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## DYNAMICS IN SUBDIVIDED POPULATIONS OF NEOTROPICAL MIGRATORY BIRDS IN A FRAGMENTED TEMPERATE FOREST<sup>1</sup>

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**Abstract.** To study the hierarchy of variables involved in the year-to-year dynamics in the distribution of Neotropical migratory birds, we compared observed numbers of local extinctions and recolonizations to those expected under six hypothetical mechanisms of settlement by returning spring migrants. These mechanisms were (1) random dispersal among forest fragments; (2) passive sampling of spring migrants according to fragment area; (3) dispersal among fragments between years according to the distance to the nearest fragment occupied the 1st yr; (4) resettlement of spring migrants according to the vertical structure of the vegetation in the fragments; (5) site fidelity of experienced breeders; (6) a combination of mechanisms 2, 3, 4, and 5. We selected four target species: Wood Thrush (*Hylocichla mustelina*), Black-and-white Warbler (*Mniotilta varia*), Ovenbird (*Seiurus aurocapillus*), and Scarlet Tanager (*Piranga olivacea*). In 50 fragments of mature deciduous forest (3.0–129.8 ha, median = 11.8 ha) within a 10 × 10 km square, we recorded the presence of any target species and an abundance index in two successive breeding seasons. Absences were validated using song playbacks. Except for the random dispersal model, each hypothetical mechanism was simulated using logistic regressions on empirical data. Frequencies of population turnovers (local extinctions + recolonizations) were 16–28% between the two breeding seasons, varying with species. Observed numbers of population turnovers were best approximated by the combination model (model 6). Expected numbers of population turnovers were consistently higher than observed numbers for models 1–4, suggesting that between-year dynamics were constrained by some process(es). Our simulations suggest that site fidelity might be an important constraint on the distributional dynamics of these species, even when effects of fragment area and habitat on site fidelity are factored out. This finding has important implications for the response of Neotropical migrant birds to the fragmentation of their habitat.

**Key words:** dispersal; habitat fragmentation; *Hylocichla mustelina*; landscape structure; local extinction/recolonization; metapopulation; *Mniotilta varia*; Neotropical migrant birds; Ontario; *Piranga olivacea*; *Seiurus aurocapillus*; site fidelity.

### INTRODUCTION

Few attempts have been made to determine the process through which migratory passerine birds reoccupy their breeding range every spring. Do individuals return directly to their birth place or breeding site of the previous year? Do they home to very large regions or to specific sites? Do they drift haphazardly until they find high-quality habitat that is unoccupied? Studies on the dispersal of passerine birds (including long-distance migratory species) indicate that natal dispersal, the movement of individuals from their birth site to their first breeding site, is always more extensive than breeding dispersal, the movement of adult birds between successive breeding sites. According to Greenwood and Harvey (1982), the median natal dispersal

distance for both sexes is usually less than 10 territories away from the birth site. However, the validity of this generalization is unclear since recapture rates of passerine birds banded as nestlings are usually lower than 10% (M.-A. Villard, unpublished manuscript).

During migration, passerine birds are often found in large multispecies flocks in small, isolated habitat patches. Based on this phenomenon, Ambuel and Temple (1983) and Blake (1991) concluded that the rarity of Neotropical migrants in small forest fragments is unlikely to reflect differences in the ability of these species to locate and colonize habitat patches. These authors thus equate vagility, the physical ability of a species to move certain distances, and dispersal ability, the ability of a species to move to a certain site and settle there to breed. To our knowledge, a positive correlation between vagility (e.g., extent of migratory movements) and dispersal ability has yet to be demonstrated for passerine birds.

In forest patches of central Illinois, Robinson (1992)

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observed that bird species had a very low reproductive success, mainly because of intense nest predation and brood parasitism. He suggested that populations of Neotropical migrants in his study area are maintained by immigrants from source populations over 200 km away. It is conceivable that the naturally fragmented woodland of the edge of the prairies would have favored the evolution of long-distance dispersal. The fact that no isolation effects were observed on the species richness of, or species abundance in, forest fragments in regional studies conducted in Wisconsin (Ambuel and Temple 1983) and Illinois (Blake and Karr 1987) would be consistent with longer dispersal movements by woodland birds at the edge of the prairies. In contrast, isolation effects have been observed in the Middle Atlantic States (Lynch and Whigham 1984, Robbins et al. 1989), in New England (Askins et al. 1987, Askins and Philbrick 1987) and in Ontario (Villard 1991). These comparisons are rather crude, however, since isolation metrics were not always consistent among studies.

Without a detailed knowledge of dispersal movements in fragmented landscapes, our opening questions about the mechanisms through which migratory birds reoccupy their breeding range every spring will remain unanswered. However, the local extinctions and recolonizations observed in the distribution of particular species in fragmented habitats (Villard et al. 1992, Haila et al. 1993) provide an opportunity to test predictions generated from a variety of hypothetical mechanisms of spring resettlement by migratory birds.

In this study, we compare the year-to-year dynamics observed in the landscape-scale distribution of four Neotropical migrant bird species to those expected based on the following hypotheses about the mechanism of spring resettlement of fragmented forests by Neotropical migrants: (1) completely random dispersal among fragments; (2) passive sampling of spring migrants according to fragment area; (3) resettlement pattern reflecting the distance to the nearest potential source of immigrants; (4) resettlement reflecting structural characteristics of the vegetation of the fragments; (5) resettlement pattern determined by the probability of return of experienced breeders; and (6) a combination of mechanisms 2, 3, 4, and 5. We used computer simulations to examine the probability of obtaining the observed numbers of local extinctions and recolonizations under each hypothetical mechanism. This approach can be viewed as successive approximations of a complex phenomenon. Our objective is not to identify a specific mechanism of resettlement of spring migrants proper to each target species, but rather to assess the relative contribution of each mechanism within and among species. Understanding this phenomenon is critical if we are to model the response of different species to the fragmentation of their habitat.

## METHODS

### *Study area*

This study was conducted in an agricultural landscape south of Ottawa, Ontario (45°11' N, 75°26' W) (Fig. 1). Aerial photographs indicate that woodland has been fragmented in this area at least since the mid 1930s. Clearing of woodland for agriculture and settlement probably reached its maximum extent at the turn of the century (Middleton and Merriam 1983). The study area is a 10 × 10 km square where all forest fragments of at least 3 ha were surveyed in two successive breeding seasons (area range: 3.0–129.8 ha, median = 11.8 ha,  $n = 50$ ). The location of this square was selected to minimize variation in the structural and floristic composition of the stands. Woodland covers 15% of the area within the square. Cultivated fields cover most of the remaining area.

Forest fragments were defined as continuous areas of woodland separated from surrounding fragments by gaps of at least 30 m, or connected to other fragments by wooded strips <30 m wide. The ecological justification behind these arbitrary criteria is that territories of forest-specialist bird species are unlikely to encompass open gaps of this extent, or to extend into habitat strips of that width. This threshold distance had to be defined arbitrarily since, to our knowledge, no detailed analysis of this aspect is available in the literature.

All forest fragments were characterized by relatively mature deciduous stands. On well-drained sites, the dominant tree species were Sugar Maple (*Acer saccharum*), White Ash (*Fraxinus americana*), American Basswood (*Tilia americana*), and Ironwood (*Ostrya virginiana*). A few sites with imperfect to poor drainage were dominated by Red Maple (*Acer rubrum*). The only common conifer, White Cedar (*Thuja occidentalis*), occurred mainly along forest-field edges. Between the two breeding seasons, a house was built along the edge of a forest fragment and some firewood cutting was noted in another. These disturbed sites were included in subsequent analyses since the direction of the year-to-year dynamics of the target species appeared unaffected (one recolonization in each of two target species). However, historical perturbations such as grazing could not be avoided. This resulted in some forest fragments having a sparse sapling layer. None of the forest fragments included permanent water bodies visible on 1:15 000 aerial photographs.

### *Bird censusing techniques*

Wood Thrush (*Hylocichla mustelina*), Black-and-white Warbler (*Mniotilta varia*), Ovenbird (*Seiurus aurocapillus*), and Scarlet Tanager (*Piranga olivacea*) were selected as target species. These species had intermediate incidences (0.62, 0.36, 0.64, and 0.53, respectively) in 45 forest fragments (2.8–57.5 ha, median = 20.1 ha) censused with point counts in previous years (Villard 1991), making them good candidates for ex-

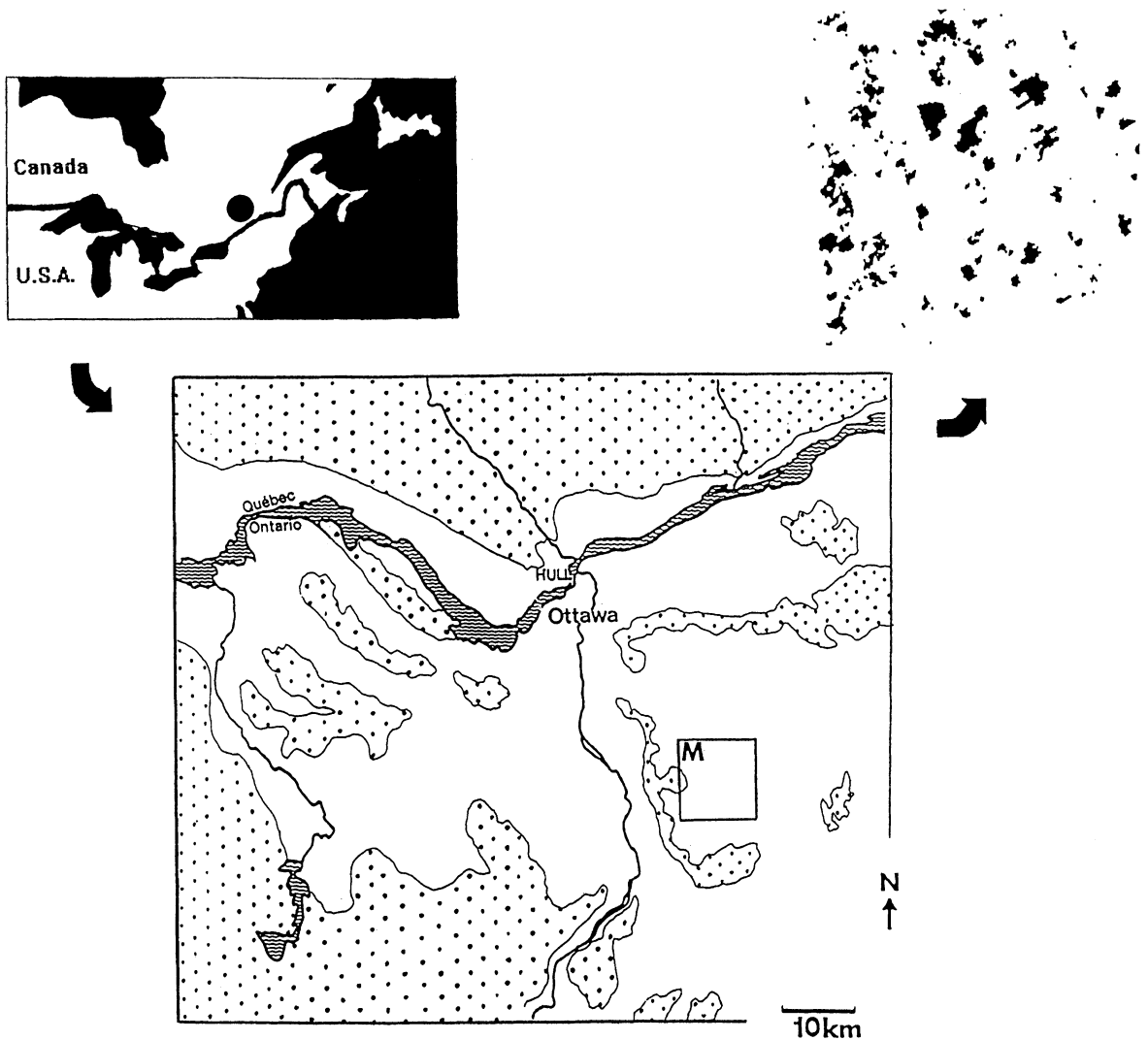


FIG. 1. Map of the study area. Top left: geographic location indicated by a dot. Center: Metcalfe landscape (M) and its location relative to large fragments of woodland (>1000 ha, stippled). Top right: configuration of woodland (solid black) in Metcalfe landscape.

hibiting spatiotemporal shifts in their distribution in small to medium-sized forest fragments. The incidence of a species was calculated as the proportion of forest fragments where it was recorded. The incidence or abundance of these target species have been found to increase with the area of forest fragments in various parts of their breeding ranges (Hayden et al. 1985, Blake and Karr 1987, Askins et al. 1987, Robbins et al. 1989). Robbins et al. (1989) also found that the abundance of these species in forest fragments decreased with their isolation from surrounding woodland with the exception of the Wood Thrush, whose abundance actually increased with fragment isolation.

The target species vary widely in their habitat use (Freemark and Merriam 1986, Smith and Shugart 1987; M.-A. Villard, *personal observation*). Wood Thrushes

nest in the sapling layer and forage on or close to the ground. Ovenbirds and Black-and-white Warblers are ground nesters, although the latter occasionally build elevated nests. Ovenbirds feed primarily by picking invertebrates on the leaf litter, whereas Black-and-white Warblers search the bark of woody branches and trunks to glean insects. Finally, Scarlet Tanagers are canopy nesters and forage at various heights in the canopy or subcanopy.

To determine the status (presence or absence) of the target species and obtain an index of their abundance in a large number of sites, we used the field check method (Villard et al. 1992), which consists in recording any visual or auditory contact with any of the target species while walking slowly along the long axis of a forest fragment. The time spent in each fragment was

TABLE 1. Descriptive statistics for the different variables included in the stepwise logistic regressions used in the simulation of the combination model (model 6).

Variable	Description	Mean or median	SD/range	Units
LOGA	Area of the forest fragments (log-transformed for the analyses).	Med. = 11.75	23.57	ha
NNWT	Distance to nearest forest fragment occupied by the Wood Thrush in 1989.	Med. = 0.40	0.03–1.20	km
NNBW	Same as NNWT, but for the Black-and-white Warbler.	Med. = 0.65	0.03–3.70	km
NNOB	Same as NNWT, but for the Ovenbird.	Med. = 0.40	0.03–2.40	km
NNST	Same as NNWT, but for the Scarlet Tanager.	Med. = 0.60	0.03–3.60	km
ABWT	Indexed abundance of Wood Thrush in 1989 (residuals from a generalized linear model of abundance vs. LOGA and PCA1—see <i>Methods</i> ).	Med. = 1	0–4	no. pairs per fragment
ABBW	Same as ABWT but for Black-and-white Warbler	Med. = 0	0–3	as above
ABOB	Same as ABWT but for Ovenbird	Med. = 1	0–4	as above
ABST	Same as ABWT but for Scarlet Tanager	Med. = 0	0–1	as above

thus proportional to its area. Absences were validated using playbacks of prerecorded songs. Playbacks also induced singing in late morning surveys, when singing rates tended to drop.

In the 1st yr of this study (1989), three visits were made to each forest fragment between the last week of May and the 1st wk of July. In the 2nd yr (1990), surveys were started during the 1st wk of June and a third visit was added only in fragments where a difference in the status of any of the target species was noted between the previous visits. In fragments where absences were noted on previous visits, we made special efforts to survey additional portions of the fragments during subsequent visits. Field checks were conducted between sunrise and 1130, at intervals of  $\approx 2$  wk. The vast majority of the individuals recorded were territorial males. Individuals recorded only at the first visit in 1989 were considered as transients and, accordingly, an absence was recorded for that species. Abundance data were ranked as follows: 0, 1, 2, 3, and 4 or more territorial males. This truncated scale reflects the incompleteness of our surveys in the largest forest fragments. The abundance index represents the maximum number of territorial males recorded in a given fragment on a single visit. One of the 50 fragments was surveyed using point counts with unlimited distance (Blondel et al. 1970, 1981). We assumed that probabilities of detection of the target species were similar for the field check and point count methods. This assumption is discussed in Villard et al. (1992).

Neither field checks nor point counts indicated the pairing status of territorial males. In a study that was conducted in some of the forest fragments included here, pairing success of territorial male Ovenbirds was found to be lower in fragments than in a plot within an extensive forest nearby (Villard et al. 1993). Hence, the presence of territorial males of a target species in a fragment does not necessarily mean that this species is actually breeding. In this study, we are interested in

the settlement pattern of territorial males and its relation to local (fragment) and regional (landscape) characteristics. We assume that the same settlement mechanism(s) can lead to successful reproduction or reproductive failure.

#### *Vegetation sampling*

Vegetation structure and floristic composition were quantified in 42 of the 50 forest fragments surveyed in the study area using the point-centered quarter method (Mueller-Dombois and Ellenberg 1974). At each vegetation sampling point, we measured the distance to the nearest tree in each of the four quadrants. For each tree, we recorded the species and diameter at breast height (dbh). The distance to the nearest sapling ( $< 8$  cm dbh) and its species were also recorded. Vegetation structure was quantified at each point using semiquantitative variables. Sampling points were located at 25-m intervals along transects following the long axis of large fragments, or the diagonals of smaller fragments. In large fragments, 25 points were sampled along a 625-m transect, and as many points as possible were fitted in small fragments. Descriptive statistics for each habitat variable are provided in Table 2.

Tree and sapling densities were calculated from the mean distance to the nearest individual of any species in a given forest fragment. Importance values were calculated for each tree species following the method described in Mueller-Dombois and Ellenberg (1974), except that only relative density and relative dominance were included in the calculation, and not relative frequency, because of its correlation with the former. Hence, these values were calculated out of 200 instead of 300. Relative frequency is the percentage of individuals of a given species recorded, out of the total number of individuals sampled (100 in most fragments). Relative dominance is an approximation of the percentage of the total basal area represented by a given species. Canopy height was measured at each sampling

TABLE 2. Descriptive statistics and factor loadings of habitat variables on the first axis (PCA1) of a principal components analysis of vegetation structure data.

Variable	Description	Mean or median	SD/range	Units	PCA1
LOGBA	Average basal area of trees (log-transformed)	Med. = 293.40	164.54	cm <sup>2</sup>	0.51
CC	Canopy closure	$\bar{X}$ = 71.69	10.59	%	0.16
CH	Canopy height	$\bar{X}$ = 17.31	3.21	m	0.52
HGC	Herbaceous ground cover	$\bar{X}$ = 22.88	12.63	%	-0.22
WGC	Woody ground cover	$\bar{X}$ = 12.61	7.03	%	0.40
FD	Foliage density (0–5 m)	$\bar{X}$ = 19.29	8.47	%	-0.21
SD	Shrub density	$\bar{X}$ = 31.35	15.78	no./100 m <sup>2</sup>	-0.37
TD	Tree density	$\bar{X}$ = 8.26	2.45	no./100 m <sup>2</sup>	-0.24
Eigenvalue (PCA1):					2.88
Variance explained (%):					36.06

point with a clinometer. Mean basal area per tree was also used as a separate variable.

Canopy closure, percent cover of woody and herbaceous ground vegetation, and foliage density were estimated using a semiquantitative scale (0–1, 1–5, 5–25, 25–50, 50–75, >75%). Canopy closure was defined as the proportion of the field of vision of an observer looking up that was masked by canopy foliage. Percent ground cover was estimated in a 1-m radius circle around each sampling point. Foliage density was measured as the proportion of a 5 m high vertical stick that was hidden by foliage (Haila et al. 1987). Foliage density was estimated by looking at the reference stick from 5 m on either side of it, and selecting the appropriate percent cover class. These semiquantitative variables were grouped for analyses using the midpoint of each percent cover class.

Habitat data were summarized to include a description of both the vertical structure of the vegetation and the floristic composition of tree stratum. Associations between bird species diversity or distribution and vegetation structure have been widely documented (e.g., MacArthur and MacArthur 1961, James 1971). However, the taxonomic composition of the vegetation has recently been shown to be more strongly associated with bird community composition than various habitat structure variables in grassland habitats (Rotenberry 1985) and riparian woodland (Rice et al. 1984). We used a principal components analysis (PCA) to extract independent composite variables from the highly intercorrelated set of descriptors of vegetation structure (listed in Table 2). We only retained the first axis of this PCA for subsequent analyses since it was the only interpretable principal component according to the broken-stick method (Frontier 1976, Jackson 1993). To obtain composite variables reflecting tree species composition in each fragment, we used importance values as indices of species abundance in a detrended correspondence analysis (DCA) (ter Braak 1988). This technique produces an ordination of species and sites using a two-way weighted averaging procedure. A score is calculated for each sampling site using the importance values (scores) of the species present multiplied by

arbitrarily assigned weightings. Scores are then calculated for each species by multiplying the sampling site scores previously obtained by the total number of sampling sites occupied by the species. This procedure is repeated until species and sampling site scores stabilize (Jongman et al. 1987).

#### SIMULATING DYNAMICS IN FRAGMENT OCCUPANCY

The extinction and recolonization of local populations is a stochastic process that involves the decisions made by individual birds in selecting forest fragments. Because of the stochastic nature of this process, we developed a series of simulation models to mimic various kinds of stochastic events and constraints on them that might be relevant to Neotropical migratory birds. We begin our modelling procedure with the simplest case of unconstrained randomized selection of forest fragments and proceed to models that incorporate increasing numbers of factors that may affect probabilities of fragment selection, such as habitat structure or fragment isolation.

Since we assume that local extinction and recolonization are stochastic processes, we expect a distribution of annual local extinction and recolonization rates (measured in number of fragments per year). The nature of this distribution is determined by the assumptions made about factors constraining the selection of forest fragments by individuals. By making assumptions regarding how fragment characteristics affect the probability of a site being occupied in a given year, we constructed probability distributions of expected local extinctions and recolonizations by comparing the simulated occupation of forest fragments under six main sets of assumptions in 1990 with the observed occupation status of fragments in 1989. The validity of the assumptions used to construct each distribution was assessed by comparing the observed number of local extinctions or recolonizations between 1989 and 1990 to the corresponding distribution of local extinctions and recolonizations obtained from the simulation process (Fig. 2). If the observed value was in the extreme tails of the distribution (i.e., in the lower 2.5% or upper

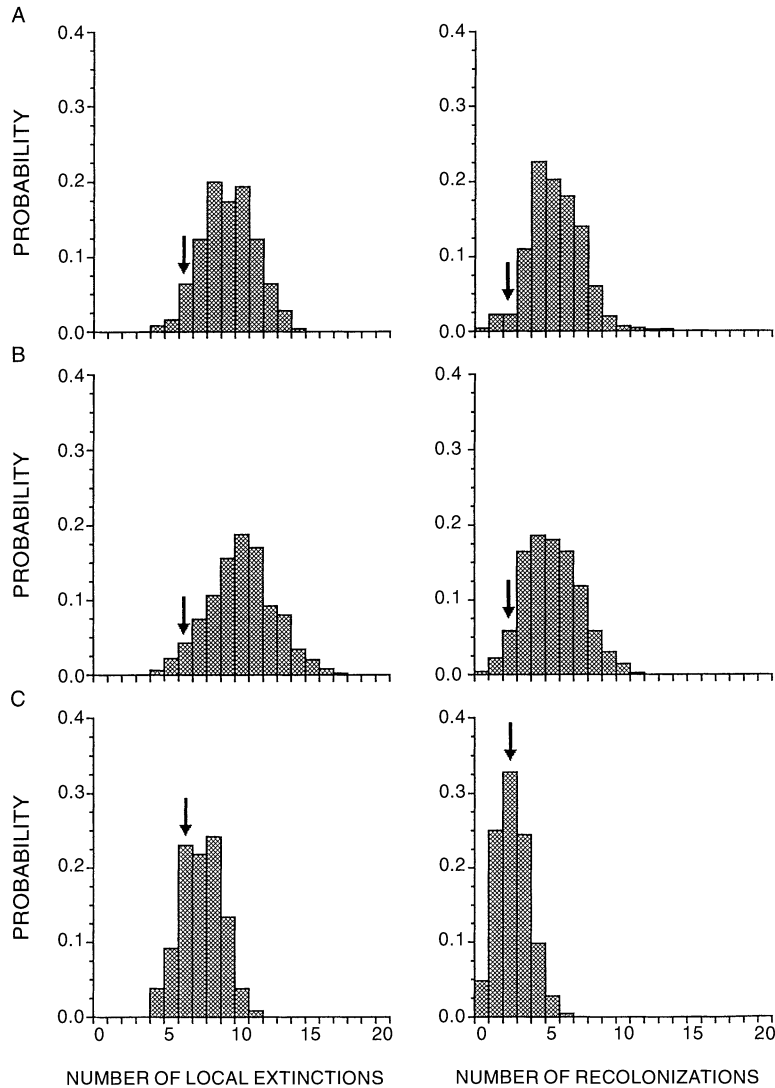


FIG. 2. Frequency distributions of expected numbers of local extinctions and recolonizations for the Ovenbird in the study landscape under (A) passive sampling, (B) site fidelity, and (C) combination models. Arrows indicate observed numbers of local extinctions and recolonizations.

2.5%), then the assumptions used to construct the distribution were rejected because they did not provide an adequate description of the factors affecting local extinction and recolonization dynamics.

#### *Variables included in the simulations*

The variables we used in the simulations were selected based on their significance as predictors of the presence or absence of the target species. In our initial set of variables, there were three pairs of intercorrelated variables: (1) fragment area (log-transformed) and perimeter to area ratio (an index of fragment shape) ( $r = 0.87$ ;  $P < 0.001$ ;  $n = 42$ ); (2) scores for forest fragments on the first axis of a PCA on vegetation structure (PCA1) and on the first axis of a DCA on tree species composition ( $r = 0.52$ ;  $P < 0.001$ ;  $n = 42$ ); and (3)

distance to nearest fragment occupied in 1989 and the sum of the distances to the nearest fragment occupied in each quadrant around a focal site ( $r = 0.68$  to  $0.86$ ;  $P < 0.001$ ;  $n = 42$ ). We found that fragment area, PCA1, and distance to the nearest occupied site were consistently better independent predictors of presence or absence in 1990 than their correlate in univariate logistic regressions, and so we used these variables in our simulations.

#### *Simulation models*

The first simulation model (random dispersal) represents completely random selection of forest fragments by returning migrants without regard to any biological or physiographic characteristics of the fragments. Thus, each fragment occupied in 1989 had

the same probability of experiencing a local extinction event in 1990, and each unoccupied fragment had the same probability of being recolonized. We used the incidence of each of the four target species in 1990 as an estimate of the probability that a fragment would be occupied that year. For each forest fragment, we drew a random variate from a uniform distribution between 0 and 1. If that variate was less than the incidence, the fragment was scored as occupied in 1990; if not, it was scored as unoccupied. This simulated set of presence-absences was compared to the 1989 presence-absence data and when a forest fragment that was occupied in 1989 was scored in the simulation as being unoccupied in 1990, we counted this as a simulated local extinction. Likewise, when a fragment unoccupied in 1989 was scored in the simulation as being occupied in 1990, we counted this as a simulated recolonization. The total number of recolonizations and local extinctions in the simulated data were obtained for that simulation run. This procedure was repeated for 500 runs, and the resulting data were used to calculate probability distributions for the number of local extinctions and recolonizations expected under the null expectation that all fragments were equally likely to be occupied in any given year.

The second model (passive sampling) assumed that occupation of a fragment in 1990 depended only on its area. The probability of a species occupying a fragment in 1990 was estimated from a logistic regression with presence or absence in 1990 as the dependent variable and the logarithm of fragment area (LOGA) as the independent variable. Predicted values from this regression were used as estimates of the probability that a fragment would be occupied in 1990 based on its area. In every simulation run, a random uniform variate was obtained for each fragment, as in the previous simulation. If that variate was less than the predicted probability of occupancy from the logistic regression, the fragment was scored as occupied, otherwise, it was scored as unoccupied. The numbers of simulated local extinctions and recolonizations were counted, and the procedure repeated for a total of 500 simulations. Probability distributions of local extinctions and recolonizations (Fig. 2) were obtained from these simulations under the expectation that turnover dynamics depended only on fragment area.

The same procedure was used for the other models. In the isolation by distance model, we assumed that fragment occupancy in 1990 depended solely on the distance from that fragment to the nearest site occupied by the same species in 1989. This model assumes that migratory birds (particularly males) select the general site where they will return to breed in year  $t + 1$  during the postfledging/postbreeding season of year  $t$  (Löhrl 1959, Adams and Brewer 1981, Morton et al. 1991, Morton 1992). The vegetation structure model assumes that birds select fragments according to the vertical structure of the vegetation (summarized by PCA1), ir-

respective of other fragment characteristics or landscape context. There is evidence that the vertical structure of the vegetation may be used by some bird species to assess prey availability and select territory sites (Smith and Shugart 1987). The first principal component represents a gradient of increasing canopy height and basal area of trees, and decreasing density of woody stems (Table 2).

Finally, the site fidelity model is based on the assumption that fragment occupancy in 1990 depends on the degree of philopatry of birds that bred in the study landscape in 1989. We expect that the probability that at least one experienced breeder of a given species will return to the same fragment in 1990 will increase as a function of its abundance in 1989. With the exception of the Black-and-white Warbler, the number of territorial males present in the different forest fragments in 1989 increased significantly with the logarithm of fragment area (generalized linear models,  $P < 0.01$ ; McCullagh and Nelder 1989). Because abundance values depend in part on fragment area and probably on habitat characteristics, we used the residuals of generalized linear models with the abundance index of each target species as the dependent variable and LOGA and PCA1 as independent variables. These residuals are a measure of abundance in a fragment after controlling statistically for the area and habitat structure of that fragment. Residuals were then used as predictors of the presence or absence of each target species in 1990 in logistic regressions. For the Scarlet Tanager, the generalized linear model we used was equivalent to a logistic regression with the binomial as the error distribution and the logit as link function, since its abundance index was either 0 or 1. For other species, where abundance varied between 0 and 4 (Table 1), we used a log link and Poisson errors.

We did not expect that the random dispersal model or any of the univariate models alone would predict the observed landscape-scale distributions of the target species in 1990. We simulated each of these hypothetical mechanisms in an attempt to compare their relative influence on the observed dynamics. A more realistic model is one that combines the effects of fragment characteristics (area, vegetation structure) to those of the behavior or life history characteristics of the bird species (site fidelity) and landscape context (isolation from occupied sites). To simulate this more complex scenario, we used logistic regressions with presence or absence of each target species in 1990 as the dependent variable and we successively entered the following independent variables in the model: LOGA, PCA1, residual of abundance in 1989, and distance to nearest fragment occupied in 1989. The contribution of each independent variable to the overall fit of the model was assessed at each step, using the likelihood ratio chi-square test (Hosmer and Lemeshow 1989).

We could have used our 1989 data set to simulate area and vegetation effects, but we had to use 1990



TABLE 3. Probability of obtaining as many or fewer local extinctions (LE) and recolonizations (R) as recorded in the study landscape according to six hypothetical mechanisms of spring resettlement by four Neotropical migrants. Probabilities falling within a 95% confidence interval around the mean are indicated in bold. See Table 4 for details on the combination model.

Model	Wood Thrush		Black-and-white Warbler		Ovenbird		Scarlet Tanager	
	LE	R	LE	R	LE	R	LE	R
Random dispersal	0.016	0	0.014	<b>0.070</b>	<b>0.082</b>	<b>0.042</b>	0	0.006
Passive sampling	<b>0.060</b>	<b>0.050</b>	0.010	<b>0.090</b>	<b>0.084</b>	<b>0.068</b>	0.014	<b>0.048</b>
Isolation by distance	0.006	0	<b>0.030</b>	<b>0.068</b>	0	0.002	0.010	0.020
Vegetation structure	0	0.004	0.002	<b>0.076</b>	0.004	0	0	0.016
Site fidelity	0	<b>0.262</b>	0.004	<b>0.216</b>	<b>0.070</b>	<b>0.084</b>	0.010	<b>0.222</b>
Combination	0	<b>0.604</b>	0.002	<b>0.346</b>	<b>0.360</b>	<b>0.626</b>	<b>0.090</b>	<b>0.664</b>

data to simulate site fidelity and isolation by distance models. Consequently, we preferred to maintain the comparability between univariate and multivariate models by using 1990 data for all simulations. We did not test independent predictions since we used our own data set to obtain expected numbers of population turnovers. Instead, we determined the goodness of fit of models based on a small number of parameters of fragment characteristics and their context.

Numbers of fragments occupied and unoccupied were unequal in every target species. Given these unbalanced designs, we chose to build models that would be identical across species to facilitate comparisons. Our goal was not to select the "best" model as judged by its goodness of fit, but rather to compare the relative contribution of each variable to the models among the four target species. The sequence in which variables were entered in the models was chosen a priori to reflect a hierarchy of influences on fragment occupancy.

Logistic regression is known to be sensitive to observations taking extreme values (Pregibon 1981). Statistical packages like SAS (SAS 1989) provide a series of diagnostic statistics for identifying cases that have a strong influence on regression parameters. For the multivariate logistic regression models representing the combination of mechanisms, we focused on cases with influence diagnostic  $C > 1$  (Cox and Snell 1989). When these cases appeared consistently influential according to the other diagnostic statistics provided by SAS, we ran additional logistic regressions in which these cases were excluded, and contrasted predicted values obtained with the original model and the model with one or two influential cases excluded. Three of the four models had consistently influential cases. However, their removal did not significantly alter the predicted values (Pearson correlation coefficients,  $r > 0.90$ ,  $n = 40$  or  $41$ ). Furthermore, there was no indication that the data points in question were erroneous. Therefore, we feel that the simulations based on our logistic regression models are robust enough to influential cases to retain these cases in the final analyses.

## RESULTS

### *Observed and expected numbers of population turnovers*

The incidence of all four target species did not change significantly in the study landscape between 1989 and 1990, even though population turnovers (local extinctions or recolonizations) were recorded in 16–28% of the 50 forest fragments surveyed (M.-A. Villard, *unpublished data*). This pattern is consistent with that reported by Villard et al. (1992) for Wood Thrush, Ovenbird, and Scarlet Tanager in previous years.

When comparing observed numbers of local extinctions and recolonizations to those expected according to the different models simulated, we find that expectations fit observed numbers in at least one case in each model (Table 3). For the random dispersal model, a relatively good fit to the observed data was obtained for the number of recolonizations in Black-and-white Warblers, and for both local extinctions and recolonizations in Ovenbirds. Among the first five models, site fidelity and passive sampling were the most accurate based on the goodness of fit of their expected values. The site fidelity model gave a substantially better fit than passive sampling for recolonizations, but not for local extinctions (Table 3).

If adult birds exhibit a strong fidelity to their previous breeding site, we would expect that models assuming unconstrained dispersal (random dispersal, passive sampling, and vegetation structure) would overestimate numbers of population turnovers. Indeed, over 90% of the simulated numbers of population turnovers were greater than observed values in all of the 24 species  $\times$  model combinations. The isolation by distance model, which assumes partially constrained dispersal, also overestimated the observed numbers of population turnovers. The combination model gave a better fit to observed values, especially for recolonizations. Numbers of local extinctions were still overestimated.

The relative importance of the four variables included in the combination model as predictors of fragment occupancy by each target species in 1990 was

TABLE 4. Logistic regressions of the relationship between presence or absence of a target species in 1990 and four independent variables. The likelihood ratio chi-square test, based on the difference in deviance ( $\Delta D$ ) between two models, is used to assess the effect of additional variables entered.  $\Delta D$  has a chi-square distribution with 1 df for the effects of individual variables, and 4 df for the models including all independent variables. Parameter estimates and their standard error (SE) refer to models including the four independent variables. See Table 1 for meaning of variable codes.

Species	Variable entered	Parameter estimate	SE	D	$\Delta D$	P
Wood Thrush	Intercept only	-2.277	2.476	43.645	...	...
	LOGA	5.135	2.642	32.424	11.221	0.0008
	PCA1	0.254	0.381	32.419	0.005	0.9456
	ABWT	1.812	0.762	23.327	9.092	0.0026
	NNWT	-1.778	2.150	22.602	0.725	0.3945
	Model	...	...	22.602	21.043	0.0003
Black-and-white Warbler	Intercept	-0.046	1.349	58.129	...	...
	LOGA	1.089	1.028	55.364	2.765	0.0963
	PCA1	-0.641	0.292	53.915	1.449	0.2287
	ABBW	0.749	0.486	47.945	5.970	0.0146
	NNBW	-1.327	0.624	41.884	6.061	0.0138
	Model	...	...	41.884	16.245	0.0027
Ovenbird	Intercept	-5.135	2.305	58.129	...	...
	LOGA	6.789	2.391	37.777	20.352	0.0001
	PCA1	-0.712	0.379	37.531	0.246	0.6199
	ABOB	1.490	0.698	32.182	5.349	0.0207
	NNOB	-4.634	1.946	22.226	9.956	0.0160
	Model	...	...	22.226	35.903	0.0001
Scarlet Tanager	Intercept	-0.428	1.729	58.129	...	...
	LOGA	1.956	1.410	53.114	5.015	0.0251
	PCA1	1.274	0.532	43.485	9.629	0.0192
	ABST	0.814	0.492	34.651	8.834	0.0296
	NNST	-2.445	1.202	28.099	6.552	0.0105
	Model	...	...	28.099	30.030	0.0001

assessed using logistic regressions (Table 4). We examined the effect of the influential cases identified using regression diagnostics on the significance of the variables included in the models. Influential cases were found in all species except Scarlet Tanager. Removing one influential case did not change the effects recorded for the Wood Thrush model. However, changes were observed when we removed two influential cases in simulation models of Black-and-white Warbler and Ovenbird. The contribution of PCA1 to the Black-and-white Warbler model became significant, while the significance of ABOB in the Ovenbird model dropped to  $P = 0.0730$ . No apparent reason was found for this slight change in the Ovenbird model. The two influential cases considered in the Black-and-white Warbler model represented the highest values of PCA1 recorded in the 42 fragments included in this analysis, yet both of these fragments were occupied in 1990. PCA1 was negatively related to fragment occupancy by Black-and-white Warblers in 1990 (Table 4).

Likelihood ratio chi-square tests indicate that LOGA and abundance contributed significantly to the fit of the models for each species (although marginally for the Ovenbird), which is consistent with our simulation results (Table 3). The positive sign of the parameter estimates of abundance (Table 4) indicates that the probability of presence of a species in a given fragment increased as a function of its abundance in 1989. This

relationship was also significant in the Scarlet Tanager, even though its abundance index only varied between 0 and 1. Results for the distance variable and PCA1 differed from simulations: (1) distance to nearest occupied fragment contributed significantly to all but one model (Wood Thrush), while it was only important in the Black-and-white Warbler in the simulations; (2) PCA1 did not contribute significantly to the fit of the model for the Black-and-white Warbler, while it did in the simulations; the opposite was found for the Scarlet Tanager. These inconsistencies between the multivariate logistic regression models and simulation results are hardly surprising since the latter are based on univariate logistic regression models. They may also partly reflect the stochastic element introduced in the simulations through the use of random uniform variates.

#### DISCUSSION

The processes involved in the assembly of species on islands or in terrestrial habitat fragments have been the object of a long debate in ecology (see Strong et al. 1984 and references therein). Several authors have argued that area effects on species composition can be attributed to passive sampling from the regional collection of individuals (Haila et al. 1987, 1993 and references therein), and that the absence or scarcity of suitable habitat can often be invoked to explain species absences in small or isolated habitat fragments (Jär-

vinen and Haila 1984, Haila et al. 1987, 1993). These conclusions contrast with the "conventional wisdom" that has emerged from North American studies suggesting that habitat fragmentation leads to a nonrandom impoverishment of species assemblages reflecting the life history characteristics of the species involved (Whitcomb et al. 1981, Ambuel and Temple 1983, Askins and Philbrick 1987, Blake and Karr 1987, Blake 1991). These authors have found that Neotropical migrant birds were consistently rare or absent in smaller forest fragments, or were selectively extirpated from forest tracts becoming increasingly isolated due to deforestation in the surrounding landscape (Askins and Philbrick 1987).

In this paper, we used these contrasting views to define and compare a range of mechanisms of resettlement of fragmented breeding habitat by returning migrant birds. These mechanisms cover a gradient of increasing ecological and/or behavioral constraints. This approach allowed comparing the relative accuracy of expectations under different assumptions about the way migratory birds recolonize their breeding habitat every spring. However, it must be pointed out that observed values located within the 95% confidence interval around the mean expected value do not necessarily indicate support for a particular mechanism. For example, a good fit of observed values for recolonizations was obtained from all simulation models in the Black-and-white Warbler. This urges caution in the interpretation of simulation results. However, the use of four different species in the analyses allowed identifying consistent trends in the data.

As shown by our multiple logistic regressions, we could obtain accurate expectations of occupancy patterns in 1990 and, thus, we could simulate distributional dynamics between 1989 and 1990 based on a knowledge of the effects of fragment area, vegetation structure, proximity to fragments occupied in 1989, and local population size in 1989 on occupancy in 1990. Observed landscape-scale dynamics in the distribution of the four Neotropical migrant bird species studied were best approximated by the combination model, followed by the site fidelity and passive sampling models. Many of the hypothetical mechanisms of resettlement we simulated probably cannot explain the patterns unless they are combined with others. For example, the isolation by distance model may only fine-tune the goodness of fit of the models after effects of fragment area or abundance in 1989 are taken into account. However, the very fact that this isolation variable significantly improved the goodness of fit of multivariate models in three of the four target species is particularly insightful when considering that these species migrate every year to wintering ranges several thousands of kilometres to the south.

One of the most consistent patterns revealed by our simulations was their tendency to overestimate the actual numbers of population turnovers recorded in the

field. This tendency was particularly strong in the models that did not include abundance in 1989, suggesting that some constraints exist on the number of local extinctions or recolonizations that can take place between years. Site fidelity could be one of these constraints. By statistically controlling the effect of fragment area and vegetation structure, we have ruled out the possibility that our abundance index values merely represent a surrogate of fragment area or habitat availability. However, the possibility that apparent site fidelity actually reflects the presence in some forest fragments of microhabitat features critical to nesting or foraging cannot be ruled out. We suspect that open-nesting species are less likely to experience such limitations than cavity-nesting species (especially secondary cavity nesters), but the possibility that the target species have microhabitat requirements that are currently unknown is always present.

Another interesting pattern, most obvious in site fidelity and combination models, was the tendency of expected values to be closer to observed values for recolonizations than for local extinctions. This suggests that local extinctions have a more stochastic character than recolonizations. A single bird establishing a territory in a previously unoccupied fragment of suitable habitat is enough to constitute a recolonization while a local extinction implies that none of the territory holders in year  $t$  returned to the site in year  $t + 1$  and no dispersing bird established a territory in year  $t + 1$ .

#### *Generality of our findings*

Turnover in the occupancy of habitat fragments or patches by birds generally has been documented as an annual community turnover rate (e.g., Diamond 1969, Lynch and Whitcomb 1978, Williamson 1983), a number expressing the proportional change in the species composition of an avian community. Unless the actual list of species becoming locally extinct and recolonizing a site is examined, this parameter is of little use for conservation (Merriam and Wegner 1992).

Population turnovers have rarely been documented over a large number of sites and, to our knowledge, only Villard et al. (1992) and Haila et al. (1993) have reported population turnovers in migratory bird species. Do most forest bird species exhibit these landscape-scale dynamics? We observed local extinctions and recolonizations in the forest bird assemblages of six forest fragments (25.3–53.3 ha) surveyed with point counts over four successive years (Villard 1991). Although absences were not validated with song playbacks, these data clearly suggest that local extinctions and recolonizations occur even in fairly large fragments.

Haila et al. (1993) monitored population turnovers in the avifauna of forest fragments in Finnish taiga. They used Poisson series to test the null hypothesis of random sampling of individuals in fragments of varying area. Their study differs from ours in four respects:

(1) their forest fragments were very small (0.7–4.4 ha) relative to the ones we surveyed; (2) the matrix surrounding their forest fragments was composed of clearcuts and early successional stands rather than cultivated fields; (3) they surveyed all species present in 13 study sites for four successive years, compared to our 2-yr survey of four target species in 50 forest fragments; and (4) they compared observed dynamics to random expectations, rather than the expectations from several different models. Haila et al. (1993) concluded that, for most of the species they examined, the distribution of pairs in their study sites could be predicted using Poisson series. In other species, divergence from random expectations was attributed to habitat selection. They pointed out that local extinctions and recolonizations in habitat fragments hosting single pairs of various species are ecologically meaningless, and stressed the importance of distinguishing these individual-scale phenomena from metapopulation dynamics whereby “genuine, semi-independent subpopulations” go extinct or are recolonized.

Where does one draw the line between sampling colonization and “genuine” metapopulation dynamics? This distinction is a moot point when one is concerned with the mechanisms ensuring the persistence of bird populations in fragmented landscapes. In fact, systems where habitat fragments are occupied by one or a few pairs of birds are ideal for isolating temporal dynamics that would be indistinguishable from stochastic fluctuations in larger populations. Because of the subjectivity involved in the delimitation of local populations in many systems, distinguishing between sampling colonization and metapopulation dynamics is an elusive pursuit (Fahrig and Merriam 1994). The distinction made by Haila et al. (1993) can actually be viewed as a warning against the use of the relative equilibrium between numbers of local extinctions and recolonizations as an index of metapopulation stability in systems with small local populations.

#### *The role of dispersal in the observed landscape-scale dynamics*

None of the birds recorded in our study area were individually marked during this study. Hence, inferences on the role of dispersal (and the corollary phenomenon of site fidelity) in producing the patterns observed here are based on indirect evidence. The dispersal movements of long-distance migratory passerines have been well documented for adults, where percent recapture often approximates the proportion of individuals deemed alive, at least for males (Hann 1937, Walkinshaw 1953, 1966, Nolan 1978, Gavin and Bollinger 1988, Bensch and Hasselquist 1991, Reijnen and Foppen 1991, Payne and Payne 1993, but see Thompson and Nolan 1973, Holmes and Sherry 1992). Median distances reported for the breeding dispersal of Neotropical migratory passerines are <350 m (Ken-deigh 1941, Drilling and Thompson 1988, Holmes and

Sherry 1992), which indicates that the median distances of 400–650 m to nearest occupied sites measured in this study (Table 1) might decrease the frequency of these movements. Movement patterns of birds surviving their 1st yr are still essentially unknown because of the very low recapture rates obtained. However, these low recapture rates themselves suggest that natal dispersal movements are substantially longer than the movements of adults between breeding sites.

The apparent importance of site fidelity and dispersal in the landscape-scale dynamics of the Neotropical migrant species included in this study are particularly intriguing given what is known about natal dispersal in passerine birds. If natal dispersal movements are an order of magnitude longer than breeding dispersal movements, then the distances we recorded between occupied sites should have had no measurable effect on between-year distributional dynamics unless mortality was very high in the 1st-yr cohort. High mortality in the 1st yr would be consistent with important roles of both site fidelity and dispersal in year-to-year dynamics, since the majority of territorial males settling in a given fragment would have held a territory there the previous year (Ruiter 1941, Walkinshaw 1953, 1966, Bairlein 1978, Nolan 1978, Blancher and Robertson 1985, Leck et al. 1988, Holmes and Sherry 1992, Payne and Payne 1993) and breeding dispersal movements are normally very short, as indicated earlier. Lower survival rates in 1st-yr birds than in adults have been reported in parids (Dhondt 1979, Ekman 1984, Loery et al. 1987) and in wood warblers (Nolan 1978, Probst 1986, Sherry and Holmes 1991).

Whitcomb et al. (1981) and Leck et al. (1988) proposed that gradual declines in local populations of Neotropical migrants may result from a net emigration from isolated habitat fragments. Their model, formalized by May (1981), assumes that at equilibrium, all experienced breeders of a local population that survive until the next spring will return to the same habitat fragment to breed, and that immigration by 1st-yr birds fledged elsewhere will balance mortality. Thus, any decrease in survival rates of previous breeders and any reduction in the pool of immigrants to the site (e.g., lower survival of 1st-yr birds; habitat destruction around the site; reduced accessibility of the site through increased isolation) would lead to a decline in local population size (May 1981). This model would hold if natal and breeding dispersal movements are extensive enough that they can lead to emigration from individual fragments, yet are short enough that isolated fragments have a lower immigration rate than those located closer to sources of dispersers. Net emigration from isolated fragments would mainly be associated with natal dispersal since adult passerines generally exhibit high site fidelity. However, consistently high frequencies of reproductive failure can result in low return rates by adults in subsequent years, as shown in a long-term study of a Wood Thrush population (Roth and Johnson 1993).

Processes other than dispersal and site fidelity undoubtedly play a role in the distributional dynamics we observed in our study area. Fragment area was a significant predictor of 1990 occupancy patterns in all species and the passive sampling model gave fairly good approximations of observed numbers of population turnovers, although over 90% of expected numbers were larger than observed ones in all species. The actual process(es) through which fragment area affects the resettlement of returning migrants remain(s) unclear, however. This process could be purely probabilistic (passive sampling), or it could be influenced by various correlates of fragment area, including the abundance of the target species, the presence of critical microhabitat features, or habitat heterogeneity. Free-mark and Merriam (1986) found that their indices of heterogeneity in species composition of tree and shrub strata were positively correlated with fragment area. Hence, a large fragment would have a greater probability of including at least a small patch of suitable habitat for a given species, and would thus be more likely to be occupied in 1990.

Other habitat characteristics not necessarily correlated with fragment area also are important in determining the relative suitability of fragments for a given bird species. The rather minor role played by vegetation structure and composition in our models probably reflects the low variability existing among the forest fragments surveyed. The particular location of the square was selected specifically to minimize variability in habitat and woodland cover.

#### *Conservation implications*

Several studies from eastern deciduous forests of North America have shown that forest reserves (including tracts > 25 ha) are often inefficient at maintaining populations of breeding birds, including many Neotropical migrants (Lynch and Whitcomb 1978, Askins and Philbrick 1987, Leck et al. 1988, reviewed in Terborgh 1989 and Askins et al. 1990). In this study, we focused on four species of forest birds that have maintained subdivided populations in a landscape where woodland was fragmented at least 60 yr ago by the intensification of agriculture. Local extinctions and recolonizations were frequent (Villard et al. 1992; M.-A. Villard, *unpublished data*) and population turnovers depended in part on the site fidelity of experienced breeders and on the isolation of fragments from other occupied sites. Even though this study only provides indirect evidence for the importance of site fidelity and dispersal in the spatiotemporal dynamics of Neotropical migrant birds, the potential conservation implications of this finding deserve attention since area and habitat suitability of forest fragments are irrelevant if these fragments systematically "leak" birds through an imbalance between emigration and immigration.

Clearly, conservation strategies designed for Neotropical migrant birds must extend beyond the selection

of individual "reserves." Assuming that conservation issues on the wintering grounds and along major migratory flyways can be effectively addressed, we still need to determine whether subdivided populations of Neotropical migrants can persist on the breeding grounds without immigration from less fragmented populations. There is evidence that at least some species can persist over several decades as subdivided populations (Villard et al. 1992; M.-A. Villard, *unpublished data*). In addition, this study suggests that Neotropical migrants may not disperse as far as previously thought. However, mortality of yearlings may have been particularly high in these subdivided populations during our study, or long-distance dispersal might have been exceptionally infrequent. Large-scale studies on natal dispersal are critically needed to obtain more robust distributions of dispersal distances, based on large fractions of returning yearlings. Alternatively, indices of gene flow among populations separated by increasing distances (from local to continental scale) could be used to assess the relative frequency of long-distance dispersal and, thus, its role in the persistence of moderately to severely fragmented populations.

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