

DISTRIBUTION, TERRITORIAL LIMITATIONS, AND PATCH
COLONIZATION DYNAMICS OF BIRD SPECIES IN A FRAGMENTED
TEMPERATE- ZONE WOODLAND LANDSCAPE

DISSERTATION

Presented in Partial Fulfillment of the Requirements for
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By

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ABSTRACT

I examined three aspects of forest fragmentation to determine how they impact resident and migrant bird species. The first aspect was the relationship between habitat patch area and species presence and richness. I performed an observational study along riparian woodlands to determine the abundance and distribution of bird species and avian guilds. Woodland area better predicted bird species presence than woodland width. In addition, the probability of detection was positively correlated with woodland area for 11 bird species and negatively correlated with woodland area for eight species. A management simulation of woodland riparian corridor width indicated that current management suggestions were inadequate to provide habitat for a variety of Neotropical woodland migrant bird species.

In the second aspect of my research, I examined the ability of two species of birds to supplement their habitat requirements by incorporating disjunct habitat patches on either side of a watercourse into a single territory. I found the probability of eastern wood-pewees (*Contopus virens*) crossing water gaps to reach simulated singing conspecific to be negatively associated with vegetation gap width. Red-eyed vireos (*Vireo olivaceus*) demonstrated no significant trend. However, the strength of red-eyed vireo vocal responses after crossing was inversely proportional to the width of waterway.

These results suggest that species may differ in their response to simulated conspecific vocalization, and that water gaps less than 30 m wide may not hinder all avian species from crossing to reach playbacks, but may still curtail territorial responses.

The third aspect of my work was to determine the ability of a species to colonize empty habitat patches. I simulated patch extinction events by removing Carolina chickadees (*Poecile carolinensis*) from woodland fragments. I found that chickadees arrived sooner in woodlots connected to other woodland by habitat corridors. I also found that individual chickadees were more often temporarily absent from smaller woodlots, suggesting that these birds utilized woodlots that insufficiently meet foraging and / or breeding requirements. And finally, although chickadees appeared in all woodlots at some point during the study, they were more likely to remain to breed in larger woodlots.

Dedicated to Jessica and Shoshana

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CHAPTER 1

INTRODUCTION

This dissertation utilizes the patchily distributed woodlands of central Ohio to answer questions related to the behavior of bird species within fragmented habitat. Anthropogenic habitat fragmentation is a common worldwide occurrence and has three components (Andrén 1994). As habitat fragmentation proceeds, overall habitat area is lost, patches of remaining habitat are reduced in size, and existing habitat patches are increasingly isolated from each other. Our understanding of the long-term impacts of such fragmentation on resident populations is limited. The ability to assess the impact of fragmentation on the individual and population levels for a species that evolved in areas of continuous habitat may offer a powerful management tool for mitigating adverse aspects of fragmentation.

The concepts of metapopulation biology have been extensively employed to determine the impact of fragmentation on species persisting in habitat patches in human-altered landscapes. A metapopulation is a collection of populations, each inhabiting a discontinuous patch of suitable habitat characterized by a probability of extinction and maintained by immigration from other populations (Levins 1969). Such patches are surrounded by inhospitable habitat, or matrix (McCullough 1996). Individual-patch

extinction and recolonization characterize a metapopulation. The persistence of a metapopulation relies not only on individual patch persistence, but on inter-patch movements as well (Lidicker & Koenig 1996). Stochastic events cause populations in patches to become extinct independently of one another. A stable metapopulation has equal frequencies of extinction and colonization events, with the colonization events being a result of immigration from other patches.

In terms of the metapopulation biology framework, habitat patch area is often assumed, for a given species, to be causal for the likelihood of patch use, patch population size, and probabilities of patch extinction and colonization events. Habitat area is also related to the diversity of organisms within a patch (Diamond 1973). Studies have demonstrated repeatedly that forest area is positively correlated with breeding-bird species diversity (Ambuel & Temple 1983; Opdam et al. 1985; Freemark & Merriam 1986; Blake & Karr 1987; Hinsley et al. 1995; Villard et al. 1999). However, evidence also indicates that the distribution and connectivity of habitat patches within a landscape may impact both species diversity and the probability of species colonization and persistence. Connectivity, according to Taylor et al. (1993), is “the degree to which the landscape facilitates or impedes movement among resource patches.”

In three phases, I investigated potential effects of habitat fragmentation on Ohio birds. The first phase (Chapter 2) was an observational study determining the relationships between local riparian woodland abundance and the distribution of individual bird species and avian guilds. Although habitat area is often associated with species diversity (MacArthur & Wilson 1967), a correlate of area, such as forest width,

has often been used in species – area analyses when examining species richness or population densities along riparian habitats (Stauffer & Best 1980; Keller et al. 1993; Darveau et al. 1995; Kilgo et al. 1998; Whitaker & Montevecchi 1999). Understandably, in regions in which riparian woodland is continuous and its width changes gradually or not at all along considerable sections of a river (Darveau et al. 1995), riparian woodland width should be highly correlated and therefore analytically interchangeable with woodland area. However, in regions where riparian woodland width is highly variable within relatively short sections of river, woodland area may be a more appropriate predictor of species richness or abundance.

Along Ohio's Big and Little Darby Creeks, woodland area appeared to be a better predictor of bird species presence than woodland width. Landsat Thematic Mapper data were used to determine woodland area and width surrounding each of 135 point-count stations along the two watercourses. Probability of detection was positively correlated with woodland area for 11 bird species and negatively correlated with woodland area for eight species. The proposed Little Darby National Wildlife Refuge located within the study area includes restoration of riparian forest habitat along the Darby Creeks. If the riparian habitat zones are not sufficient in area, species already common, rather than declining Neotropical migrants, may be the only species to benefit.

For the second phase of the dissertation (Chapter 3) I performed a manipulative experiment designed to determine the tendencies of two bird species to make use of habitat on both side of a habitat gap. Dunning et al. (1992) referred to this phenomena as "landscape supplementation." Theoretically, an animal population may be sustained at a

higher density than the patch resources can support if, in the landscape surrounding the patch, habitat patches or resources are nearby and available. Thus, if individuals of a species are able to move between patches in a fragmented landscape, habitat patch area will not as strictly limit a patch's population size as it would for less mobile organisms. However, the degree to which resources or nearby habitats are available depends on the intervening matrix.

Riparian waterways may effectively serve as a habitat matrix feature for birds, potentially limiting the likelihood of territories spanning the water gaps. I performed a playback experiment along waterways in central Ohio to determine the extent to which individual birds cross a body of water to respond to a simulated singing conspecific. Logistic regression indicated that the probability of eastern wood-pewees (*Contopus virens*) crossing the gap was negatively associated with vegetation gap width. The red-eyed vireo (*Vireo olivaceus*) demonstrated no significant trend. However, the strength of red-eyed vireo vocal response after crossing was inversely proportional to the width of waterway. These results suggest that 1) species may differ in their gap-crossing response to simulated conspecific vocalization, and 2) gaps less than 30 m wide may not hinder all avian species from crossing to reach playbacks, but may still curtail territorial responses. Riparian habitat conservation plans should consider the impact and importance of waterway and habitat corridor width on territory size for Neotropical migrant species.

The persistence of a metapopulation relies not only on the tenure of a population within a patch, but on inter-patch movements as well (Lidicker & Koenig 1996). In ecological “snapshot” studies, the best predictors of the species composition of individual patches are patch area and connectivity with other patches (Opdam et al. 1985; Blake & Karr 1987; Fitzgibbon 1993; McIntyre 1995).

Patch size may be important in determining the length of time until patch colonization. Lima and Zollner (1996) suggested that dispersing animals moving through a landscape should selectively move toward large patches if they are able to discern differences in dimensions of distant patches. For invertebrates, Simberloff and Wilson (1969) found island size positively related to the rate of species colonizations.

Connectivity between patches may be vital for maintaining species compositions within patches similar to that of the original undisturbed habitat. Connectivity is assessed by determining whether habitat corridors link otherwise disjunct habitat patches (Laurance & Gascon 1996; Anderson & Danielson 2001). A habitat corridor, according to Beier and Noss (1998), is a linear habitat embedded in a dissimilar matrix, connecting two or more habitat blocks. Habitat corridors offer insufficient resources for reproduction by focal organisms.

The third and final phase of my dissertation (Chapter 4) simulated habitat patch extinctions to investigate the ability of a species to colonize empty habitat patches. I simulated patch extinction events by removing Carolina chickadees (*Poecile carolinensis*) from woodland fragments in an Ohio agricultural landscape. I monitored woodlands to determine their date(s) of reoccupation, and subsequent usage by the birds.

Over the course of the project, all woodlots were eventually reoccupied, regardless of their size or degree of isolation. Woodlots connected to other woodland by habitat corridors were reoccupied sooner than were unconnected sites. Birds reoccupied woodlots throughout the winter, but usually during periods of relatively benign wind chill. Chickadees were more likely to remain to breed in larger woodlots. Individual chickadees reoccupying small woodlots were more often temporarily absent, suggesting they utilized woodlots that insufficiently meet foraging and / or breeding requirements. Results from this experiment indicate that habitat connectivity affects the tendency of a species to move through a fragmented landscape. Habitat corridors may be important management tools for maintaining movement between patches for threatened or endangered species.

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CHAPTER 2

BIRD SPECIES ASSOCIATED WITH FRAGMENTED TEMPERATE-DECIDUOUS RIPARIAN WOODLAND

Groom, J.D., Grubb, T.C., Jr., 2002. Bird species associated with fragmented temperate-deciduous riparian woodland. *Conservation Biology*, 16:832-836.

ABSTRACT

Forest area is known to be correlated to bird species diversity. Most researchers of riparian forest avifauna have used riparian woodland width as an index of forest area. However, along Big and Little Darby Creeks, Ohio, woodland area appeared to better predict bird species presence than woodland width. We conducted point counts at 135 locations along Big and Little Darby Creeks. Landsat Thematic Mapper data were used to determine woodland area and width surrounding each point count station. Probability of detection was positively correlated with area for 11 bird species and negatively correlated with area for 8 species. The proposed Little Darby National Wildlife Refuge located

within the study area includes restoration of riparian forest habitat along the Darby Creeks. If the riparian habitat zones are not sufficient in area, already common species, rather than declining Neotropical migrants, may be the only species to benefit.

INTRODUCTION

Past studies have demonstrated repeatedly that forest area is positively correlated with breeding-bird species diversity (Ambuel & Temple 1983; Freemark & Merriam 1986; Blake & Karr 1987; Villard et al. 1999). In North and South America, fragmentation has been implicated in the decline of Neotropical bird species (Robbins et al. 1989). Riparian habitats, in particular, may be important because they may support higher densities of Neotropical migrants than do other habitats (Stauffer & Best 1980; Gates & Giffen 1991; Kinley & Newhouse 1997). The ability to properly assess the importance of riparian habitat quantity and individual bird species abundance may aid in management decisions.

The purpose of our project was to study the relationship between riparian forest fragmentation and the probability of detection of bird species. We measured the potential influence of fragmentation by determining how forest area was related to the presence of individual species along two creeks. Woodland width appeared to be highly variable along the creeks, so we examined the relative effectiveness of both woodland area and width in predicting avian presence.

METHODS

The study took place along Little and Big Darby Creeks in Franklin, Madison, and Union Counties, Ohio. The creeks pass through tilled fields, pasture, wooded areas, and wetland, and have an average width of 30 m. Although deforestation has been severe in the Darby watershed and elsewhere in central Ohio, pockets of riparian forest still exist. The Ohio Chapter of The Nature Conservancy, Columbus Metro Parks, and the U.S. Fish and Wildlife Service are collaborating on a management plan to protect a portion of the Little Darby Creek watershed. Goals include creating a 9300-ha National Wildlife Refuge and increasing the area of riparian forest leading into the refuge (U.S. Fish and Wildlife Service 2000).

Roughly 48 km of Little Darby Creek and 8 km of Big Darby Creek were sampled by canoe from 31 May - 24 June 1998. We used United States Geological Survey 1:7500 topographical maps to select point-count stations every 0.4 km. The location of point-count stations along the creeks was determined by comparing local geographical features with those delineated by topographical maps. We monitored Big and Little Darby creek in a randomized block design. We divided the 48 km of Little Darby Creek into six sections, each section 8 km long. A seventh 8-km section, along Big Darby Creek, was included in this block design. Twenty point counts spanning 8 km of river were surveyed daily beginning at the count site farthest upstream in a section continuing downstream sequentially for the remaining 19 point counts. All seven sections were sampled, in random order, before any section was resampled.

Point counts lasted 5 minutes and took place between 0530 and 1030 hours from a canoe. Each site was sampled three times following the protocols in Kilgo et al. (1998) and Whitaker and Montevecchi (1999). Two observers per canoe performed the point counts for each of the creeks. J.D.G. and T.C.G. performed at least two of the three counts per site (17 of the 21 count days). Three other teams collected records on the remaining four count days.

Birds estimated to be within a 50-m radius of the count site were recorded (Hodges & Krementz 1996; Kilgo et al. 1998). Those observed only in flight during a sampling period were not included in the analysis. Although bird species occurrence was recorded at all 119 sites along Little Darby Creek, 4 sites were excluded from the analysis due to excessive vehicular noise (Keller et al. 1993). No sites were removed from the 8-km stretch of Big Darby Creek. We did not survey during periods of strong wind or heavy rain (Ambuel & Temple 1983; Rich et al. 1994; Kilgo et al. 1998). The distance of 400 m between point-count sites guarded against the possibility that the same bird would be recorded at more than one site (Freemark & Merriam 1986; Blake & Karr 1987; Schmiegelow et al. 1997; Kilgo et al. 1998).

Using ARC / INFO 7.1 (Environmental Systems Research Institute, Redlands, California) and a 1994 Landsat Thematic Mapper image (25 x 25 m resolution), we created circular grid sample areas of 200-m radius around individual point sites along Big and Little Darby creeks. This procedure permitted a large area for analysis and avoided sampling overlapping areas. We used FRAGSTATS 2.0 (McGarigal & Marks 1995) to determine the number of woodland grid cells within 200 m of each grid point, woodland

being one of the seven habitat types (woodland, agriculture, development, open water, wetland, barren land, and shrub) depicted by the Landsat imagery. Woodland area ranged from 0 to 90 percent. The frequency distribution of woodland area was less skewed if no log transformation was used (Kolmogorov-Smirnov normality test; $n = 135$; untransformed woodland area $p = 0.079$; log-transformed woodland area $p < 0.01$). Therefore, we did not log transform woodland area for analysis. No other habitat type was included in the analysis, as the two most abundant types (woodland and agriculture) were strongly correlated (Pearson's correlation = -0.970 , $p < 0.001$).

To reduce the number of correlated parameters included in a model, we used two separate regression procedures. The models examined relationships between 1) bird species richness and woodland area and 2) bird species and two measures of woodland abundance. We used SPSS 9.0 and MINITAB 12.0 for conducting statistical analyses. Logistic regression fits were calculated with STATISTICA 5.0. For logistic regressions, we minimized type II errors by restricting analyses to species detected at $> 10\%$ of survey points (Drolet & Desrochers 1999). Using linear regressions, we examined correlations between number of species and woodland area. Probability of detection based on our sampling method of individual species in relation to woodland area was examined with logistic regression. In addition, we used these logistic regression equations to predict changes in individual species detection probabilities according to potential alterations in riparian forest width. The area of forest entered into the equations was determined from simulated grid coverages of different riparian buffer zone widths.

We compared two logistic regression models measuring different aspects of surrounding woodland to determine which better described variation in the probability of bird detection: (1) woodland area within 200 m of a point-count location and (2) the mean of the woodland widths on the two banks measured perpendicular to the river at the point-count location. Woodland width ranged from 0 to 950 m. The comparison was accomplished by calculating Akaike's information criterion (AIC) values (Burnham & Anderson 1998) for logistic models of area and width for every bird species included in the analysis. We used the Wilcoxon signed ranks test to determine relative ranks of AIC values between models blocked on species. All species in the study were included. This analysis demonstrated which of the two independent variables usually better approximated the information in the data, but it had two weaknesses: 1) it included many species for which neither model approximated the data well and 2) the size of AIC differences (Δ AIC) was not taken into account. A second Wilcoxon signed ranks test addressed these problems by again comparing the two models, but examining only those species for which Δ AIC were > 2 . Models with Δ AIC < 2 are thought to explain data equally well (Burnham & Anderson 1998).

RESULTS

The surveyed section of Big Darby Creek was more forested than the average sample section of Little Darby (Mann-Whitney U test, $Z = 3.754$, two-tailed asymptotic significance < 0.001). The frequency distribution of woodland area was less skewed

when no log transformation was used (Kolmogorov-Smirnov normality test; $n = 135$; untransformed woodland area $p = 0.079$; log-transformed woodland area $p < 0.01$). Therefore, log transformations were not used in the final models.

Eighty-one avian species were detected along Big and Little Darby Creeks (list available upon request from first author). There was no correlation between overall species richness and woodland area ($\beta = 0.197$, $r^2 = 0.026$, $p = 0.062$).

Presence of certain bird species was significantly positively correlated with the amount of woodland around a site (Table 2.1). Of the 35 species included in the analyses, 11 demonstrated positive relationships with woodland area. Negative correlations with woodland area were found for eight species (Table 2.2).

The creation of riparian buffer zones of varying widths is predicted to impact individual Neotropical migrant species differently (Fig. 2.1). We used species-specific logistic regression models and simulated grids of differing riparian corridor widths to arrive at these predictions. Five species would likely increase their probability of detection if riparian buffer widths were widened (Fig. 2.1A), while two would likely decline (Fig. 2.1B). These projections are merely qualitative speculations, as the actual prediction intervals for each species in Fig. 2.1 would overwhelm any theoretical predictive ability.

Using logistic regression, we compared individual species detection relationships with woodland area and woodland width to determine which independent variable accounted for more variation in the data. The model examining individual species detection against the independent variable woodland area was the better approximation

| Species | <i>n</i> | β | <i>p</i> | |
|--------------------------|----------|---------|----------|----|
| Yellow-billed Cuckoo | 21 | 0.089 | 0.284 | |
| Red-bellied Woodpecker | 46 | 0.149 | 0.023 | ** |
| Downy Woodpecker | 82 | 0.089 | 0.136 | |
| Eastern Wood Pewee | 67 | 0.336 | 0.001 | ** |
| Acadian Flycatcher | 37 | 0.452 | 0.001 | ** |
| Great Crested Flycatcher | 50 | 0.183 | 0.005 | ** |
| Carolina Chickadee | 80 | 0.157 | 0.01 | ** |
| Eastern Tufted Titmouse | 80 | 0.192 | 0.002 | ** |
| White-breasted Nuthatch | 55 | 0.118 | 0.054 | |
| Carolina Wren | 37 | 0.287 | 0.001 | ** |
| Blue-grey Gnatcatcher | 68 | 0.155 | 0.011 | ** |
| Wood Thrush | 17 | 0.102 | 0.268 | |
| Yellow-throated Vireo | 34 | 0.234 | 0.003 | ** |

continued

Table 2.1. Positive relationships between bird species presence and woodland area. Shown are results of logistic regression analysis of Little and Big Darby Creek point count records. N refers to the number of the 135 point count locations where a species was detected. Analysis was limited to species detected at > 14 points.

Table 2.1 continued

| Species | <i>n</i> | β | <i>p</i> | |
|--------------------|----------|---------|----------|----|
| Red-eyed Vireo | 37 | 0.244 | 0.001 | ** |
| Blue Jay | 54 | 0.012 | 0.836 | |
| Scarlet Tanager | 14 | 0.322 | 0.011 | ** |
| Northern Cardinal | 121 | 0.161 | 0.092 | |
| Baltimore Oriole | 56 | 0.026 | 0.654 | |
| American Goldfinch | 69 | 0.028 | 0.629 | |

** = Significant value

| Species | <i>n</i> | β | <i>p</i> | |
|----------------------|----------|---------|----------|----|
| Mourning Dove | 15 | -0.171 | 0.067 | |
| House Wren | 95 | -0.016 | 0.798 | |
| American Robin | 82 | -0.296 | 0.001 | ** |
| Gray Catbird | 49 | -0.141 | 0.022 | ** |
| European Starling | 23 | -0.227 | 0.005 | ** |
| Cedar Waxwing | 41 | -0.042 | 0.499 | |
| Warbling Vireo | 27 | -0.173 | 0.02 | ** |
| Common Yellowthroat | 33 | -0.099 | 0.043 | ** |
| Field Sparrow | 27 | -0.071 | 0.325 | |
| Song Sparrow | 96 | -0.578 | 0.001 | ** |
| Indigo Bunting | 104 | -0.021 | 0.759 | |
| Red-winged Blackbird | 34 | -0.353 | 0.001 | ** |
| Common Grackle | 51 | -0.047 | 0.434 | |
| Brown-headed Cowbird | 91 | -0.093 | 0.147 | |

continued

Table 2.2. Negative relationships between bird species presence and woodland area. Shown are results of logistic regression analysis of Little and Big Darby Creek point count records. N refers to the number of the 135 point count locations where a species was detected. Analysis was limited to species detected at > 14 points.

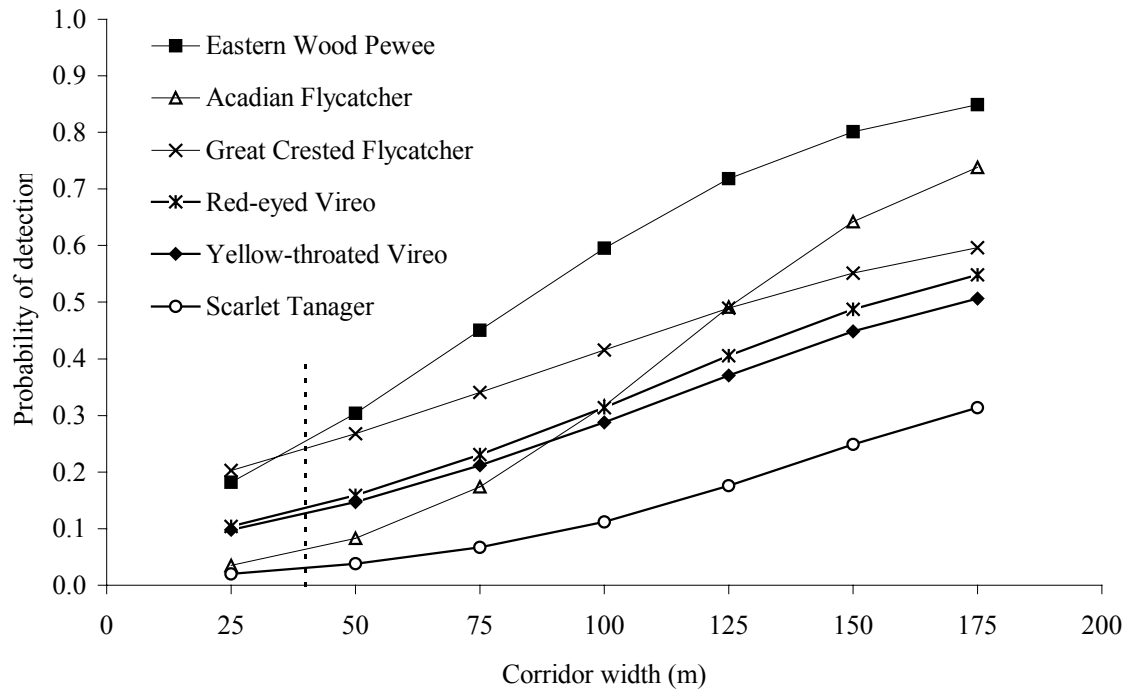
Table 2.2 continued

| Species | n | β | p | |
|---------------|----|---------|-------|----|
| House Sparrow | 14 | -0.312 | 0.003 | ** |
| Mourning Dove | 15 | -0.171 | 0.067 | |

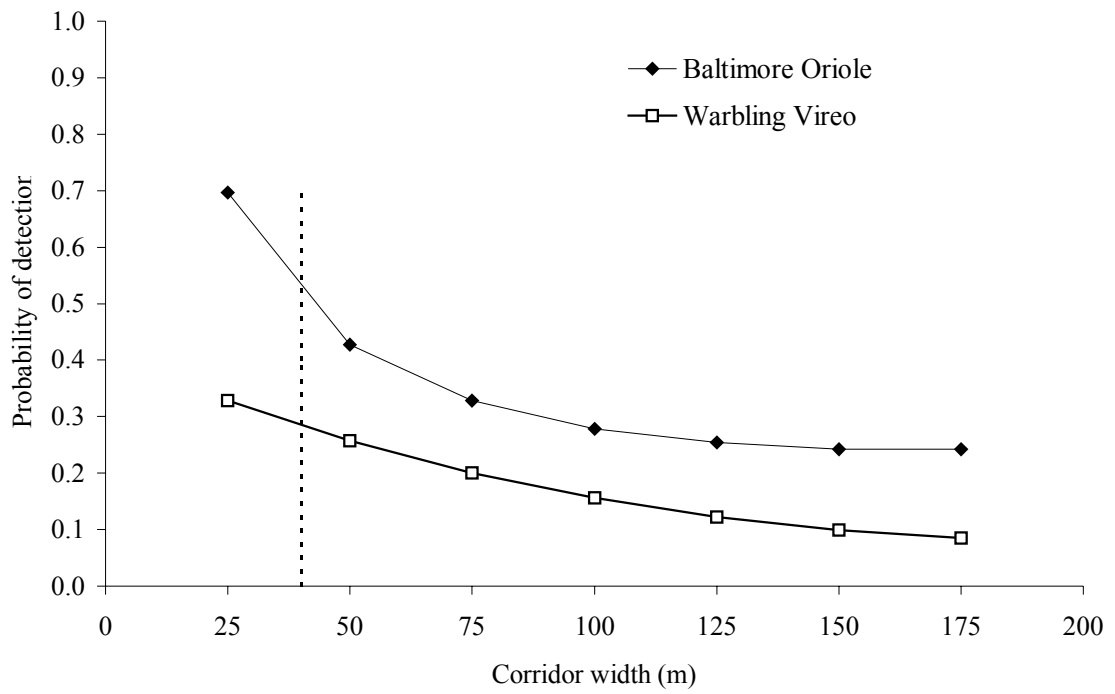
** = Significant value

Figure 2.1. Detection probabilities for Neotropical species positively (A) and negatively (B) associated with increased woodland width. The amount of woodland within simulated grids of riparian forests of different widths was entered into previously determined species-specific logistic regression models to generate detection probabilities. Indicated corridor width is the extent of woodland on one side of the river. The dashed vertical line in each panel denotes the 40-m corridor width planned for proposed Little Darby Nation Wildlife Refuge.

A



B



for the information in the data when we examined AIC values for all 35 species involved in the analysis ($n = 35$; Wilcoxon signed ranks test $Z = -3.063$; $p = 0.002$). When we compared only the models for those species with $\Delta AIC > 2$, woodland area was again the better approximation for the information in the data ($n = 16$; Wilcoxon signed ranks test $Z = -2.172$; $p = 0.030$).

DISCUSSION

Linear regression revealed no significant relationship between the total number of species detected at a site and woodland area. This result may indicate that the habitat surrounding a point-count station was inhabited by a similar number of species, from different guilds. However, woodland area was a significant predictor of occurrence for individual bird species (Tables 2.1 - 2.2).

Woodland area had lower AIC values than did woodland width in correlations with occurrence of individual species. This result indicates that in riparian systems, width may not always be the most biologically relevant measure of the amount of woodland in a given area. For many studies, width may be a good index of woodland quantity (Stauffer & Best 1980, Keller et al. 1993; Hodges & Krementz 1996; Kilgo et al. 1998; Whitaker & Montevecchi 1999) because the woodland in such studies is often continuous and its landward edge more or less parallel to the watercourse. However, in the Darby

watershed, the edges of woodland areas bordering agricultural land use were often highly convoluted and woodland plots were often noncontiguous. Thus, use of woodland area gave more meaningful results.

CONSERVATION IMPLICATIONS

In central Ohio, and throughout the eastern Corn Belt, riparian woodlands are likely important for many woodland species as virtually all of the remaining woodland lies along riparian areas. Development is the single largest threat to the Darby riparian system, as much of the surrounding agricultural land is within commuting distance of the Columbus metropolitan area. One goal of the proposed Little Darby National Wildlife Refuge is to restore and protect native riparian communities from degradation due to development. An important aspect of this proposal is the creation and maintenance of a riparian woodland corridor 40 m wide on each side of Big and Little Darby creeks (Edwards 1997; U. S. Fish and Wildlife Service 2000), creating an aggregate riparian woodland width of 80 m. This area is to be created through both land purchase agreements and voluntary conservation easements. Based on our results, creating woodland corridors even wider than the proposed 40 m per side could have positive effects on the probability of detecting many Neotropical migrant species. We suggest managing riverine habitats for those species most adversely affected by forest fragmentation, namely those Neotropical migrant species that nest predominantly in extensively forested areas.

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CHAPTER 3

RIVER WIDTH AND TERRITORIALITY IN BIRDS: IMPLICATIONS FOR MANAGEMENT OF RIPARIAN HABITAT

To be submitted to the journal *Biological Conservation* by J. D. Groom and T. C. Grubb,
Jr.

ABSTRACT

In a fragmented landscape, we examined the conditions under which a body of water may serve as a territory barrier for breeding birds. We performed a playback experiment along waterways in central Ohio to determine the extent to which individual birds cross a body of water to respond to a simulated singing conspecific. Logistic regression indicated that the probability of eastern wood-pewees *Contopus virens* crossing the gap was negatively associated with vegetation gap width. The red-eyed vireo *Vireo olivaceus* demonstrated no significant trend. However, the strength of red-eyed vireo vocal responses after crossing was inversely proportional to the width of waterway. These results suggest that 1) species may differ in their response to simulated conspecific vocalization, and 2) gaps less than 30 m wide may not hinder all avian species from

crossing to reach playbacks, but may still curtail territorial responses. Riparian habitat conservation plans should consider the impact and importance of waterway and habitat corridor width on territory size for Neotropical migrant species.

INTRODUCTION

Several studies have examined birds crossing terrestrial habitat gaps (Haas 1995; Désrochers and Hannon 1997; Rail et al. 1997; Grubb and Doherty 1999). Rail et al. (1997) addressed the question of whether territories of birds span gaps of unsuitable habitat. In a fragmented landscape we examined the conditions under which a body of water may serve as a territory barrier for breeding birds. Presumably, at some threshold width of a watercourse, a bird of a given species will no longer establish a territory straddling the watercourse, instead confining its territorial activities to a single bank. Watercourses could therefore further fragment existing habitats into effectively smaller patches for a given species. It is conceivable that if riparian buffers are narrow and the watercourse is wide, species that would otherwise cross and make use of habitat on both banks may be constrained to utilize suboptimal elongated territories on one side, or may avoid the area altogether. Thus, watercourse width and a species' gap-crossing propensity would interact to determine whether the two banks of a watercourse should be managed independently of each other.

Birds become more reluctant to forage the farther they are from preferred habitat (Todd and Cowie 1990). Dominant tits (*Parus* sp.) forage on parts of trees where insect prey is only fairly abundant, while subordinates feed at the branch extremities where insect prey is more abundant, but predation risk is higher (Suhonen 1993; Suhonen et al. 1993). Birds also become more vigilant the farther away from cover they are (Lima and Dill 1990).

We hypothesized that the tendency of a bird of a particular species to defend a territory straddling a watercourse declines as the width of the watercourse increases. If this hypothesis is true, then the fall-off with distance in response to playback of conspecific vocalizations should be steeper across watercourses than across continuous habitat.

We performed a playback experiment to determine the extent to which birds of two species, the red-eyed vireo *Vireo olivaceus* and the eastern wood-pewee *Contopus virens*, would tend to cross a body of water to incorporate areas on both sides into one territory. We also studied vocalizations on the assumption that a bird holding a territory straddling a watercourse would be likely to sing after gap-crossing. We selected these species for study because both are common forest-dwelling Neotropical migrants (Blake and Karr 1987; Groom and Grubb 2002). Red-eyed vireos are additionally of interest as Villard (1998) claimed that they might be one of the few “true” forest interior birds that actually demonstrate forest edge avoidance.

A decreasing probability of response by either species to simulated conspecifics singing from across waterways of increasing widths would indicate that waterways may serve as territory delineators. This in turn would suggest that for species for which habitat configuration matters, a water barrier that behaviorally constrains a species to maintain an elongated territory along a single bank may reduce reproductive success along that waterway.

METHODS

From 1– 30 June 2000, we canoed to study sites along reservoirs and rivers in Franklin, Delaware, and Madison Counties, Ohio. We avoided repeated sampling of the same individuals by including only conspecifics separated from one another by at least 200 m. Upon detecting by ear a singing eastern wood-pewee or red-eyed vireo, we landed the canoe either on the opposite bank or on the same bank as the singing individual, depending on whether the bird was to be an experimental or control subject. For experimental trials, we performed playbacks of conspecific vocalizations across water body gaps. Control trials occurred along the same bank as vocalizing target individuals.

The order of experimental and control trials was pre-determined, with a control trial occurring at every fifth conspecific encountered. For each species, we conducted 4 experimental trials for every control trial. Rail et al. (1997) justified using more than 10 experimental trials for every 1 control playback trial because of the dramatic difference

birds exhibited in response to playbacks during the two treatments. In control trials with three forest specialists, golden-crowned kinglet (*Regulus satrapa*), Swainson's thrush (*Catharus ustulatus*), and black-throated green warbler (*Dendroica virens*), Rail et al. (1997) found that 93% of the target birds approached to within 5 m of the speakers. Even when the tape was first played 100 m away, 90% of control birds responded with approach. By contrast, all three species demonstrated marked declines in response at wider habitat gaps.

We performed playbacks from sunrise to 1100. We did not conduct trials before sunrise as predation risk may be greater at this time for most small birds (Lahti et al. 1997), leading to reduced gap-crossing tendencies (Lima and Dill 1990). To preserve equipment and to avoid extraneous changes in sound attenuation, trials were not conducted in rain or strong wind.

We broadcast playbacks from a portable compact disk (CD) player equipped with an Audix PH-3 self-amplified speaker, placed on a 1.5-m tripod. We used preliminary measurements of red-eyed vireo and eastern wood-pewee distance and vocalization decibel level (Realistic sound-level meter) to estimate the amplitude at which these species on average sang (80 dB at 16 m for eastern wood-pewee, 80 dB at 20 m for red-eyed vireo). We broadcast all of our pre-recorded vocalizations at close to 80 dB at 2 m. Red-eyed vireos and eastern wood-pewees sing at roughly 4 kHz (McCarty 1996; Cimprich et al. 2000).

We obtained digitized red-eyed vireo and eastern wood-pewee vocalizations from the Borror Laboratory of Bioacoustics, The Ohio State University. Twenty archived recordings of 40 – 60 secs from each species were copied onto a CD. Each recording was of a separate bird and all recordings were birds singing within Ohio. We edited and standardized dB level of recordings using the program SoundForge 4.0. During a 5 – min playback period we broadcast 5-7 of the 20 conspecific recordings. To avoid inadvertent between-site effects due to recording order, we randomly determined the recordings used in each playback. In no playback was the same recording repeated.

Trials lasted 15 minutes. Each trial was composed of three 5-min phases: pre-playback, playback, and post-playback. This protocol provided a design with which we could compare pre- and post-playback phases for differences in subject activity. We also recorded vocal and behavioral data during the intervening playback phase, but we recognized that such data could generally not be compared to the other phases as the playback may have affected our ability to detect simultaneous vocalizations. During each phase we entered verbal descriptions of vocal and other behavioral activity onto a Sony microcassette recorder. The entries were later consolidated with the 15-minute sampling period broken into 30 30-second intervals.

We grouped the red-eyed vireo's vocalizations into two categories. (1) "Song" is an extended series of notes that is easily audible to the human ear at 100 m. (2) "Quiet calls" are vocalizations that we could only detect < 20 m from a vocalizing vireo. Quiet calls were only detected during playback and post-playback, and apparently occurred in place of song, as we never heard the two interspersed. Those vireos that did sing on the

playback bank often prefaced such singing with quiet calls. In such incidences, the volume of the quiet calls post-playback would rise swiftly and soon the birds would commence singing.

Changes in behavior between pre- and post- playback indicate that the playback phase influences the behavior of the target animal (Lemon 1967; Brooks and Falls 1975; Lindquist and Hetherington 1996). We examined the frequency (occurrence per minute) of eastern wood-pewee and red-eyed vireo vocalizations during pre- and post-playback periods. A change in the frequency of vocalization or the frequency of a particular vocalization type may indicate a reaction by a target bird to playbacks. Variation in such responses may be related to environmental features such as gap width, ultimately relating to the level of the target bird's territorial response. We compared pre- and post-playback rates of vocalization with Wilcoxon Signed Rank tests.

We conducted experimental trials by performing playbacks directly across a body of water from a singing individual. For control trials, we landed on the same bank as the singing individual and performed playbacks through forest instead of across water. The sound attenuation should have been more severe through the forest than across water so playback results of the control trials should be conservative. Target birds were observed and followed during all phases of a playback.

River and vegetation gap widths were determined with a Bushnell YardagePro 600 laser rangefinder (accuracy +/- 1 m). The vegetation gap was the narrowest distance between canopies of trees on the two banks. Playback locations and distances among playback sites were determined using a Magellan Global Positioning System 315. We

also determined riparian corridor width along each bank because habitat width on one bank could potentially influence the likelihood that birds would incorporate both banks into one territory. We employed 1994 LANDSAT imagery and aerial photographs to determine the width of forest on both banks at each playback location.

Using logistic regression analyses (Minitab 13.0 and SPSS 11.0), we estimated the propensity of experimental birds of both species to cross gaps. Responses to playbacks were more complex than we had anticipated. We had originally considered a positive response to be the crossing of a habitat gap and the subsequent approach to a speaker by a target bird. However, in both species, birds would sometimes cross a gap and approach the speaker, but not vocalize on the playback side during either a playback or post-playback period. For this reason, we include as positive responses, a) crossing a water gap, and b) both crossing and then singing on the playback bank. Both types of response are binary. We assessed the amount of variance explained by logistic models with Nagelkerke's R^2 (Nagelkerke 1991). We used multiple logistic regression analysis to further examine the relationship between responses to playback and habitat variables like bank woodland width as well as gap width. We used a paired t -test to determine whether birds were more likely to be singing from the watercourse bank with the wider riparian woodland.

We used linear regression to investigate the possibility that birds may vocalize less after crossing wider gaps to the playback bank. We included in the analysis only crossings after which vocalizations were detected. For eastern wood-pewees and red-eyed vireos, two results are reported for each analysis, one concerning just those

playback-bank vocalizations made during the post-playback period, and one including the sum of playback-bank vocalizations made during both the playback and post-playback period. It could be argued that our perception of vocalizations made during the playback phase could have been inaccurate, as we might have interpreted playback vocalizations as having come from the target bird. However, we believe we were accurate in counting nearby playback-bank vocalizations.

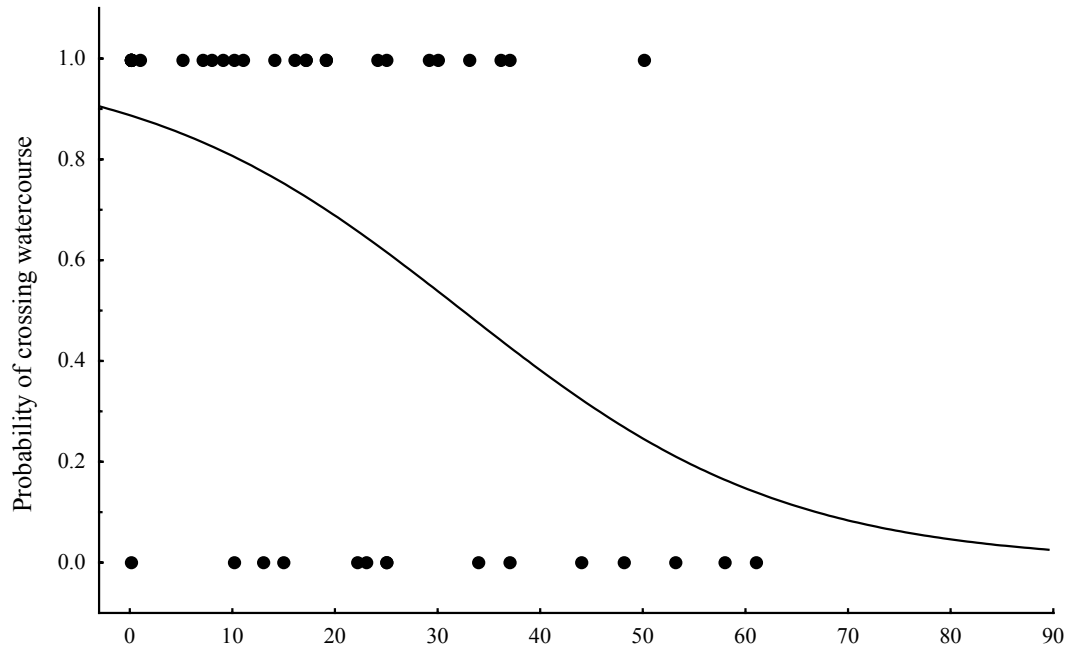
RESULTS

Gap-crossing. We found that at experimental-trial locations, the water gap and the minimum vegetation gap were positively correlated (eastern wood-pewee playback sites, $R^2 = 0.811$, $P < 0.001$, $n = 44$; red-eyed vireo playback sites, $R^2 = 0.913$, $P < 0.001$, $n = 48$). Both species typically crossed gaps at canopy level, so we employed vegetation gaps in the analysis. For experimental playbacks, vegetation gaps ranged from 0 to 61 m (mean = $20.2 \pm \text{sd } 17.4$ m) for eastern wood-pewees and from 0 to 86 m (25.3 ± 21.5 m) for red-eyed vireos.

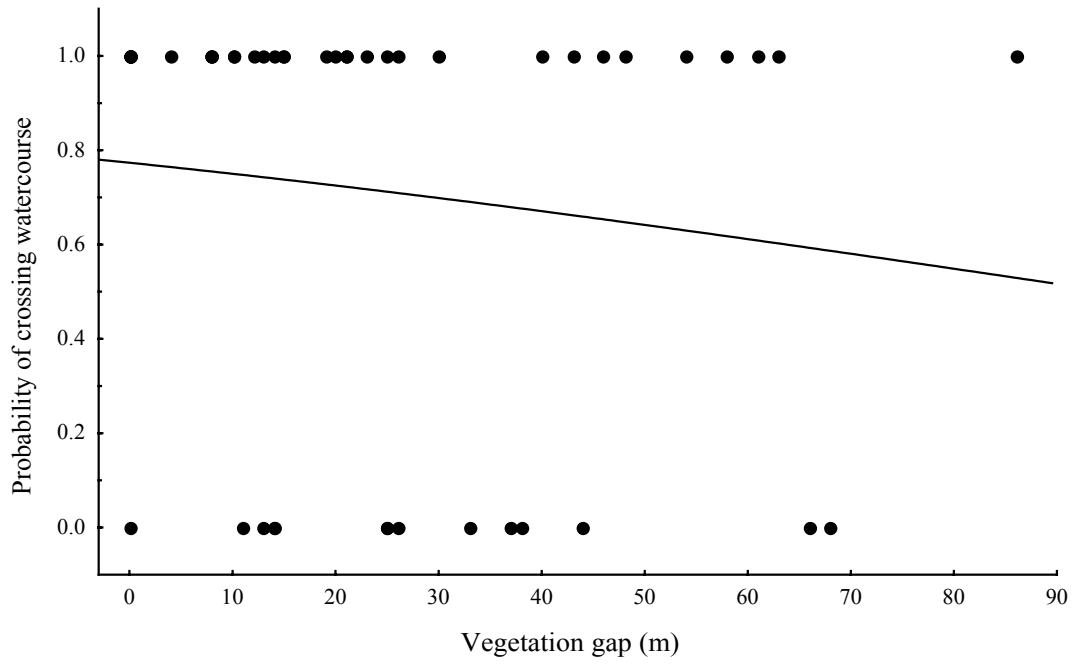
Eastern wood-pewees were less likely to cross wider vegetation gaps to playbacks (logistic regression, $P = 0.002$, $n = 44$, $R^2 = 0.276$, Fig. 3.1A), with a calculated 50% probability of crossing occurring at 33 m (95% CI = 19 m, 114 m). By contrast, red-eyed vireos demonstrated no significant trend ($P = 0.378$, $n = 48$, $R^2 = 0.023$, Fig. 3.1B). For birds of both species that crossed, the time (sec) elapsed between

Figure 3.1. Eastern wood-pewees (A) were less likely to cross wide vegetation gaps while red-eyed vireos (B) were equally likely to cross all tested gap widths.

A



B



the beginning of the playback and a crossing was not related to vegetation gap width (linear regressions: eastern wood-pewee, $P = 0.202$, $R^2 = 0.070$, $n = 25$, red-eyed vireo, $P = 0.314$, $R^2 = 0.063$, $n = 18$).

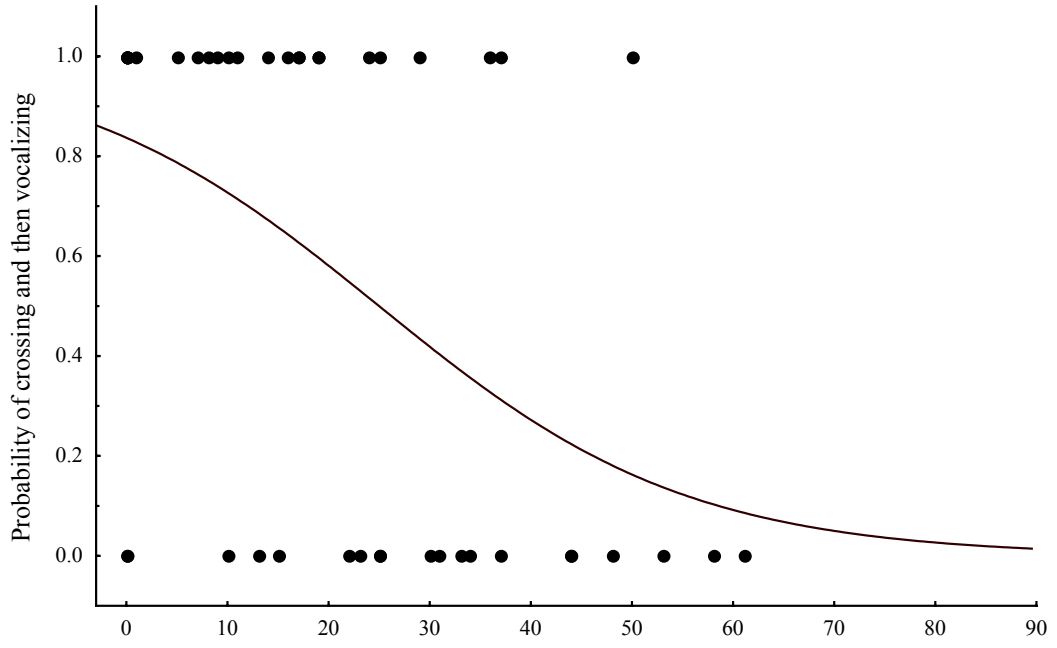
When we performed the analysis again, this time requiring both crossing and vocalizing on the playback bank for a positive response, eastern wood-pewees were less likely to cross and vocalize on the playback bank at wide vegetation gaps (logistic regression, $P = 0.003$, $n = 43$, $R^2 = 0.252$, Fig. 3.2A, 50% probability of crossing and singing at 27 m, 95% CI = 15 m, 106 m). Red-eyed vireos also demonstrated a marked decline in the probability of crossing and singing as gap width increased (when quiet calls were excluded, $P = 0.001$, $n = 48$, $R^2 = 0.275$, Fig. 3.2B, 50% probability of crossing at 15 m, 95% CI = 14 m, 46 m; all vocalizations included in the analysis, $P = 0.329$, $n = 48$; when quiet calls included and singing excluded, $P = 0.128$, $n = 48$).

During pre-playback, neither species sang more on the bank with the greater woodland width parallel to the watercourse (paired t -test, eastern wood-pewee, $t = -0.444$, $P = 0.659$, $n = 46$; red-eyed vireo, $t = -1.29$, $P = 0.204$, $n = 48$). Likewise, neither species' gap-crossing response to playback was influenced by the amount of wooded habitat on either watercourse bank (Table 3.1).

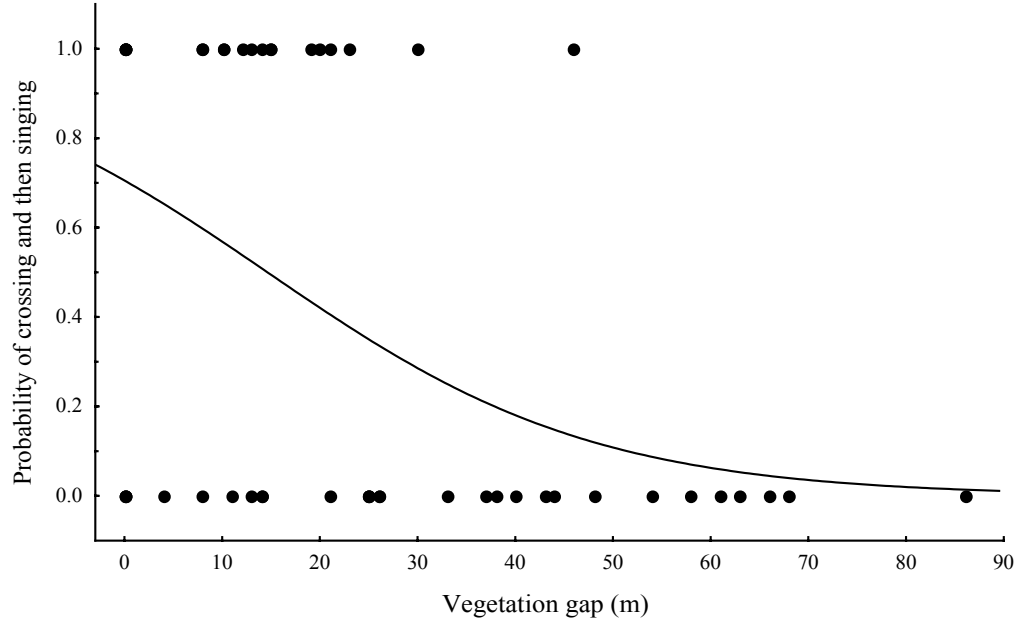
Control trials. Control trials indicated that the observed decline in response with distance during experimental trials was not simply a function of distance between playback and singing individuals. All eastern wood-pewees (initially 8 – 87 m from speaker) except one approached to within 5 m of a speaker mounted on the same

Figure 3.2. Eastern wood-pewees (A) were less likely to cross and vocalize as vegetation gap over a watercourse increased, and red-eyed vireos (B) were less likely to cross and sing as vegetation gap over a watercourse increased.

A



B



| Species | Response | <i>n</i> | Vegetation gap | | | Woodland width | | |
|--------------------|----------------|----------|----------------|--------------------|---------|----------------|---------|----------|
| | | | β | <i>P</i> | β | <i>P</i> | β | <i>P</i> |
| | | | Playback side | | | Origin side | | |
| Eastern wood-pewee | Cross | 44 | -0.066 | 0.006 ^a | -0.004 | 0.375 | 0.007 | 0.217 |
| Eastern wood-pewee | Cross and sing | 43 | -0.065 | 0.009 ^a | -0.007 | 0.137 | 0.008 | 0.167 |
| Red-eyed vireo | Cross | 48 | -0.014 | 0.360 | 0.001 | 0.867 | 0.001 | 0.879 |
| Red-eyed vireo | Cross and sing | 47 | -0.058 | 0.011 ^a | -0.005 | 0.258 | -0.004 | 0.369 |

^a Significant p-values (sequential Bonferroni $\alpha=0.025$).

Table 3.1. Relationships between the likelihood of positive responses to conspecific playback and habitat distribution. Shown are results of logistic multiple regression models. Each model includes three independent variables, vegetation gap width, woodland width on the playback bank, and woodland width on the bank of origin for the target bird. For both species, we examined two response variables, crossing only and crossing followed by singing on the playback bank.

bank (logistic regression: $P = 0.385$, $n = 11$, $R^2 = 0.040$). Similarly, all red-eyed vireos but one approached the speaker from same-bank distances ranging from 14 – 96 m (logistic regression: $P = 0.558$, $n = 12$, $R^2 = 0.036$).

Vocalizations. Eastern wood-pewees, taken in the aggregate, vocalized more post-playback than pre-playback ($n = 38$, $Z = 53.5$, $P < 0.001$). Those pewees that crossed a watercourse also sang more post-playback than pre-playback ($n = 25$, $Z = 12.5$, $P < 0.001$). Eastern wood-pewees that did not cross also vocalized more post-playback ($n = 13$, $Z = 13.0$, $P = 0.025$), indicating that pewees responded to playbacks even if they remained on their original bank throughout the playback trial.

Considering both songs and quiet calls together or just songs alone, the red-eyed vireo did not vocalize more or less frequently post-playback than pre-playback (songs and quiet calls together, $n = 48$, $Z = 591.0$, $P = 0.779$; songs only, $n = 48$, $Z = 628.5$, $P = 0.339$). While quiet calling occurred only in the post-playback period and only from birds that crossed (quiet calls, $n = 14$, $Z = 0.0$, $P = 0.001$), a majority (34 of 48) of red-eyed vireos did not perform quiet calling.

Red-eyed vireos that crossed the gaps did not differ in vocalization rate between post-playback and pre-playback periods ($n = 34$, $Z = 297.5$, $P = 0.768$). Of the two vocalization types, song did not vary in rate between post- and pre- playback periods ($n = 34$, $Z = 323.0$, $P = 0.274$). Singing rate did not differ post-playback from pre-playback for red-eyed vireos that crossed but did not vocalize at all on the playback bank ($n = 13$, $Z = 58.0$, $P = 0.147$). Quiet calls were detected on the bank opposite the

playback during only 4 of the 14 trials. Birds that did not cross did not quiet-call at all, nor did they sing more frequently during the post-playback period ($n = 14$, $Z = 53.0$, $P = 1.000$).

Vocalizations and gap width. Eastern wood-pewee vocalization rate on the playback bank during the post-playback period did not vary with gap width ($P = 0.714$, $R^2 = 0.007$, $n = 23$). Similarly, no pattern between vocalization frequency on the playback bank and gap distance was detected when playback and post-playback vocalizations were combined ($P = 0.917$, $R^2 = 0.001$, $n = 24$).

We found a significant relationship between red-eyed vireo playback-bank vocalization frequencies and gap width. During the post-playback period, all vocalizations combined (song plus quiet calls) were marginally negatively related to gap width ($P = 0.052$, $R^2 = 0.168$, $n = 23$; song, $P = 0.088$, $R^2 = 0.224$, $n = 14$; quiet calls, $P = 0.924$, $R^2 = 0.010$, $n = 14$). When we combined vocalizations from playback and post-playback periods and examined results using a sequential Bonferroni analysis (Holm 1979, as cited in Rice 1989), frequencies of all vocalizations were negatively related to gap width ($k = \text{number of comparisons} = 3$, $\alpha/k = 0.013$, $P = 0.009$, $R^2 = 0.272$, $n = 24$), although frequencies of individual vocalization types were not ($k = 2$, $\alpha/k = 0.025$, song, $P = 0.030$, $R^2 = 0.262$, $n = 18$; quiet calls, $P = 0.703$, $R^2 = 0.070$, $n = 22$).

DISCUSSION

Eastern wood-pewees were less likely to cross gaps as gap width increased, supporting our alternate hypothesis, but red-eyed vireos demonstrated no such trend, indicating that for this species we failed to reject our null hypothesis. When we considered a positive response to consist of a bird both crossing and then singing on the playback bank, the probability of red-eyed vireo responses decreased as gap width increased. According to the regression equation, the 50% probability of a vireo both crossing and singing occurred at gap widths of only 15 m, indicating, perhaps, that a watercourse of > 15 m would result in fewer straddling territories.

Control trials demonstrated that both species almost always (~90%) approached the speaker when the playback was conducted through continuous forest. Therefore, it appears that for experimental subjects playback distance alone was not responsible for a decline in response. They were responding to the width of a habitat gap.

Habitat gap widths could affect the response strength of territorial birds. It is possible that for certain species territorial responses do not abruptly cease beyond a particular point, but fade as one gets farther from the center of a territory. However, those eastern wood-pewees that did cross vegetation gaps did not vocalize less at wider gap widths, even when playback and post-playback vocalizations were included. By contrast, when playback and post-playback vocalizations were included, red-eyed vireos that crossed did tend to vocalize less at wider habitat gaps.

Neither species initially vocalized primarily from the bank with the wider swath of forest, nor was a relationship found between the likelihood that a bird would both cross and vocalize and the amount of forest on either wooded bank. This may indicate that these species are not more likely to hold territories that span waterways when 1) there is more habitat on the opposite shore, or 2) there is limited habitat available on either shore. Such a result would suggest that wide riparian vegetation gaps act as severe territory boundaries. However, our study sites may not have adequately sampled enough narrow riparian forest corridors to have properly addressed these possibilities.

The vocal reactions to a simulated singing conspecific differed between the eastern wood-pewee and the red-eyed vireo. We compared pre- and post-playback vocalizations for eastern wood-pewees and found that they were more likely to vocalize during the post-playback phase, even if they did not cross a habitat gap. This increase in post-playback vocalization rate by birds that did not cross indicates that they not only detected the playback, but also responded to it. Red-eyed vireos did not respond in a similar fashion. They did not vocalize more during the post-playback phase except for those that crossed and vocalized on the playback bank at some point during the trial.

In our analyses of vocalizations, for both species we included total vocalizations and for red-eyed vireos two separate vocalization types. For the eastern wood-pewee, all vocalizations increased post-playback. Red-eyed vireos that crossed and sang on the playback bank would often begin vocalizing with quiet calls of increasing decibel level. Birds sometimes would cross, give several quiet calls, and then cross back to their original bank. If we counted a positive territorial response as a red-eyed vireo crossing a

watercourse and then giving either a song or quiet call on the playback bank, watercourse width was not related to the probability of a positive response. However, when we dropped quiet calls and considered only songs as positive responses, a significant reduction in response with increased gap width emerged. No quiet vocalizations were detected pre-playback.

This study has several implications. Our main finding is that the width of a watercourse may influence the position of local territory boundaries. A secondary finding is that the two species studied did not respond similarly to conspecific playbacks. Eastern wood-pewees vocalized more post-playback while, in general, red-eyed vireos did not. While eastern wood-pewees did not cross at the widest habitat gap widths, red-eyed vireos would often cross gaps as wide as 87 m to approach the speaker. However, once near a speaker, vireos that had crossed gaps wider than 50 m did not vocalize at a normal volume.

Our results underscore the need for researchers to exercise caution when generalizing and interpreting behavioral responses to playbacks among species. For example, always interpreting gap-crossing as defending territory on both sides of a watercourse may be erroneous. Habitat gaps may be more important for certain species in determining a territory boundary than it would appear from the behavioral response of birds to simulated territorial encroachment.

Several studies have examined the response of multiple species to playbacks of mobbing calls (Désrochers and Hannon 1997; St. Clair et al. 1998). Mobbing calls are likely effective for eliciting responses from a wide variety of species, but the inference of

such studies relates to depredation risk, not territoriality. The gap-crossing behavior of a species may dramatically differ in response to conspecific song versus mobbing vocalizations. Based on the difference in response to conspecific playback that we observed between red-eyed vireos and eastern wood-pewees, we urge that researchers exercise caution when interpreting gap-crossing behavior of several species to conspecific playback trials (i.e. Rail et al. 1997), as not all species may respond similarly. Misinterpretation of gap-crossing behavior in response to conspecific playbacks may result in under- or over-estimation of species' abilities to hold territories straddling habitat gaps.

A question that emerges from this study concerns the identity and intentions of non-vocalizing birds that gap-crossed. The vocalizations that we played might represent potentially intruding strangers to local territorial conspecifics. The responding male bird might have traveled outside of his territory to investigate the potentially intruding stranger (Falls 1981). Alternatively, the non-vocalizing gap-crossing bird may have been a female, possibly seeking extra-pair copulations. Evidence for this possibility was the finding that during trials pairs of birds would sometimes cross gaps (pewees, $n = 4$; vireos, $n = 13$), with one bird 1 – 5 m behind the other. Such pairs might indicate a mate-guarding effort by a male of his gap-crossing mate.

CONSERVATION IMPLICATIONS

Our study demonstrates that otherwise vagile organisms may be limited behaviorally in their ability to incorporate opposite banks of a watercourse into a single territory. If a riparian habitat is fragmented and discontinuous, watercourses may effectively increase the degree of fragmentation of the habitat by further subdividing remaining habitat patches. Thus, managers should not necessarily consider terrestrial habitat to be continuous across a watercourse for all resident species; some species may be physically or behaviorally limited in their gap-crossing tendencies (Lima and Zollner 1996).

Habitat managers often protect buffers of riparian habitat of a certain width along waterways. In locations where water gaps impose territory barriers for species, resident species may only be able to hold elongated territories along a single bank. Empirical evidence indicates that for some species, the shape of available habitat may influence bird distributions (McGarigal and McComb 1995, Villard et al. 1999). As a water gap widens, a breeding pair of birds may require additional habitat protected on a single bank to realize the same fitness they would garner on both banks if the water gap were narrower. If managers wish to avoid compromising either the diversity of species along a given waterway or the reproductive success of a given species, the effect of water gap width on breeding bird territories should be considered. Additionally, individual species may vary in the amount of habitat required for successful breeding.

To illustrate this idea empirically, we amalgamated the results of this experiment with a re-analysis of data from an earlier point-count survey of the avifauna along Big and Little Darby Creeks, Ohio (Groom and Grubb 2002). At each point-count site of that survey, we retroactively measured waterway gap width using digitized 1:24000 USGS topographical maps. Then, employing logistic regressions of water gap and vegetation gap widths in the present experiment, we determined the water gap width at which each species exhibited a 50% probability of crossing and singing on the playback bank (eastern wood-pewees = 36 m [95% CI = 13 m, 70 m], red-eyed vireos = 27 m [20 m, 205 m]). We could not use the 50% probability of crossing a vegetation gap, as we had no access to vegetation gap data from the point-count survey. We used these results to find Little and Big Darby Creek point-count sites that had narrower water gaps than these cut-off widths for both species. Results from logistic regression analyses of our point-count data at these sites indicated the width of wooded habitat at which we experienced a 50% probability of detecting each of the two species (logistic regression, eastern wood-pewee, $P < 0.001$, $n = 124$, $R^2 = 0.293$, combined width = 215 m [95% CI = 146 m, 349 m], or 108 m on each bank; red-eyed vireo, $P = 0.010$, $n = 122$, $R^2 = 0.085$, combined width = 545 m [315 m, 1900 m], or 273 m on each bank). Figure 3.3 depicts the amount of habitat necessary, according to these estimates (and ignoring their confidence intervals), to maintain at least a 50% probability of detecting either species as a waterway widens past the water gap width at which each species has a 50% probability of maintaining both banks in one territory.

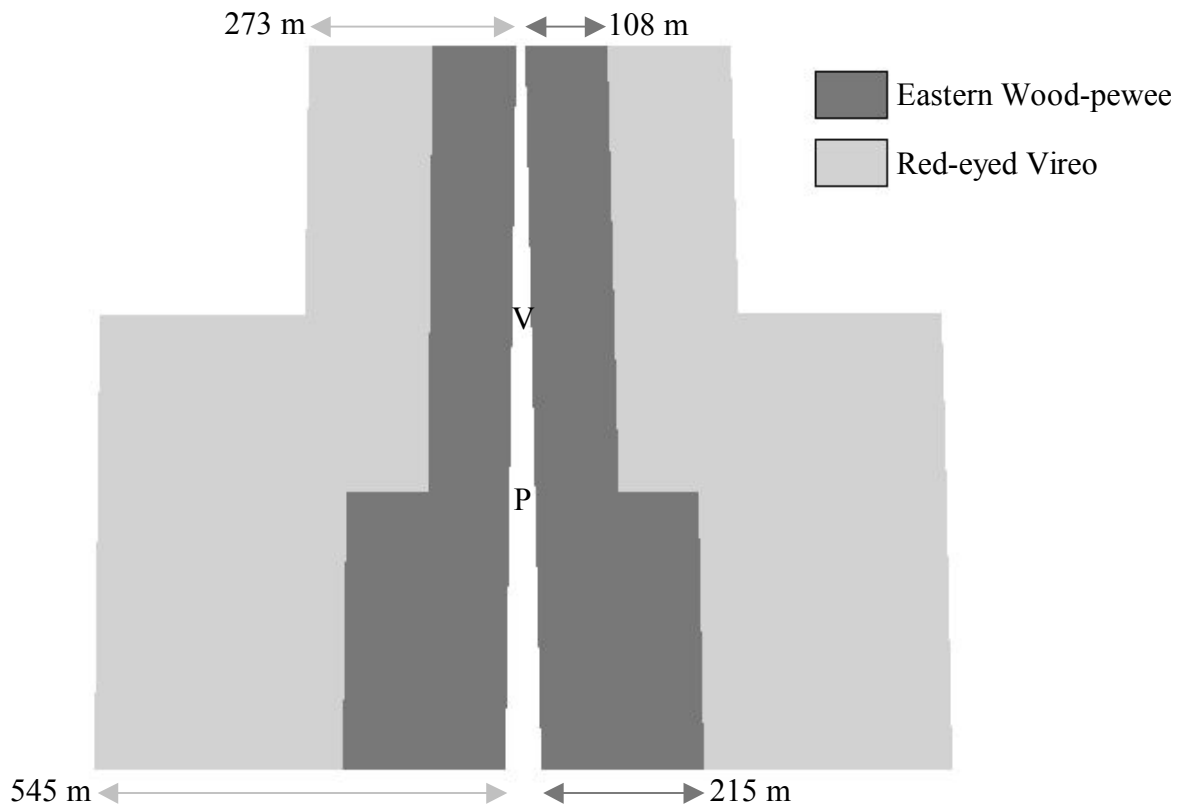


Figure 3.3. Influence of watercourse width on riparian habitat requirements of eastern wood-pewee and red-eyed vireo in Ohio. An earlier study (Groom and Grubb 2002) found that the minimum total width of riparian habitat required for a 50% probability of species detection at a survey point was 215 m for the peewee and 545 m for the vireo. From the present study, we know that peewees and vireos behaving territorially had a 50% chance of crossing watercourses 36 m (P) and 27 m (V), respectively. Thus, beyond these watercourse widths, single-bank habitat width would need to double to retain 50% occurrence rates for the two species, as illustrated in the figure.

Due to the large confidence intervals surrounding both our estimation of gap widths and riparian woodland widths and the low amount of variance these variables explain, the above results cannot be interpreted as predictive. Rather, they serve to illustrate the concept that the amount of habitat necessary to maintain a species density that allows observers a certain probability of detecting a species may differ dramatically between species. Red-eyed vireos may require wider riparian habitat than eastern woodpeewees (Fig. 3.3). Furthermore, depending on the river width, the point at which wider riparian habitat should be protected along one or both banks may vary greatly among species. These results underscore the need to relate the width of riparian habitat corridors to the ability of individuals of a given species to utilize available habitat on both banks. Thus, amount of habitat available may not be the only factor of importance to the target species. Both natural abiotic landscape features such as water gaps and anthropogenic habitat gaps may themselves discount the value of the habitat to the breeding species.

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CHAPTER 4

DYNAMICS OF PATCH COLONIZATION IN A PERMANENT-RESIDENT BIRD SPECIES IN A FRAGMENTED LANDSCAPE: A MANIPULATIVE STUDY

To be submitted to the journal *Ecology* by J. D. Groom and T. C. Grubb, Jr.

ABSTRACT

Habitat and landscape features that influence rate of inter-patch movement and colonization may determine the likelihood of species persisting in fragmented landscapes. We simulated patch extinction by removing Carolina chickadees (*Poecile carolinensis*) from woodland fragments in an Ohio agricultural landscape. We then monitored the woodlands to determine their date(s) of reoccupation, and subsequent usage by the birds. While all woodlots were eventually reoccupied regardless of their size or degree of isolation, woodlots connected to other woodland by habitat corridors were reoccupied sooner than were unconnected sites. Birds reoccupied woodlots throughout the winter, but usually during periods of relatively benign wind chill. Individual chickadees were more often temporarily absent from smaller woodlots, suggesting they utilized woodlots

that insufficiently meet foraging and / or breeding requirements. Chickadees were more likely to remain to breed in larger woodlots. Results from this experiment indicate that habitat connectivity affects the tendency of this species to move through a fragmented landscape. Habitat corridors may be important management tools for maintaining movement between patches for threatened or endangered species.

INTRODUCTION

The ability of individual organisms to move through a landscape and recolonize a patch after a patch-level extinction event may play an important role in maintaining species within a landscape (Burkey 1989, Gonzalez et al. 1998). Theoretical models suggest that recolonizations of habitat patches in which extirpations have occurred can be critical for the long-term survival of a metapopulation (Fahrig and Merriam 1994). Observational (Pettersson 1985) and experimental (Warren 1996, Gonzalez et al. 1998, Tewksbury et al. 2002) studies support these findings.

Anthropogenic habitat fragmentation is a common worldwide occurrence and has three components (Andrén 1994). As habitat fragmentation proceeds, overall habitat area is lost, patches of remaining habitat are reduced in size, and existing habitat patches are increasingly isolated from each other. Our understanding of the long-term effects of such fragmentation on resident populations is limited. Commonly, computer simulations are used to investigate consequences of fragmentation for hypothetical or selected species (e. g., Burkey 1989, Hanski 1994, Doherty et al. 1999, Anderson & Danielson 2001).

However, it is not known to what extent such models are applicable to real-world situations. The ability to assess the impact of fragmentation on individual organisms of species that have evolved in areas of continuous habitat may offer a powerful management tool for mitigating adverse aspects of fragmentation.

A metapopulation has been defined as a collection of populations, each inhabiting a discontinuous patch of suitable habitat characterized by a probability of extinction and maintained by immigration from other populations (Levins 1969). Such patches are surrounded by inhospitable habitat, or matrix (McCullough 1996). Individual-patch extinction and recolonization characterize a metapopulation. The persistence of a metapopulation relies not only on individual patch persistence, but on inter-patch movements as well (Lidicker & Koenig 1996). Stochastic events cause populations in patches to become extinct independently of one another. A stable metapopulation has equal frequencies of extinction and colonization events, with the colonization events being a result of immigration from other patches.

Patch size may be important in determining the length of time until patch colonization. For invertebrates, Simberloff and Wilson (1969) found island size positively related to the rate of species colonization events. In ecological “snapshot” studies, the best predictors of the species composition of individual patches are patch area and isolation from other patches (Opdam et al. 1985, Blake & Karr 1987, Fitzgibbon 1993, McIntyre 1995). Such indirect evidence may be related to the ability of species to

recolonize and persist in fragmented landscapes. For example, Hames et al. (2001) conducted a 3-year observational study of scarlet tanagers (*Piranga olivacea*), finding the probability of recolonization to be negatively associated with patch isolation.

It is poorly known to what extent inter-patch movement is guided by perceptual abilities and resulting decisions. Lima and Zollner (1996) suggested that dispersing animals moving through a landscape should selectively move toward large patches if they are able to discern differences in dimensions of distant patches. Sciurids oriented and moved towards habitat patches detected at a distance (Zollner 2000), but whether sciurid dispersers exhibit pre-immigration patch selectivity based on their perceptive abilities remains unknown.

Connectivity, the degree to which a landscape allows movement among resource patches (Taylor et al. 1993), may be vital for maintaining species compositions within patches similar to the species composition of the original undisturbed habitat. Genetic composition of populations can be affected by degrees of connectivity (Hale et al. 2001) and biodiversity may be better maintained if corridors are present (Gonzalez et al. 1998, Tewksbury et al. 2002). Immigration rates by invertebrates to habitat patches appear to be negatively related to the distance of such patches from continuous habitat areas (Simberloff and Wilson 1969). However, the degree to which inter-patch connectivity exists between habitat patches appears to differ among matrix types (Ferrerias 2001), taxa (Simberloff and Wilson 1969, Rosenblatt et al. 1999, Collinge 2000), and even between sexes of the same species (Aars and Ims 1999).

While the concept of linking habitat patches by corridors has been embraced by managers for some time, the conservation utility of such connections is debated (Hobbs 1992, Simberloff et al. 1992, Mann and Plummer 1993, 1995). However, recent empirical evidence indicates that for certain species corridors increase movements between patches (Haas 1995, Haddad 1999a, b, Tewksbury et al. 2002, but see Andreassen and Ims 2001) and may facilitate colonizing of patches uninhabited by conspecifics (Van Apeldoorn et al. 1994). Corridors may facilitate reoccupation of habitat patches in which extirpations have occurred.

We are not aware of any previous manipulative studies examining habitat patch colonization by vertebrates following controlled extinction events. Our study was designed to determine the relative importance of different patch and landscape variables in affecting probability of patch colonization by a bird species. Such information may offer insight regarding factors influencing inter-patch movement, potentially enabling models to incorporate added degrees of realism in predicting the persistence of threatened species currently existing in fragmented habitats. Results from this experiment may also indicate what types of conservation measures would best increase the probability that a species would be able to reoccupy habitat patches if patch-level extinction events occurred.

We simulated extinction events by removing Carolina chickadees (*Poecile carolinensis*) from woodlots in the agricultural landscape of Ohio. Birds of this species commonly inhabit fragments of previously continuous woodland and may exist as isolated pairs in woodlots of only a few hectares (Grubb and Bronson 2001). By

removing Carolina chickadees from woodlots, we simulated patch extinction events. We then observed the length of time that passed before a patch became reoccupied and whether it was subsequently colonized. We defined a patch as reoccupied if at least one new chickadee was detected post-extirpation, and colonized if chickadees attempted to breed in the patch. The distinction between reoccupation and colonization is important, as the observation that organisms are within a patch does not necessarily indicate that they will remain in the patch to breed. Evidence from a mark-recapture study of the bay checkerspot butterfly (*Euphydryas editha bayensis*) indicated that empty patches were unlikely to become colonized unless multiple immigration (i.e., reoccupation) events had occurred (Harrison 1989). We determined which climatic, patch, and landscape variables were associated with reoccupation and colonization by the chickadees.

This study examines the hypothesis that the rate at which habitat patches are reoccupied decreases with increased local habitat fragmentation (Weins 1997). If this hypothesis is true, then the amount of forest and the presence of woodland habitat corridors in the landscape surrounding a woodlot from which chickadees have been removed should be negatively correlated with the time interval between removal and reoccupation. If the reverse is true, namely that the rate at which habitat patches are reoccupied increases with increased local habitat fragmentation, then amount of forest and presence of habitat corridors should be positively correlated with the amount of time after removal until patch reoccupation and colonization. This situation is plausible if a low number of patches in a local landscape promotes a greater frequency of visits by dispersers per woodlot relative to a landscape that is less fragmented. We further

hypothesized that reoccupation events during the winter are more likely to occur during periods of relatively mild wind chill when thermoregulation and movement have lower metabolic costs. From this hypothesis, we predicted that we would be more likely to detect new immigrants during or immediately following periods of relatively mild wind chill.

METHODS

From December 2001 to May 2002 we studied chickadees within 28 privately-owned woodlots in central Ohio (Delaware, Union, Madison, and Marion Counties). The study encompassed a time frame beginning during occurrence of winter flocks and ending with mated-pair territories. All habitat patches used were < 12 ha, and while all were located within a 2840-km² area, none was closer than 5 km from any other. We believe > 5 km between study woodlots effectively maintained statistical independence, as black-capped chickadee (*Poecile atricapilla*) dispersers in a similarly fragmented landscape settled a median of 1 km from natal sites (Weise & Meyer 1979). Two woodlands were considered the same patch if they were < 30 m apart (Villard & Merriam 1995) or if there was a vegetation strip wider than 10 m connecting them.

Between 2 and 22 January, we captured chickadees from occupied woodlots in feeder traps or in mist-nets surrounding caged decoys and vocalization playbacks. A woodlot was considered empty of chickadees if none responded to post-capture playback,

and none was seen or heard within resident mixed-species flocks. We wished to avoid altering the value of woodlots for potential immigrants, so we removed feeders after removing residents.

We banded chickadees slated for removal with USFWS bands and transported them to and released them within the suburban “bird-feeder belt” of Columbus, OH. All birds were released within 10 hours of capture unless sunset was < 1 hour off in which case birds were held overnight and released at dawn. During transport, all birds were housed in individual containers with adequate ventilation and ad libitum sunflower seeds, mealworms, and water.

After removing all chickadees from a woodlot, we visited at 3-day intervals to determine whether immigrants had arrived in the interim. If immigrants had reoccupied the woodlot, a feeder was briefly redeployed to capture them. In 24 woodlots, all initial immigrants were banded with USFWS bands, color-streamered for individual identification, and then released on site. In the remaining 4 woodlots, not all of the initially reoccupying chickadees could be color-streamered. Some did not enter the trap and to capture them would have 1) required food-supplementing the birds for a longer period of time in order to draw them to the feeder, or 2) risked recapturing the already-streamered chickadees in mistnets, which could have constituted aversive conditioning towards responding to playbacks and thus have affected the efficacy of our subsequent resighting efforts. For these reasons, additional immigrants were not captured if streamered individuals remained in the woodlot. After immigrant chickadees in a woodlot had been streamered, feeder-traps were removed.

Woodlots with color-streamered chickadees were observed on average every 5 days to determine their length of stay. To determine instances of colonization, we followed color-streamered individuals until it was evident they were initiating breeding (courtship feeding observed and/or female begging calls detected) or until 3 May by which time the breeding season of Ohio chickadees is well underway (Grubb and Bronson 2001). Villard and Merriam (1995) validated absences of birds in woodlots by broadcasting playback tapes of conspecific vocalizations. We censused woodlots throughout the study using this method. We used only playbacks comprised of Carolina chickadee calls, not the characteristic “fee-bee, fee-bay” song, to avoid simulating the presence of a resident territorial male. Otherwise we might have risked triggering behavioral responses by neighboring chickadees, enhancing or dampening their probability of moving into the study woodlot. We used an Aiwa CSD-A120 portable CD player to broadcast chickadee calls. We made 3 CDs of Carolina chickadee calls from the collection in The Ohio State University Borror Laboratory of Bioacoustics. Each CD had four tracks of chickadee calls, and all tracks were roughly 45 seconds long. To inhibit the habituation of birds to the tracks of an individual CD, we alternated which CDs we broadcast in the field. During each visit, in the absence of response, we broadcast playbacks throughout the entire woodlot. On calm days, we could hear the playback through 100 m of woodland.

Once we detected the presence of chickadees, we ceased broadcasting the playback. We noted the number of chickadees detected and resightings of individual streamered birds. We also looked for USFWS bands, in case relocated birds had managed to return to their original woodlot.

We related the amount of time between induced extinction and subsequent reoccupation to such variables as patch area, distance to nearest woodland, total woodland area within 1 and 2 km of the habitat patch, and the existence of fencerows connecting the focal patch to other patches in the landscape. While fencerow connectivity was determined from aerial photographs, the other variables were determined by analyzing USGS Landsat Thematic Mapper data with ArcGIS 8.1 and Fragstats 3.2 (McGarigal et al. 2002).

The three response variables of interest were whether a patch was reoccupied, the length of time from patch extinction to patch reoccupation, and whether a reoccupied patch was subsequently colonized. We also determined the residency time for chickadees that disappeared (left or died) before breeding. Immigrant pairs that arrived at an empty patch during the winter but disappeared before the beginning of the breeding season were not considered colonists because they failed to attempt to breed in that patch.

We used linear regression for analyses involving continuous response variables (i. e., time from extinction to reoccupation), and we addressed incidence of woodlot colonization using logistic regressions. In the logistic regression, the response variable was binomial, while the independent variables were either discrete or continuous. All independent variables were transformed to correct for non-normal residual distributions.

We used an information-theoretic approach with both linear and logistic regression models. Nested model sets were constructed a priori and compared using Akaike's Information Criterion (AIC; Burnham and Anderson 1998). The best models were those with $\Delta\text{AIC} < 2$ and fewest parameters (most parsimonious). Since model comparisons are relative, the best models may not explain much variance, so P -values and r^2 values are reported, but were not used in model evaluation. For logistic models we reported Nagelkerke's r^2 values (Nagelkerke 1991).

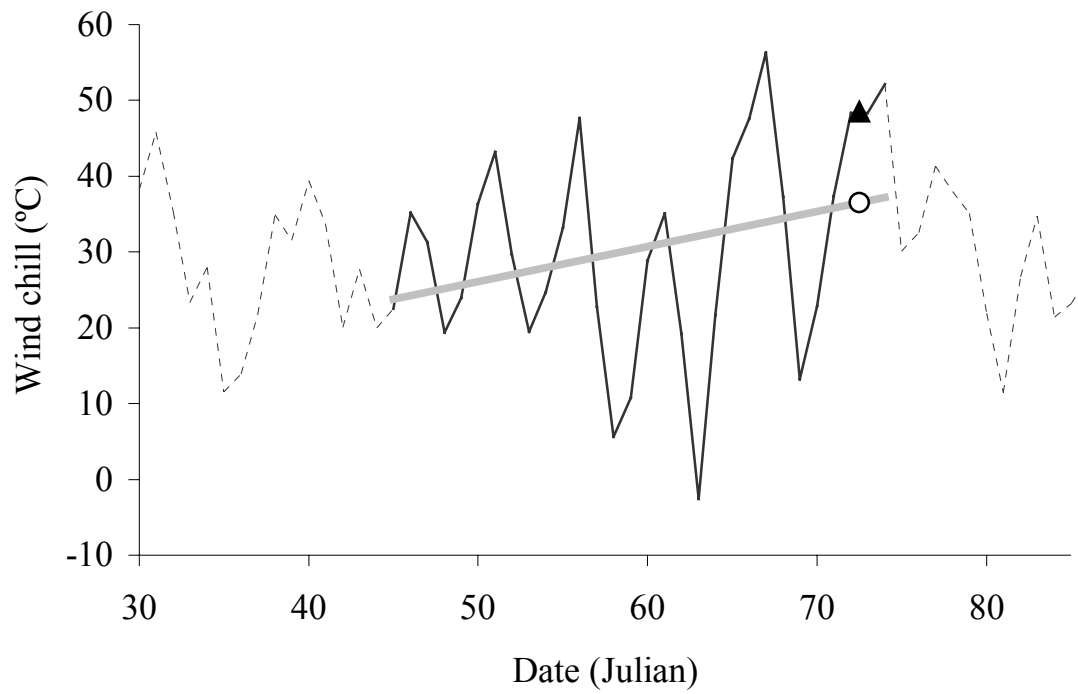
Potential habitat patch quality for chickadees was measured using vegetation sampling sensu Grubb and Bronson (2001). We quantified nine variables, average tree diameter (dbh), average dbh of 10% largest trees, average dbh of 20% largest trees, percent shrub cover, and densities of saplings, snags, logs, trees, and trees with poison ivy (*Rhus radicans*) vines. Poison ivy berries are an important winter food of chickadees (TCG, pers. obs.). We condensed vegetation data with Principal Components Analysis (PCA) and employed PC scores as independent variables in analyses incorporating vegetation data. Subjective variable interpretation and hindered repeatability are two concerns with using PCA scores as variables (Ramsey and Schafer 1997). To address these concerns we performed the same analyses using replacement variables (those that loaded highly with their respective component). Vegetation variables which violated normality assumptions were log-transformed (Anderson-Darling normality test; D'Agostino 1986).

We did not determine whether repopulation was related to average daily temperature or wind speed alone because wind chill, the interaction of the two, was most likely to matter to vagile homeothermic organisms. Weather data were averaged from daily weather summaries recorded at The Ohio State University Airport in Columbus and the Marion County Airport (National Oceanic and Atmospheric Administration 2003), sites that bracketed the locations of the study woodlots. We calculated average daily wind chill using an equation provided by the National Weather Service (2003), where $\text{wind chill (}^\circ\text{F)} = 35.74 + 0.6215 T - (35.75 V^{0.16}) + 0.4275 T (V^{0.16})$, where $T =$ temperature ($^\circ\text{F}$) and $V =$ velocity (miles/hr), and then converted to $^\circ\text{C}$. For every woodlot, we first determined the wind chill for the 30 days prior to woodlot repopulation, and then determined the linear regression equation for those wind chill values. By extending the equation to the day of repopulation, we determined the wind chill value predicted for that day by the long-term trend. To obtain an observed wind chill value for each instance of repopulation, we averaged the average wind chill conditions on the day of detection and the two days preceding detection when we had not visited. Using Wilcoxon Signed Ranks Tests, we tested the prediction that if chickadees reoccupy woodlots during periods of relatively benign weather, the observed wind chill values should be milder than the predicted values (Figure 4.1).

Streamered birds did not always respond to playback and thus may have gone undetected. We performed an analysis of detection to estimate whether lack of detection was due to observer error or bird absence. If lack of detections was due to observer error, we predicted that either detection ability would not vary predictably with habitat patch

Figure 4.1. Technique for calculating predicted and observed wind chill values related to woodlot reoccupation by chickadees. Predicted wind chill is from the regression of wind chill on Julian date for the 30 days prior to observed reoccupation. Observed wind chill is the average of mean daily wind chills on the day of reoccupation and all days since the most recent observer visit when the woodlot was empty.

- Background average daily wind chill
- Average daily wind chill for 30 days prior to reoccupation
- ▲ Wind chill regression
- Predicted wind chill



and landscape features or that observer error would be higher in larger habitat patches because of the greater chance of missing birds. Detection data were analyzed from the first sighting of a reoccupying bird either to the end of the field season or to the visit prior to the final sighting of the bird. The latter procedure was employed to avoid including inherent detection bias in the analysis, as we could never know whether a final absence was due to mortality, emigration, or an inability to detect birds that were present. For each reoccupied woodlot, we arcsine-square-root-transformed the proportion of visits when we detected target birds. The total number of visits differed among woodlots, so we assigned weighting factors (\sqrt{n}) for the proportion of visits marked birds were detected at each woodlot. For landscape variables in this detection analysis we considered the total amount of wooded area within 1 km of the focal woodlot (Area_1K), the nearest woodlot distance (Dist), and the presence / absence of a fencerow connecting the focal woodlot with another woodlot in the vicinity (Fence). Patch variables included patch area (Ln_Area), patch shape (Shape, an area:edge index that controls for raster format of data [McGarigal 2002]), PC1, PC2, and PC3. We log-transformed non-linear variables to better approach linearity requirements for regression analysis.

RESULTS

The nine vegetation variables entered into the PCA are detailed in Table 4.1. Principal Component 1 (PC1) was positively related to size of trees, PC2 was positively related to density of logs (Logs) and negatively to density of saplings (Saplings), and PC3 represented the average percent shrub cover (Ln_Shrub).

| | Components | | |
|-------------------------------|------------|--------|--------|
| | 1 | 2 | 3 |
| Eigenvalues | 3.547 | 1.676 | 1.568 |
| % variance explained | 39.409 | 18.621 | 17.423 |
| Cumulative variance explained | 39.409 | 58.030 | 75.453 |
| Variables | | | |
| Ln_Shrub | -0.049 | -0.277 | 0.826 |
| Ln_PI | -0.368 | 0.138 | 0.815 |
| Ln_DBH | 0.872 | 0.270 | 0.080 |
| Ln_20% | 0.775 | 0.487 | 0.138 |
| Ln_10% | 0.832 | 0.494 | 0.169 |
| Logs | -0.616 | 0.587 | 0.054 |
| Saplings | 0.203 | -0.616 | 0.233 |
| Snags | -0.647 | 0.485 | 0.239 |
| Trees | -0.718 | 0.259 | -0.229 |

Table 4.1. Variance explained and component matrix of vegetation Principal Components Analysis (PCA). Ln_Shrub = ln (average percent shrub cover); Ln_PI = ln (density of trees with poison ivy vines); Ln_DBH = ln (average dbh); Ln_10% = ln (average dbh of 10% largest trees); Ln_20% = ln (average dbh of 20% largest trees); Logs = average number of fallen trees / ha; Saplings = average number of saplings / ha; Snags = average number of dead upright trees / ha; Trees = average number of trees / ha.

None of the 115 birds transported from 28 woodlots ever returned. Over the course of the winter, all 28 woodlots were reoccupied. We examined the length of time between induced extinction and reoccupation using AIC analysis of regression models (Table 4.2), employing AIC_c due to small sample size. When PCA scores represented vegetation variables, the “best” model by parsimony was Fence ($r^2 = 0.179$, Fence $\beta = -0.423$, $\Delta AIC_c = 1.810$, $\omega_i = 0.141$), indicating that birds moved sooner into woodlots connected to a fencerow. Two other models worthy of consideration ($\Delta AIC_c < 2$) contained the variables, Area_1k and Fence ($r^2 = 0.302$, Area_1k $\beta = 0.419$, Fence $\beta = -0.653$, $\Delta AIC_c = 0$, $\omega_i = 0.347$) and Area_1K, Fence, and PC1 ($r^2 = 0.331$, Area_1K $\beta = 0.450$, Fence $\beta = -0.643$, and PC1 $\beta = 0.191$, $\Delta AIC_c = 0.154$, $\omega_i = 0.160$). Less woodland within 1 km and the presence of a fencerow may shorten the time a woodlot remains empty.

When the single best primary variable value was substituted for each of the three principal components, the “best” model based on parsimony contained Fence and Saplings ($r^2 = 0.357$, Fence $\beta = -0.404$, Saplings $\beta = 0.422$, $\Delta AIC_c = 0$, $\omega_i = 0.552$). No other model received consideration (second lowest $\Delta AIC_c = 3.27$). It appears that Fence and Saplings are important and make a much stronger model when together than separately. Birds reoccupied woodlots earlier if a fencerow connected them to other woodlands, and later if a high density of saplings was present. When Logs replaced Saplings, the results were similar to those of the original analysis of PC scores.

| Model | K | r^2 | AIC_c | ΔAIC_c | ω_i |
|--------------------------------|----------|--------------|----------------|----------------|--------------|
| Area_1k**, Fence*** | 4 | 0.302 | 172.453 | 0.000 | 0.347 |
| Area_1k*, Fence**, PC1 | 5 | 0.337 | 174.002 | 1.548 | 0.160 |
| Fence** | 3 | 0.179 | 174.263 | 1.810 | 0.141 |
| Area_1k*, Fence*, Ln_area | 5 | 0.314 | 174.979 | 2.526 | 0.098 |
| Fence**, Ln_area | 4 | 0.209 | 175.953 | 3.500 | 0.060 |
| Fence**, PC1 | 4 | 0.198 | 176.349 | 3.896 | 0.050 |
| Fence**, PC3 | 4 | 0.182 | 176.918 | 4.465 | 0.037 |
| Fence**, PC2 | 4 | 0.181 | 176.933 | 4.480 | 0.037 |
| Area_1k*, Fence*, Ln_area, PC1 | 6 | 0.342 | 177.070 | 4.617 | 0.035 |

continued

Table 4.2. Ranked- AIC_c multiple linear regression models for the length of time woodlots remained empty between removal of resident chickadees and reoccupation by immigrant chickadees. Models are evaluated by comparisons of ΔAIC_c values and the number of model parameters (K). The best model, by parsimony, is shown in boldface. Akaike weight, ω_i , is the probability that a model is the best model of the set, discounting parsimony. See Table 4.1 for definitions of variables.

Table 4.2 continued

| Model | K | r^2 | AIC_c | ΔAIC_c | ω_i |
|---|-----|-------|---------|----------------|------------|
| PC1 | 3 | 0.039 | 178.693 | 6.240 | 0.015 |
| Ln_area | 3 | 0.014 | 179.403 | 6.950 | 0.011 |
| PC1, PC3 | 4 | 0.039 | 181.412 | 8.959 | 0.004 |
| PC1, PC2 | 4 | 0.039 | 181.425 | 8.972 | 0.004 |
| PC1, PC2, PC3 | 5 | 0.040 | 184.394 | 11.941 | 0.001 |
| Area_1k*, Fence**, Ln_dist, Ln_area, PC1, PC2, PC3 | 9 | 0.374 | 187.679 | 15.226 | 0.000 |
| Area_1k, Area_2k, Ln_Prox, Fence**, Ln_dist, Ln_area, Shape, PC1, PC2, PC3 | 12 | 0.481 | 197.235 | 24.782 | 0.000 |

* $P < 0.10$, ** $P < 0.05$, *** $P < 0.01$.

Using the 3-May criterion, we found that chickadees bred in 21 of the 28 woodlots. We examined breeding occurrence using logistic regression models followed by AIC analysis (Table 4.3), employing QAIC_c due to the modest sample size and slight overdispersion of data ($\hat{c} = 1.103$). The model with the most support ($\Delta\text{QAIC}_c = 0$; parsimony) contained only the variable Ln_Area (Nagelkerke $r^2 = 0.337$, Ln_Area $\beta = 2.462$, $\omega_i = 0.552$). All other models resulted in $\Delta\text{QAIC}_c > 2$, so were not considered further. Use of replacement variables (LN_20%, Saplings, Logs, Ln_Shrub) for PC scores did not change the findings of the AIC analysis, nor did any of these variables significantly contribute to any model. The model Ln_Area best accounted for the probability of birds staying to breed in a woodlot.

We examined the date of reoccupation in relation to weather conditions by comparing the predicted and observed wind chill values for each woodlot. Independent of calendar date, birds were more likely to reoccupy woodlots during periods when observed wind chill was more benign than that predicted by a long-term trend ($P = 0.004$, $Z = -2.874$).

We performed a logistic regression analysis to examine changes in the probability of detection of birds responding to vocalization playback. Overall, there was no indication that birds went undetected because of habituation to repeated playbacks or because of seasonal progression. On average, we detected previously banded birds 73.6% of the time (SD = 20.1%, Range = 23.5 - 100%). We experienced 100% detection in four woodlots (three < 15 visits, one = 29 visits). To check for habituation, we compared the response data to patch visit number. Fifteen woodlots were visited 15 or

| Model | K | Nagelkerke r^2 | QAIC _c | Δ QAIC _c | ω_i |
|----------------------------------|----------|------------------|-------------------|----------------------------|--------------|
| Ln_area** | 3 | 0.337 | 31.260 | 0.000 | 0.550 |
| Ln_area**, Shape | 4 | 0.354 | 33.575 | 2.315 | 0.173 |
| Area_1k, Ln_area** | 4 | 0.338 | 33.978 | 2.718 | 0.141 |
| Area_1k, Fence, Ln_area** | 5 | 0.367 | 36.241 | 4.981 | 0.046 |
| Ln_area**, PC2, PC3 | 5 | 0.350 | 36.661 | 5.401 | 0.037 |
| Area_1k | 3 | 0.017 | 38.160 | 6.900 | 0.017 |
| Ln_area**, PC1, PC2, PC3 | 6 | 0.386 | 39.048 | 7.788 | 0.011 |
| Area_1k, Fence, Ln_area**, Shape | 6 | 0.383 | 39.107 | 7.847 | 0.011 |
| PC2, PC3 | 4 | 0.050 | 40.270 | 9.010 | 0.006 |
| | | | | | continued |

Table 4.3. Ranked QAIC_c multiple logistic regression models for the probability of immigrant chickadees colonizing (breeding in) study woodlots. Models are evaluated by comparisons of Δ QAIC_c values and the number of model parameters (K). The best model is shown in boldface. Akaike weight, ω_i , is the probability that a model is the best model of the set, discounting parsimony. See Table 4.1 for definitions of variables.

Table 4.3 continued

| Model | K | Nagelkerke r^2 | QAIC _c | Δ QAIC _c | ω_i |
|--|-----|------------------|-------------------|----------------------------|------------|
| Ln_area**, Shape, PC1, PC2, PC3 | 7 | 0.399 | 42.306 | 11.046 | 0.002 |
| Area_1k, Ln_Prox, Fence | 5 | 0.089 | 42.491 | 11.231 | 0.002 |
| Shape, PC2, PC3 | 5 | 0.070 | 42.861 | 11.601 | 0.002 |
| PC1, PC2, PC3 | 5 | 0.052 | 43.208 | 11.948 | 0.001 |
| Area_1k, Fence, Ln_area**, Shape, | 9 | 0.421 | 50.121 | 18.861 | 0.000 |
| PC1, PC2, PC3 | | | | | |
| Area_1k, Area_2k, Ln_Prox, Fence, | 12 | 0.436 | 66.532 | 35.272 | 0.000 |
| Ln_dist, Ln_area, Shape, PC1, PC2, PC3 | | | | | |

* $P < 0.10$, ** $P < 0.05$, *** $P < 0.01$.

more times. Fourteen of these were individually analyzed (we excluded the woodlot with 29 visits, 100% detection success), with a (positive) significant result for only one woodlot (patch visits: $N = 29$, $\beta = 0.029$, $P = 0.040$). Of the 13 non-significant analyses, 7 β values were negative and 6 positive.

When we performed a linear regression of the arc-sine-transformed proportion of our visits during which chickadees were present at a woodlot and examined models using AIC (Table 4.4), we found that the model with $\Delta AIC_c = 0$ was Shape and Ln_Area ($r^2 = 0.347$, Shape $\beta = -0.496$, Ln_Area $\beta = 0.358$, $\omega_i = 0.635$). Parsimony dictates that Ln_Area alone be considered the best model ($r^2 = 0.208$, Ln_Area $\beta = 0.265$, $\Delta AIC_c = 1.963$, $\omega_i = 0.238$), although there is some distance between it and the model with the lowest AIC value. All other models achieved $\Delta AIC_c > 4$, so were not considered further. Use of replacement variables (Ln_20%, Saplings, Logs, Ln_Shrub) for PC scores did not change the findings of the AIC analysis, nor did any of these variables significantly contribute to any model. In a post-hoc analysis, when we included the interaction term between Shape and Ln_Area, the r^2 value improved to 0.522 (Ln_Area $P = 0.001$, Shape $P = 0.807$, Ln_Area * Shape $P = 0.011$).

| Model | K | r^2 | AIC_c | ΔAIC_c | ω_i |
|------------------------------------|----------|--------------|----------------|----------------|--------------|
| Shape**, Ln_area*** | 4 | 0.347 | -63.402 | 0.000 | 0.635 |
| Ln_area** | 3 | 0.208 | -61.439 | 1.963 | 0.238 |
| Ln_area**, PC3 | 4 | 0.216 | -58.858 | 4.544 | 0.066 |
| Area_1k, Ln_area**, PC2 | 5 | 0.223 | -55.917 | 7.485 | 0.015 |
| Ln_area**, PC2, PC3 | 5 | 0.222 | -55.883 | 7.519 | 0.015 |
| Area_1k | 3 | 0.001 | -55.649 | 7.753 | 0.013 |
| Shape**, Ln_area***, PC1, PC2, PC3 | 7 | 0.367 | -53.596 | 9.806 | 0.005 |
| Shape, PC1 | 4 | 0.027 | -53.447 | 9.955 | 0.004 |
| | | | | | continued |

Table 4.4. Ranked AIC_c multiple linear regression models for the probability of detection of marked immigrant chickadees during woodlot visits. Models are evaluated by comparisons of ΔAIC_c values and the number of model parameters (K). The best model, by parsimony, is shown in boldface. Akaike weight, ω_i , is the probability that a model is best model of the set, discounting parsimony. See Table 4.1 for definitions of variables.

Table 4.3 continued

| Model | K | r^2 | AIC_c | ΔAIC_c | ω_i |
|---|-----|-------|---------|----------------|------------|
| PC2, PC3 | 4 | 0.012 | -53.055 | 10.347 | 0.004 |
| Fence, Area_1k | 4 | 0.001 | -52.794 | 10.608 | 0.003 |
| Fence, Area_1k, ENN | 5 | 0.063 | -51.243 | 12.159 | 0.001 |
| PC1, PC2, PC3 | 5 | 0.015 | -49.979 | 13.423 | 0.001 |
| Fence, Area_1k, ENN, Shape**, Ln_area**, PC1, PC2, PC3 | 10 | 0.442 | -41.618 | 21.784 | 0.000 |

* $P < 0.10$, ** $P < 0.05$, *** $P < 0.01$.

DISCUSSION

Regardless of their own characteristics and their degree of isolation, all 28 woodlots were reoccupied. This result indicates that Carolina chickadees in Ohio farm country, if truly a metapopulation, may represent an extreme example in which patch extinction events are rapidly followed by recolonization. For this species in this landscape, empty patches of suitable habitat are likely short-lived events.

Woodlots were reoccupied sooner if they were connected to other habitat patches by fencerows. While this evidence supports the utility of corridors for an avian species traveling through a fragmented landscape, it would be premature to generalize these results. Movement pathways through fragmented landscapes may differ between ecologically similar species. For example, the red-breasted nuthatch (*Sitta canadensis*) freely crossed gaps to reach mobbing-call playbacks, while the black-capped chickadee generally avoided crossing gaps where possible, instead traveling longer distances through woodland to reach playbacks (Desrochers & Hannon 1997). If inter-patch movements by other species are similar to those of the chickadees in this study, then habitat corridors may be worthy investments for assisting in preserving some species in fragmented landscapes. The amount of woodland habitat in the landscape may have contributed to the speed of patch reoccupation. The positive relationship between the amount of woodland within 1 km of a woodlot and the length of time a woodlot remained empty is difficult to explain. More nearby habitat patches and/or larger habitat patches should support a higher density of chickadees, providing more potential immigrants to

reach the study woodlot. Perhaps, the less wooded area in a landscape, the higher the disperser visitation rate per woodlot. This effect might be intensified if the target woodlots are relatively large in highly fragmented areas and relatively small in more heavily wooded areas of the landscape, as dispersers might perceive and preferentially move towards the largest local woodlots.

To examine these possibilities, we performed a post-hoc analysis to determine how focal woodlot size varied relative to the size of patches in the immediate surrounding landscape. Initial results indicated that focal patches were larger in landscapes that were more forested ($r^2 = 0.296$, $\beta = 1.968$, $P = 0.003$). However, with the removal of two outliers, the pattern disappeared ($r^2 = 0.080$, $\beta = 1.05$, $P = 0.162$). The natural log of the amount of woodland within 2 km of a focal woodlot was not related to the number of woodlots larger than the focal woodlot ($r^2 = 0.093$, $\beta = 1.435$, $P = 0.115$). Thus, there was no relationship between either patch area and landscape woodland cover or landscape woodland cover and the number of patches larger than the focal woodlot.

Our results indicate that large numbers of saplings in a woodlot may delay patch occupancy by chickadees. High sapling density is often a consequence of recent timber harvest (TCG, pers. obs.), and indeed we found that sapling density was negatively related to tree density. Grubb and Bronson (2001) showed that Carolina chickadees were most likely to remain and breed in woodlots that had not been recently cut over. It is likely that woodland thinning decreases both the amount of foraging substrate and number of potential nest cavities, lowering the quality of the woodland for prospecting chickadees.

Chickadees did not breed in all available woodlots, with breeding more likely to occur in the larger patches. This result might indicate that large woodlots were more likely to contain resources necessary for reproduction. Three of the seven woodlots in which no breeding occurred contained singleton male chickadees which, by the end of the study season, were observed singing continually. All three of the solo males had had putative mates at the beginning of April, and so this observation of late-winter abandonment of non-breeding habitat is similar to that of Grubb and Bronson (2001) in their study of Carolina chickadees, black-capped chickadees and Carolina x black-capped chickadee hybrids.

Abiotic factors such as weather may mediate the likelihood of a species performing inter-patch dispersal. The dispersal ability of odonates has been shown to be influenced by weather conditions (Angelibert and Giani 2003). We found that throughout our winter study birds were more likely to arrive at a habitat patch during periods of relatively mild wind chill. It is conceivable that the severity of weather during the winter will constrain to varying degrees the likelihood of inter-patch movements by chickadees. The impact of landscape fragmentation on these birds may be a temporal as well as spatial phenomenon.

We did not elicit response to playback on all post-reoccupation visits. Birds may have either been elsewhere when playbacks occurred or in the woodlot, but unresponsive to playbacks. We have two lines of evidence suggesting that birds were absent from the woodlots, and not simply ignoring our playbacks. The first is that there did not appear to be a pattern to the order of chickadee absences. Chickadees did not respond less

frequently with increasing numbers of woodlot visits. The only statistically significant logistic regression result indicated that birds were actually more likely to respond on later visits. Additionally, according to the results from the 13 non-significant logistic regression analyses, β values were as likely to be negative as positive. Therefore, it does not appear likely that bird response declined with habituation, experience, or the approach of the breeding season.

The second line of evidence relates to our being less likely to elicit a response to playback in smaller woodlots. This trend was contrary to what would be expected had our playbacks been more limited in attracting birds over distance than we assumed they were. The observed pattern is also readily interpretable biologically. Those individuals in small patches may have had the most to gain by venturing to investigate other local patches. Birds defending large woodlots would gain less by searching for better territories. Andreassen and Ims (2001) found that root voles (*Microtus oeconomus*) were more likely to emigrate from relatively smaller, more sparsely populated patches. Individuals utilizing small patches of habitat may also meet resource requirements through habitat supplementation (Dunning et al. 1992). Smaller habitat patches should be inhabited by such chickadees less often than larger patches. From a management perspective, it would be useful to know if the likelihood of birds that foray from small habitat patches is as great in landscapes where habitat fragmentation has resulted in even higher degrees of patch isolation (Blake and Karr 1987).

Our results disprove the assumption from studies of unmarked birds that winter presence indicates breeding presence (Opdam et al. 1985) or that disappearance of winter residents from a habitat patch necessarily represents a death or emigration event (Doherty and Grubb 2000). We found that marked individuals were sometimes not detected in a woodlot, but would be present during a subsequent visit. For habitat patches that support exceedingly small populations, a single finding of species absence does not necessarily indicate that a patch remains unused or is necessarily unimportant.

Much of the variance in patch absence was explained when patch size, shape, and their interaction were taken into account. Bird presence was positively associated with patch area and negatively associated with the edge:area index. Severe wind chill can reduce the amount of woodlot area a bird can forage in during cold periods (Dolby and Grubb 1999). Therefore, during winter months, chickadees in highly fragmented areas preferring woodlots with low edge:area ratios may maximize the proportion of a woodlot available for foraging. Another edge-related threat to chickadees is the house wren (*Troglodytes aedon*), an intense competitor for nest sites. Carolina chickadees preferentially nest towards the center of a woodlot (Doherty and Grubb 2002), while house wrens tend to nest close to a woodlot edge. Therefore, the closer a chickadee is forced to nest towards the edge of a woodlot, perhaps the less its fitness gain.

Conservation plans for even highly vagile species, like birds, may do well to include corridors and to protect small habitat patches. Carolina chickadees accomplish inter-patch movements in a fragmented landscape, yet we have shown that their movements are constrained. Corridors facilitated movement, possibly offering refuge

from predators such as accipitrine hawks. Once they become “residents” of a habitat patch, the degree to which chickadees exhibit site fidelity and the likelihood of breeding within the patch appear to be determined by patch features. Smaller habitat patches may not be as likely to support breeding pairs of birds, but they may serve other functions such as habitat supplementation or staging points for nearby habitat patch assessment. Small patches therefore may not necessarily function only as sink habitat, but may confer fitness benefits to dispersing organisms.

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