calling male Scarlet Tanager on both required visits. Probability of occurrence increases as fragmentation decreases and elevation increases. Model is highly significant (-2 log-likelihood $= 39.876$, df $= 2$, $P < 0.001$).

FIGURE 4. The effects of fragmentation (PC1) and elevation (PC2) on the probability of detecting a singing or calling male Veery on both required visits. Probability of occurrence increases as fragmentation and elevation decrease. Model is highly significant (-2 log-likelihood $= 35.932$, df $= 2$, $P < 0.001$).

played by the other thrushes. In addition, the Hermit Thrush showed a highly significant increase in the probability of "possible" breeding with increases in elevation. The best model also contained a significant region by canopy height interaction term, so that we can conclude that the effect of canopy height differed between eastern and western populations. The uniform response to fragmentation across species and also across genera was striking, and somewhat troubling. To test if this trend was universal and potentially an artifact of our analytic design, we also fit a logistic regression model to data for the Wood Thrush, a purely eastern species. The

Wood Thrush showed the opposite trend (Table 4), a somewhat weaker but still significant increase in probability of "possible" breeding with increases in fragmentation. The Wood Thrush was also more likely to be detected in forests with higher canopies (Fig. 6).

In both the East and the West, the Brown-headed Cowbird likewise showed an increase in the probability of occurrence with increases in fragmentation (Table 6). The best model for the cowbird also contained a significant effect of year, an indicator variable used to partition variance due to slight differences in the Project Tanager and BFL protocols as to when cowbirds could be counted. In addition, there was a highly significant year by region interaction term,
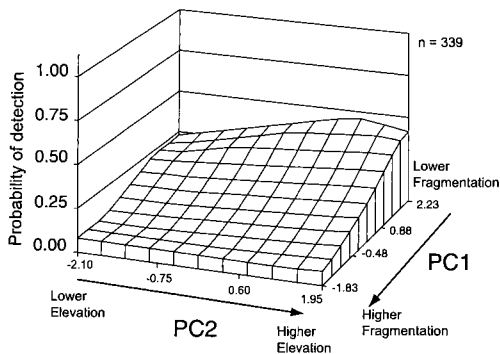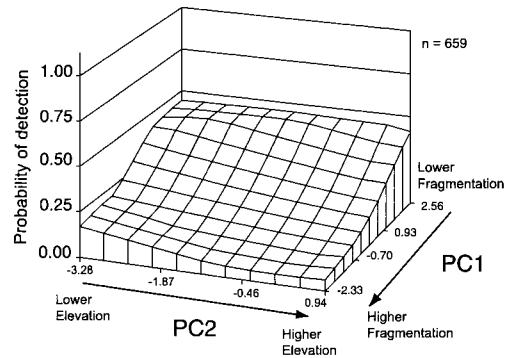

FIGURE 3. The effect of fragmentation (PC1) on the probability of detecting a singing or calling male Western Tanager on both required visits. Probability of occurrence increases as fragmentation decreases. Model is highly significant (-2 log-likelihood $= 13.757$, df $= 1$, $P < 0.001$). Note there is no significant effect of elevation; elevation is only included for comparison between graphs.
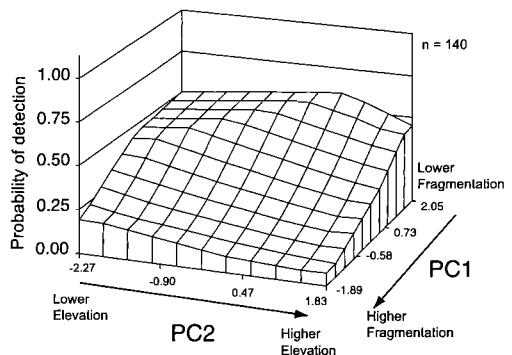

FIGURE 5. The effects of fragmentation (PC1) and elevation (PC2) on the probability of detecting a singing or calling male Swainson's Thrush on both required visits. Probability of occurrence increases as fragmentation and elevation decrease. Model is highly significant (-2 log-likelihood $= 12.588$, df $= 2$, $P = 0.002$).

TABLE 5. RESULTS OF LOGISTIC REGRESSION OF GEOGRAPHIC REGION, FRAGMENTATION, ELEVATION, VEGETATION STRUCTURE, AND THEIR INTERACTIONS, ON THE PRESENCE OF THE HERMIT THRUSH

Variable	Parameter estimate	df	SE	Wald χ^2	P
Intercept	−1.7284	1	0.1724	100.5300	<0.001
West	−0.5680	1	0.3253	3.0498	0.081
PC1	0.6793	1	0.1270	28.6187	<0.001
PC2	0.4099	1	0.1517	7.3037	0.007
PC3	−0.3452	1	0.1432	5.8130	0.016
West*PC3	0.3968	1	0.2245	3.1245	0.077

Notes: Regression based on data from 617 study sites censused for BFL from 1997 to 1998. "West" is an indicator variable: West = 0 east of the Great Plains and West = 1 west of the Great Plains. Overall model χ^2 = 57.879, df = 5, P < 0.001. Concordant pairs = 71.8%.

which showed that fewer cowbirds were detected in the West during the 1997 and 1998 BFL field seasons. Further, there were other highly significant region by fragmentation, and region by elevation interactions, as well as a region by elevation by year three-way interaction.

East/West comparisons

Because we used a standardized measure of fragmentation that included both patch size and the landscape measures proportion of forest and of edge, and because this variable had similar distributions in the East and West, we were able to directly compare fragmentation coefficients from logistic regressions. We tested for differences in the strength of fragmentation between species using a large sample, two-tailed t-test, or between populations within species by using the Wald chi-square for the region by fragmentation interaction term from the logistic regression. We also directly compared the relative strengths of the effects of fragmentation across species by comparing 95% confidence intervals for the es-
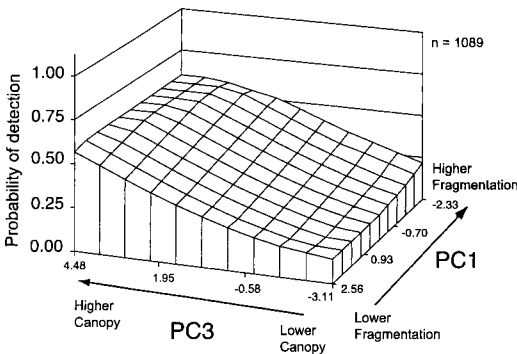

FIGURE 6. The effects of fragmentation (PC1) and canopy height (PC3) on the probability of detecting a singing or calling male Wood Thrush on both required visits. (Note that fragmentation axis is reversed from other graphs.) Probability of occurrence increases as fragmentation increases and canopy height increases. Model is highly significant (−2 log-likelihood = 26.381, df = 2, P < 0.001).

timated fragmentation coefficients. We found that the strength of the negative effects was not significantly different (z = −1.281, P = 0.176) in the Scarlet and the Western tanagers (Table 4) and that their 95% confidence intervals showed considerable overlap. Likewise, there was no significant difference in the strength of fragmentation effects (z = 0.597, P = 0.334) between the Veery in the East and the Swainson's Thrush in the West (Table 4), and the 95% confidence interval for the Veery was completely contained within that of the Swainson's Thrush. Logistic regression for the Hermit Thrush (Table 5) did not yield a significant region by fragmentation interaction term (Wald χ^2 = 0.099, P = 0.753), indicating that there was no significant difference in the strength of fragmentation effects between eastern and western populations. Thus, neither objective hypothesis testing, nor a more subjective examination of the degree of overlap in confidence intervals, provided strong evidence to reject the null hypothesis of no difference in eastern and western responses to fragmentation, at least in these tanager and thrush species.

Conversely, although the Brown-headed Cowbird, like the Wood Thrush, showed an overall increase in probability of detection with increases in fragmentation, a significant region by fragmentation interaction term showed that the response to fragmentation was stronger in the West than in the East (Table 6). Additionally, contingency table analysis of the number of sites at which the Brown-headed Cowbird was detected (Table 7) showed a somewhat higher frequency of occurrence in the East than the West, although this difference was not significant (P ≤ 0.058). For predators, however, the picture is more straightforward. Overall the East had a significantly higher proportion of sites with at least one mammalian (49.3%) or at least one avian (64.4%) predator, than did the West (39.3% and 25.4%, respectively.) In fact, the West significantly surpassed the East only in the frequency of occurrence for the red or Douglas (*Tamias-*

TABLE 6. RESULTS OF LOGISTIC REGRESSION OF PROTOCOL, GEOGRAPHIC REGION, FRAGMENTATION, ELEVATION AND THEIR INTERACTIONS, ON THE PRESENCE OF BROWN-HEADED COWBIRDS

Variable	Parameter estimate	df	SE	Wald χ^2	P
Intercept	−0.8756	1	0.0747	137.37	<0.001
Year	−0.2883	1	0.1259	5.24	0.022
West	−0.3474	1	0.2210	2.47	0.116
PC1	−0.1998	1	0.0571	12.22	<0.001
PC2	0.1398	1	0.0999	1.96	0.162
Year*West	−0.7813	1	0.3562	4.81	0.028
Year*PC2	−0.2965	1	0.1516	3.83	0.050
West*PC1	−0.5577	1	0.1604	12.09	<0.001
West*PC2	−0.7654	1	0.1798	18.12	<0.001
West*PC2*Year	0.8415	1	0.2944	7.65	0.006

Notes: Regression based on data from 2068 study sites censused for Project Tanager and BFL from 1995 to 1998. "Year" is an indicator variable that partitions variation due to differences in the protocols of the two projects. "West" is an indicator variable: West = 0 east of the Great Plains and West = 1 west of the Great Plains. Overall model $\chi^2 = 101.25$, df = 9, P < 0.001. Concordant pairs = 63.0%.

ciurus douglasii) squirrels and for *Accipiter* species. For all other predators the proportion of sites with detections was significantly higher in the East than in the West (Table 7).

DISCUSSION

Despite regional differences in topology, vegetation structure, suites of predators, and land uses past and present, compounded by differences in phylogeny, there is a surprising uniformity in the strength and direction of the responses to fragmentation across the regions and the species studied. This is particularly surprising because Rosenberg, et al. (1999) showed clear regional differences in the strength of responses to fragmentation in the Scarlet Tanager. This lack of regional effects in the present study may be due to the "lumping" of variation occurring at smaller scales, due to the extremely large regions defined for the current study. However, as measured by presence/absence of singing males, for at least the tanager and thrush species we studied, increasing fragmentation is strongly correlated with decreasing probability of detection. What is perhaps not intuitively clear is the correct interpretation of our results.

Our study measured the distribution (presence or absence) of the focal species in relation to fragmentation, not the demographic consequences of that fragmentation. However, demonstrated sensitivity to fragmentation alone (shown as changes in distribution of sensitive species) is sufficient to infer that the tanager and thrush species studied are adversely affected by fragmentation (Winter and Faaborg 1999). For example, in a recent study of fragmentation effects on grassland birds, Winter and Faaborg (1999) make a clear distinction between the distributional consequences (lower densities, lower probability of occurrence) and the demographic consequences (lower nesting success) of fragmentation. Further, their results demonstrate that some area-sensitive species may show distributional effects such as absence from small patches (Robbins et al. 1989a), while other species may show demographic effects such as lower nesting success in fragments (Donovan et al. 1995a, Winter and Faaborg 1999). This useful partitioning of the adverse effects of fragmentation can equally well be applied to forest-dwelling species. This is important because directly determining the demographic consequences of fragmentation requires a skilled field crew and is extremely labor-intensive, making it im-

TABLE 7. PERCENTAGES OF SITES, BY REGION, AT WHICH NEST PREDATORS OR BROWN-HEADED COWBIRDS WERE DETECTED DURING THE 1995, 1996, 1997 OR 1998 FIELD SEASON

	Brown-headed Cowbird	Chipmunk (any species)	Red or Douglas squirrel	Gray or fox squirrel	Crow (any species)	Jay (any species)	*Accipiter* (any species)	Mammalian predator	Avian predator
N	644	783	388	685	1148	1222	161	1429	1838
East %	21.88	29.94	9.86	26.83	44.54	45.59	4.38	49.28	64.40
West %	18.66	12.87	20.98	9.40	16.99	23.42	6.82	39.25	25.41
Δ	3.22	17.07	−11.12	17.43	27.55	22.17	−2.44	10.03	38.99
χ^2	3.603	88.687	64.622	101.356	187.665	118.740	5.058	23.390	69.124
P ≤	0.058	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001

Notes: N = Total number of sites at which predators or Brown-headed Cowbird detected; Δ = difference in percentage detected (East − West).

practical for an extensive, volunteer-based study such as this one.

In the future, repeated sampling over several breeding seasons will allow us to use rates of site occupation or turnover (Villard et al. 1992, Winker et al. 1995, Bellamy et al. 1996b), rather than simple presence/absence in one season, as a measure of the effects of fragmentation. For example, Hames et al. (2001) have demonstrated that the proportion of breeding seasons a site is occupied by a territorial male Scarlet Tanager over several years is inversely proportional to the degree of fragmentation. Thus, we eagerly await analyses of multiple-year BFL data, which will allow us to make stronger inferences by using rates of territory occupancy as a currency for the effects of fragmentation on habitat quality and reproductive success. However, although direct demographic data are necessary for a complete understanding of these effects, already documented changes in distribution due to fragmentation are sufficient to demonstrate adverse effects on sensitive species.

Our requirement that singing males be detected on both visits to the study sites reduces the probability that migrant males would be counted as "possible" breeders; that is, as resident males displaying territoriality. However, although the participants were charged to find as many nests of focal species as possible, and to monitor any nests found to determine reproductive success, very few nests were in fact found (Rosenberg et al. 1999). This lack of direct measures of reproductive success, per se, limits our ability to determine the processes that lead to the observed patterns, and hence our ability to make inferences about population effects of fragmentation. In particular, Van Horne (1983) pointed out that the use of density alone as a measure of habitat quality could give rise to misleading results, especially where territorial behavior limits access to high quality habitat. Others (Maurer 1986, Hobbs and Hanley 1990, Winker et al. 1995) have supported her conclusion, and still others (Vickery et al. 1992, Donovan et al. 1995b, Winter and Faaborg 1999) have also pointed out that density does not necessarily track reproductive success. However, although density (measured as number of birds per area) is mathematically equivalent to probability of occurrence (with the same units), probability of occurrence based on presence/absence data is a special case of density measures with density bounded by zero and one. In fact, the only reliable evidence of the effects of fragmentation available from census data is arguably based on the presence or absence of a species (Freemark et al. 1995, Winter and Faaborg 1999). Further, Boyce and McDonald (1999) point out that habitat usage involves both active habitat selection and passive persistence in a habitat. The fitness consequences of utilizing that habitat, expressed as selection on survival or reproduction (Southwood 1977), is what gives rise to the perceived patterns of distribution (Boyce and McDonald 1999). Thus, in most cases, extent of habitat use (or presence/absence) reflects fitness in those habitats (Fretwell and Lucas 1970). The patterns described above (Van Horne 1983, and others) may be exceptions to this generalization (Boyce and McDonald 1999).

Thus, at first glance, it is somewhat surprising that the high sensitivity to fragmentation shown in most of the species studied was not correlated with population trends as measured by the Breeding Bird Survey. For example, while the Veery showed a significant decline survey-wide between 1966 and 1996 (trend = -1.4%, P < 0.01; Sauer et al. 1997), the Hermit Thrush, which displayed approximately the same level of fragmentation sensitivity as the Veery, showed a survey-wide significant increase over the same period (trend = $+1.4\%$, P = 0.01; Sauer et al. 1997). The equally sensitive Swainson's Thrush displayed no significant trend at all survey-wide. Finally, the Wood Thrush, whose probability of occurrence increased with increasing fragmentation, has shown a strong and highly significant negative trend (trend = -1.8%, P < 0.01) over the same 30 years (Sauer et al. 1997). However, this is perhaps not a total surprise.

As migrant species, the thrushes' and tanagers' population trends reflect influences on the birds on their breeding grounds, during migration, and on their wintering grounds. In the case of the Wood Thrush, population decreases coincide with deforestation in their tropical wintering grounds (Morton 1989) and a decrease in the survival of non-territorial "floaters" while over-wintering (Rappole et al. 1989). In contrast, the Hermit Thrush, which is the only thrush exhibiting an increasing population trend, is also the only species we studied that does not winter in the tropics. Thus, demonstrated sensitivity to fragmentation on the breeding grounds alone may not be sufficient for prediction of population trends of these neotropical migrant species. Data from all portions of the annual cycle are important to understand changes in migratory bird demography (Danielson et al. 1997). However, at least in the case of the Wood Thrush, the preponderance of recent evidence suggests that declining trends are due, in large part, to poor reproductive success in fragmented landscapes on the breeding grounds (Robinson and Wilcove 1994, Hoover et al. 1995, Trine 1998).

Another surprising result of our analysis was the uniformly negative correlation between the

degree of fragmentation and presence of our focal species (with the exception of the Wood Thrush), which held across western and eastern regions. As recently as five years ago, Freemark et al. (1995) pointed to differences between the landscape contexts of studies of fragmentation in the East and the West as a means to explain the clear differences in levels of response between the regions. They pointed to the fact that most western studies had taken place in forested regions fragmented by silviculture, as opposed to most eastern studies that took place in landscapes where forests were fragmented by agriculture and urbanization (Freemark et al. 1995). Our current analysis did not take the nature and extent of adjacent habitat into account because these data were not always available, but instead made comparison based on patch and landscape configuration alone. Further, Freemark et al. (1995) cited an earlier study by Rosenberg and Raphael (1986), which suggested that the lack of strong reaction by western species may also be due to relatively recent fragmentation combined with a time-lag in response by sensitive birds, as well as a lack of truly isolated forest patches. It is possible that the intervening 16 years was a sufficient time for a time-lagged response to become apparent, or for levels of parasitism by Brown-headed Cowbirds to increase with increasing human populations throughout the West (Tewksbury et al. 1998). It seems just as likely, however, that our study was simply the first that undertook a large scale comparison of fragmentation effects in the East and West using the same methodology and measures of fragmentation in both regions, and that the nature of adjacent habitat has a far from negligible effect on sensitive species' response to fragmentation.

In summary, it is clear that the trends in probability of detecting tanager or thrush species in landscapes with varying proportions of fragmentation are the same, in both direction and strength, in both western and eastern landscapes. Further, this similarity in response to fragmentation occurs despite differences in both the suites and abundances of predators and of nest parasites, and despite significant regional differences shown in other analyses (Rosenberg et al. 1999). The Brown-headed Cowbird increased in all landscapes with increases in the level of fragmentation, and this effect was stronger in the West. However, all the focal species except the Wood Thrush showed strong negative effects of fragmentation on possible breeding, whatever their distribution and whatever the history of landuse in their ranges. Finally, this study demonstrates that the use of volunteer citizen scientists in conjunction with explicit, rigorous protocols using playback to verify the absence of the species of interest, can be effective at addressing a large-scale question such as this by gathering detailed distributional data about species of interest across North America.

ACKNOWLEDGMENTS