

AN EVALUATION OF SURVIVORSHIP AND HABITAT USE OF EARLY-
SUCCESSIONAL BIRDS DURING THE BREEDING SEASON:
IMPLICATIONS FOR CONSERVATION

DISSERTATION

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By

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ABSTRACT

Due to steady population declines since the 1960s, conservation of shrubland birds has become an important issue facing land managers across eastern North America. Because most shrubland habitats are ephemeral and patchily distributed, effective conservation requires knowledge of shrubland bird responses to patch characteristics and configuration. In this dissertation, we (1) tested the extent to which shrubland birds may be area sensitive, (2) evaluated evidence for 5 alternative hypotheses to explain the previously documented pattern of edge avoidance by shrubland birds, and (3) evaluated the importance of landscape configuration to shrubland birds.

To test area-sensitivity, we mist-netted and banded shrubland birds in 13 regenerating clearcuts between 2002-2006 in southeastern Ohio. After quantitatively adjusting for increased availability of birds for capture in larger patches, only four of the six species showed positive correlations between capture rate and patch size, with capture rates averaging 22% higher in the largest patch compared to the smallest patch; this relationship was only statistically significant for the Yellow-breasted Chat (*Icteria virens*).

Despite weak evidence of lower densities in smaller patches, we had strong evidence of lower densities in edge habitat during the early morning. We evaluated evidence for five hypotheses that could potentially underlie this pattern: 1) lower usage of

edge habitat over all time periods, 2) lower usage of edge habitat during the morning because of social interactions, 3) temperature regulation leading to preferred use of interior habitat during the morning, 4) lower densities in edge habitat due to passive displacement, and 5) larger territories near edge habitat. To test these mechanisms, we examined nest success, settlement, and territory size and placement of three shrubland species and radio-marked 37 males of one shrubland specialist, the Yellow-breasted Chat, during 2005 and 2006. We found little support for lower nest success near edge habitat or edge avoidance in nest or territory placement. Settlement patterns were consistent with predictions of the passive displacement hypothesis. Models strongly supported the hypothesis of larger territories near edges for only one species, the Prairie Warbler (*Dendroica discolor*). Radio-marked Yellow-breasted Chats did not avoid edge habitat based on telemetry data although there was some support for seasonal variation in edge habitat use. Collectively, results supported the passive displacement hypothesis and, to a lesser extent, the social behavior and territory expansion hypotheses.

To evaluate the importance of landscape composition to shrubland birds, we used variables at the plot, patch, and landscape level to model capture rates. Models including plot variables and the amount of shrubland habitat in the landscape received the most support. Support for amount of shrubland habitat in the landscape rather than patch size suggested higher densities of birds in clustered patches and/or that birds may have used multiple patches within the season. Banding and telemetry data also indicated that inter-patch movements were not uncommon.

Overall, we detected weak evidence of lower densities in smaller patches and no evidence of active edge avoidance by shrubland birds. Due to strong evidence of passive

displacement and the importance of landscape composition, we suggest that managers would support the highest densities of shrubland birds through the creation of larger, clustered patches with minimum edge-to-area ratios.

Dedicated to my parents

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CHAPTER 1

INVESTIGATING AREA-SENSITIVITY IN SHRUBLAND BIRDS: RESPONSES TO A PATCHY LANDSCAPE

ABSTRACT: Population declines of shrubland birds in the eastern United States have been attributed to loss of early-successional habitat. Given that shrubland habitats are often ephemeral and patchily distributed, understanding the sensitivity of shrubland birds to patch characteristics is important for conservation. We tested the extent to which patch area was related to shrubland bird density, annual survival, and productivity by examining capture rates, apparent annual survival estimates, and juvenile-to-adult-female ratios for six focal species of shrubland birds in southeastern Ohio. Identical 3 x 3 mist-net grid arrays were set at each of 13 clearcut patches ranging in size from 4 to 16 ha and visited once per week between June and August of 2002-2006. Over the five seasons, 1,428 juveniles and 2,001 adults of six species were banded. Capture rates for all six species increased with patch area (mean of 44% higher in largest than smallest patch) but this relationship was only significant for the Yellow-breasted Chat (*Icteria virens*; $F_{1,11} = 34.2$, $P < 0.001$) and the Common Yellowthroat (*Geothlypis trichas*; $F_{1,11} = 7.0$, $P = 0.023$). However, after accounting for the effect of bird movements on capture rates, capture rates for only four of the six species increased patch area (mean of 22% higher in

largest than smallest patch) and this relationship was only significant for the Yellow-breasted Chat ($F_{1,11} = 8.9$, $P = 0.012$). Patch area was not a good predictor of apparent annual survival or juvenile-to-adult-female ratios for any species. Overall, we detected limited evidence of area-sensitivity in our system and no evidence that annual survival or productivity differed by patch area.

1. Introduction

Populations of shrubland birds have been declining since the 1960s (Litvaitis 1993; Dessecker and McAuley 2001; Hunter et al. 2001; DeGraaf and Yamasaki 2003). These declines have corresponded to declining amounts of shrubland habitat in the eastern United States (Litvaitis 1993, 2001), prompting DeGraaf and Yamasaki (2003) to declare natural shrublands to be among the most endangered ecosystems in the country.

Historically shrubland habitat was created by a wide variety of natural and human-caused disturbances in forest systems, but today certain disturbance agents, such as beaver (i.e., dams) and fire, are generally suppressed. In addition, the coastal areas and major river valleys that were historically subjected to the most frequent and severe disturbances (i.e., hurricanes and floods) have been the most developed (Noss et al. 1995; Boose et al. 2001; Lorimer 2001). Although even-aged harvesting in forests creates the structure necessary for shrubland species, public opposition to clearcutting and other even-aged management techniques has increased in recent decades. Substantial gains in the amount of shrubland habitat are unlikely both on public lands given the sociopolitical climate and on private lands due to increasingly fragmented land ownership (Dessecker and McAuley 2001) and continuing urbanization (Trani et al. 2001). In light of limited and declining

habitat, effective management hinges upon our ability to identify and manage those key features to which shrubland species respond (Askins 1994).

An area-sensitive species can be defined as a species that occurs more frequently, or increases in density, as fragment area increases (Freemark and Collins 1992). Area sensitivity has been documented in breeding forest birds (Ambuel and Temple 1983; Robbins et al. 1989) and more recently in grassland species (Herkert 1994; Vickery et al. 1994; Helzer and Jelinski 1999; Johnson and Igl 2001); however, results of studies on area sensitivity in shrubland birds have been mixed. Some research indicates that small group-select cuts (<0.8 ha) may not provide habitat for shrubland specialists (Alterman et al. 2005; Annand and Thompson 1997; Costello et al. 2000; DeGraaf and Yamasaki 2003) and Bay (1996) found area-sensitivity in old fields. In Maine, Rudnicki and Hunter (1993) found that size of regenerating clearcuts (2-112 ha) was positively related to species richness of shrubland birds when the clearcuts were less than 20 ha in size. On the other hand, some shrubland birds use narrow right-of-way powerline corridors (King and Byers 2002; Confer and Pascoe 2003). In South Carolina, Krementz and Christie (2000) found no evidence for area-sensitivity of shrubland specialists in regenerating pine stands (2-57 ha in size). Similarly, King et al. (2001) found no differences between large and small clearcuts. However, King and DeGraaf (2004) found that chestnut-sided warblers (*Dendroica pensylvanica*) nesting in northern hardwoods occurred at lower densities and had later nest initiation dates in smaller patches. This led the authors to suggest that smaller patches were perceived as being lower-quality habitat by these birds.

There is strong evidence of positive area-density relationships for numerous taxa (Connor et al. 2000), but the mechanisms driving this relationship are not well known.

Understanding the mechanisms behind area sensitivity is vital to making appropriate management decisions, especially considering that area sensitivity has been observed to vary regionally within species (Johnson and Igl 2001; Bakker et al. 2002). Root (1973) proposed that area-sensitivity could result from organisms dispersing from smaller to larger patches and the tendency of organisms to remain in larger patches. Differential food availability is another proposed mechanism; Burke and Nol (1998) found that arthropod abundance was lower in mature forest fragments than in large blocks of mature forest habitat. However, Rodewald and Vitz (2005) found no differences in food resource availability (arthropod and fruit abundance) between large and small regenerating clearcuts in southeastern Ohio. Additional, non-exclusive mechanisms postulated to support the positive density- area relationship include the habitat-quality hypothesis which predicts a positive habitat-quality-to-area relationship (Matter 1997), and conspecific attraction which predicts that birds make settlement decisions based on the presence of conspecifics and that larger patches are more likely to be occupied originally (Ahlering and Faaborg 2006).

Edge avoidance is another mechanism that may lead to area sensitivity because small patches tend to have a higher proportion of edge than interior habitat (Burke and Nol 1998; Johnson and Igl 2001; Fletcher and Koford 2003). Observed edge avoidance can be caused by 1) active avoidance, in which birds place territories farther from habitat edges; 2) passive displacement, in which birds are constrained by habitat edges in territory placement, leading to lower densities within about half the diameter of the average territory from the edge (Kroodsma 1984; King et al. 1997; Ortega and Capen 1999; Fletcher and Koford 2003); and 3) territory expansion, in which territories closer to

edge habitat are larger resulting in lower densities near habitat edges (Ortega and Capen 1999; Fletcher and Koford 2003).

Our objectives were to test the extent to which patch area was related to shrubland bird density, annual survival, and productivity by examining capture rates, apparent annual survival estimates, and the number of juveniles captured per adult female.

Focusing on seven species of shrubland birds in southeastern Ohio, we predicted that (1) if shrubland birds exhibited area sensitivity, then we would detect positive associations between density and patch size, and (2) if large patches offered higher quality habitat than small patches, then birds in large patches would show higher annual survival and productivity than birds in small patches. Understanding the relationship between patch size and shrubland bird demographics in the forest matrix will contribute to effective forest habitat management for bird conservation.

2. Methods and materials

2.1. Study area

Study sites were located in southeast Ohio, USA on Zaleski State Forest (Athens and Vinton Counties) and New Page (formerly Mead-Westvaco) Forest Land (Athens, Vinton, and Jackson Counties) within the Ohio Hills Physiographic region. The region is dominated by mature oak-hickory forests (approximately 70% forest cover) and is perforated by regenerating clearcuts with small amounts of other non-forest land uses. Common tree species in the region include red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), red oak (*Quercus rubra*), white oak (*Quercus alba*), yellow-poplar (*Liriodendron tulipifera*), and black gum (*Nyssa sylvatica*). Thirteen 4-10 year-old clearcut patches were used between 2002 and 2006 (Table 1.1), although not all sites

were included every year. Two sites were dropped in 2004 due to mining activity and two additional sites were not used after 2003 and 2004, due to low capture rates.

Dominant vegetation in the clearcut patches included saplings of the mature forest trees, predominately maple and yellow-poplar, and blackberry (*Rubus* spp.), greenbrier (*Smilax* spp.), and sumac (*Rhus* spp.).

Focal species were the common shrubland species in the region: White-eyed Vireo (*Vireo griseus*), Blue-winged Warbler (*Vermivora pinus*), Prairie Warbler (*Dendroica discolor*), Common Yellowthroat (*Geothlypis trichas*), Yellow-breasted Chat (*Icteria virens*), and Indigo Bunting (*Passerina cyanea*). Additional shrubland-breeding species in our region included the Eastern Towhee (*Pipilo erythrophthalmus*), Brown Thrasher (*Toxostoma rufum*), Gray Catbird (*Dumetella carolinensis*), Chestnut-sided Warbler, Field Sparrow (*Spizella pusilla*), and Song Sparrow (*Melospiza melodia*). However, these additional species were either captured infrequently and/or occurred at densities too low to analyze.

2.2. Data collection

Bird were mist-netted from June to mid-August 2002-2006 at 9-12 sites/year in southeastern Ohio. At each site, nets were arranged in a 3 x 3 grid with nets at 20, 50, and 80 m from the mature forest edge and net lanes separated by 50 m. Sites were visited once per week for 9 weeks (June 15- August 15) during 2002 and 2003, and once per week for 11 weeks (1 June – August 15) during 2004 - 2006. We opened mist nets 30 minutes before sunrise (~0540 EST) and closed them 4.5 hours later. Burton and DeSante (2004) found that as few as 3-10 sites may be sufficient to produce

representative regional results, so we believe that this sample was sufficient for making inferences to the southeastern Ohio region.

2.3 Data analysis

2.3.1 Apparent annual survival

Nur et al. (2004) recommend restricting survival analyses to those individuals captured at least twice in a season to exclude transients. Transients are likely to have lower recapture probabilities than local birds (Chase et al. 1997; Pradel et al. 1997); such variability violates the assumption of equal probability of recapture in the mark-recapture framework (Lebreton et al. 1992). Burton and DeSante (2004) suggested that operation of nets once per 10-day period over at least 6 periods provided sufficient recaptures to discriminate between local birds and transients. For our analyses, we used only capture records of individuals that we considered to be local to the area. Locals were individuals captured at least twice in the same breeding season and/or captured in more than one year; individuals captured only once were of unknown status and likely included both floaters and individuals local to areas outside the banding grid. By excluding unknown-status individuals from the analyses, we were also able to increase the precision of our estimates.

2.3.2 Model-building

We calculated apparent annual survival (Φ) probabilities using program MARK (White and Burnham 1999). Because recapture probabilities (p) were low, capture-recapture histories were pooled by year and sex for each species. Models were ranked using Akaike's Information Criteria (AIC; Akaike 1973) adjusted for small sample size (AIC_c). Models with $\Delta\text{AIC}_c \leq 2$ were considered to have strong support (Burnham and Anderson

2002). We could not evaluate our global models ($\Phi_i p_i$) for goodness-of-fit because our models were saturated due to the use of “.” to indicate sites not sampled in a given year. Thus, we left ϕ at the default value of 1.0. The model ($\Phi_i p_i$) calculated both Φ and p as time independent, estimating each Φ and p by year except for the final year when these two parameters could not be estimated separately. For each species, we also ran models where Φ and p were constant and where Φ included a linear and a quadratic time trend. To evaluate the effect of patch size on apparent survival, we included patch size as an additive effect in Φ to the top-ranked model for each species. Using this model, we then estimated Φ for the smallest (4 ha) and largest (16 ha) patches in our study

2.3.3 Capture rates

We standardized captures by calculating the number of individuals captured per 100 net hours. We then tested for the effect of patch size on rate of capture. However, we wanted to distinguish between legitimately higher capture rates due to higher densities versus deceptively higher capture rates due to more birds being available for capture. Although the sampling grid was identical among sites, we suspected that differences in the area and shape of patches might influence the number of individuals available for capture independent of density. Nur et al. (2004) found that they captured breeding wrentits (*Chamaea fasciata*) whose nests were located up to 200 m away from the nearest mist net. Thus, we considered the number of birds captured at a site to be a function of the area of habitat sampled by the mist net grid and the density of birds at that site. We assumed that: 1) a bird’s probability of being available for capture was a function of the distance between the center of its home range and the net, 2) home ranges did not differ in size between large and small patches, and 3) males and females did not differ

significantly in distances moved or home range size. Due to the generally unimodal shape of kernel home ranges of Yellow-breasted Chats observed in a concurrent study (Appendix C), we modeled availability for capture using the half-normal function, which estimated the probability of being available for capture as approximating a half-normal distribution with increasing distance from the center of the home range.

To determine distances moved we examined the capture records of adults with at least two captures in a breeding season. For each individual bird we calculated the distance from the net of capture to the net of recapture; in cases of multiple recaptures for an individual we used the mean distance from the original net to the nets of recapture. For each species the observed distances were split into 20-m intervals and the number of observations in each interval was adjusted to account for differences in sampling intensity at different distances. We modeled availability for capture for each species using a half-normal function. To translate this into area, we multiplied the area of patch habitat at each site at 10-m intervals from the mist-netting grids by the probability of being available for capture at that interval and then summed these areas to get an effective sample area for that species at that site (e.g. 1 ha at availability probability = 1.0 is the same as 2 ha with availability probability = 0.5).

Because distance moved was derived from only those individuals captured at least twice, this distance may not be representative of the capture rates of all adults. Adults captured only once are more likely to be floaters and may have higher rates of movement. To test for differences in capture rates among local and unknown status birds in large and small patches, we used a 2 x 2 contingency *G*-test on the percentage of unknown status birds for each species (Sokal and Rohlf 1994). For the sake of this analysis, patches were

grouped into small (4-9 ha) and large (13-16 ha) categories. If the G -test did not detect differences between capture rates in large and small patches between local and unknown status birds, we then compared capture rates for all adults by species using linear least-squares regression. Variables were checked for normality and models were run in program R 2.6.2 (R Development Core Team 2006). Adjusted R^2 (R_a^2) was calculated for each model. R_a^2 provides a better estimate of the population coefficient of determination than R^2 because it accounts for the degrees of freedom (Zar 1999). With small sample sizes, R^2 tends to overestimate the amount of variance explained by the model. Whereas R^2 is the percentage of variation explained, R_a^2 is an index value that approximates R^2 when the sample size is high and the number of explanatory parameters is low but can be negative in cases in which the model explains less of the variance than expected by chance. Finally, we divided capture rates by the effective sample area for that species at that site to give capture rate per hectare. Again, variables were checked for normality and linear least-squares regression models were run in program R 2.6.2 (R Development Core Team 2006).

2.3.4. Juveniles per adult female

We calculated the number of juveniles captured per adult female for each of the six species. Adult females were included once for each year they were captured, e.g. a female captured in 2002 and recaptured in 2004 would be counted in both 2002 and 2004. The ratio of juveniles captured per adult female was then modeled using linear least-squares regression, with patch area as the predictor variable and the mean number of juveniles captured per adult female as the response variable. Variables were checked for normality and models were run in program R 2.6.2 (R Development Core Team 2006).

3. Results

3.1. Banding

Over the five-year study, 1,428 juvenile (hatch-year) and 2,001 adult (after-hatch-year) birds of the six most common shrubland species were banded (Table 1.2).

Apparent annual survival rates – There was some support for the model containing patch size as an additive effect for apparent annual survival for all species (Table 1.3).

However, most species had several models with AIC_c rankings under 2.0 and the 95% CI for estimates of the effect of patch size included zero for all species, indicating that patch size was a poor predictor of apparent annual survival. In addition, there was no consistent relationship across species between apparent annual survival rate and patch size, with three species having higher point estimates of apparent annual survival in small patches (4 ha) and three in large patches (16 ha; Figure 1.1).

3.2 Effective sample area

Of the six shrubland species we considered, 563 individuals were captured at least twice in a season over the five years of the study (Table 1.2). The estimate of availability for capture differed by species. The distance beyond which a bird with a home range at x distance from a mist net had ≤ 0.01 probability of being available for capture ranged from 140 m for the Prairie Warbler to 220 m for the Yellow-breasted Chat. Effective sample areas differed by species and site (Table 1.4) but, in general, larger patches had larger effective sample areas.

3.3 Capture rates

We detected strong evidence of increased capture rates with increased patch size for only the Yellow-breasted Chat. We did not detect significant differences between local and unknown-status individuals in rates of capture in large versus small patches for any species using the G-test (all $P > 0.77$), so we compared capture rates using all adults of each species captured. Capture rate unadjusted for effective sample size was positively related to patch size for all six species but this difference was only significant for the Yellow-breasted Chat ($F_{1, 11} = 34.2$, $P < 0.001$) and the Common Yellowthroat ($F_{1, 11} = 7.0$, $P = 0.023$; Figure 1.2). However, after accounting for the effect of effective sample area on capture rates, only four of the six species had positive associations with patch size and this relationship was only significant for the Yellow-breasted Chat ($F_{1, 11} = 8.9$, $P = 0.012$; Figure 1.3). Over the six species, the predicted capture rates from the linear regressions were a mean of 44% greater in the largest patch (16 ha) compared to the smallest patch size (4 ha). After adjusting for effective sample size, predicted capture rates were a mean of 22% higher in the largest patch compared to the smallest patch. For the Yellow-breasted Chat, capture rates were predicted to be 50% greater in the 16 ha compared to the 4 ha patch; after adjustment for effective sample size, capture rates were predicted to be 32% higher in the larger patch.

3.4 Juveniles per adult female

We detected no differences in the number of juveniles captured per adult female by patch area for any of the six species (all $P_s > 0.35$; Figure 1.4). Moreover, no consistent trends were observed; three species averaged more juveniles per adult female in larger patches

while three species exhibited the reverse pattern and the R_a^2 values were essentially zero for all models.

4. Discussion

Our results provide weak support for area-sensitivity, as only the Yellow-breasted Chat exhibited strong evidence of increased density with patch size. These findings are similar to those reported in other studies (Confer and Pascoe 2003; King et al. 2001; King and Byers 2002; Krementz and Christie 2000; Rodewald and Vitz 2005; but see Rudnicki and Hunter 1993). In addition to examining data spanning more years (5 years) than previous studies, a key difference in our current study is that we explicitly accounted for differences in capture rates based on movements of birds. Ecologists now recognize that many early studies of area sensitivity using surveys were flawed because sampling effort increased, either actively or passively, with increasing patch size. In studies that do not census every individual within the entire habitat patch, movements of individuals can increase density estimates passively in larger patches even when the area sampled in each patch is identical. This is the first study of shrubland bird area sensitivity to adjust for effective sampling area in a quantitative manner.

Our findings illustrate the importance of explicitly considering movement behavior in analyses of area sensitivity. On average, 34% of the differences between large and small patches were explained by the adjustment for effective sampling area. This percentage is conservative because it assumes that birds never make long-distance (> 122-174 m, depending on species) movements during the breeding season. Tracking of radio-marked male Yellow-breasted Chats as part of a concurrent study demonstrated that these birds did occasionally move up to 1 km from their home ranges and sometimes

left their patch to travel to nearby patches (Chapter 5). Similar movements have been observed in Common Yellowthroats (Pedersen et al. 2006) and Hooded Warblers (*Wilsonia citrina*; Neudorf et al. 1997, Stutchbury 1998) during the breeding season. Long-distance extra-territorial forays such as these could boost the capture rates in larger patches. In this way, our study illustrates the importance of measuring density or indices of density when studying area-sensitivity. Because larger patches had more suitable habitat available in the vicinity of the mist-netting grid, there were more individual birds available for capture in larger patches. If we had not accounted for bird movements, we would have overestimated the strength of the area-sensitivity evidence.

Our results provided little evidence that fitness parameters were related to patch size. If large patches represented the best breeding habitat, then we would expect that differences in habitat quality due to edge or area effects would be paralleled by differences in apparent annual survival or productivity rates. The lack of significant differences or a consistent pattern in either survival rates or juvenile:adult female ratios also suggests productivity did not vary by patch size. An important caveat of these findings is that if patches were fully occupied and settled in an ideal free manner (i.e., the best sites fill first and then density-dependent declines in fitness lead to lower quality habitats filling in order of their suitability; Fretwell 1970, 1972), then demographic parameters, such as survival and productivity, might be similar across the full range of patch sizes, even if patches differed in quality. Ideal despotic distribution, in which habitat selection by subordinate individuals is constrained by territoriality of dominant individuals (Brown 1969), is predicted to result in subordinates being forced into lower quality habitat. Lower quality habitat in this case would be expected to have lower

metrics of breeding success (Oro 2008). Based on our field work in the study area, we do not believe that populations were sufficient to allow for complete occupation of shrubland habitats, as we regularly encountered regenerating clearcuts that were unoccupied or sparsely settled by one or more of our focal shrubland species.

There remains the possibility that our focal species may exhibit area-sensitivity relationships in patches outside the range of those we considered in our study (4-16 ha) or in different regions. For example, some studies have indicated that small group-select cuts (<0.8 ha) may not provide habitat for shrubland specialists (Annand and Thompson 1997; Costello et al. 2000; DeGraaf and Yamasaki 2003). Conversely, it is possible that all the patches we considered were equally susceptible to edge effects if the effects extended more than 100 m into the habitat patches. In addition, Rosenberg et al. (1999) documented regional variation in area-sensitivity indicating the complexity of area-density relationships.

Although we had weak support of area-sensitivity in shrubland birds in our region, forest managers may still want to consider patch size of silvicultural treatments within the context of all-bird conservation in forested landscapes. Use of fewer and larger harvests rather than more and smaller harvests would not only provide large patches of habitat to shrubland birds, but also would reduce the amount of edge habitat within the landscape which is likely to benefit many mature-forest breeding species. For example, King et al. (1998) found that nest predation is higher in mature forest adjacent to group selection cuts, a finding that implies that minimizing the number of cuts by increasing harvest size might be one reasonable strategy to reduce effects of edge-related nest predation for mature forest birds. Silvicultural treatments such as group selection

cuts are also likely to displace territories of both early-successional and mature forest species away from the harvest areas (Germaine et al. 1997), an effect that will be minimized by maximizing size of harvests. Consolidating mature and regenerating forest into larger blocks as a “shifting mosaic” would maximize the utility of the resulting habitat for mature forest species and may benefit early successional species as well (Hagan et al. 1997; King et al. 2001).

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Site	Year cut	Size (ha)	Ownership	Years Used				
				2002	2003	2004	2005	2006
Green Gate	1996	4.1	Mead/New Page	x	x	x	x	x
Connaut Road	1996	5.7	Mead/New Page	x	x	x		
Will Tract 2	1996	5.7	Zaleski	x	x			
Will Tract 3	1996	6.9	Zaleski		x	x	x	x
CCC	1997	7.7	Zaleski	x	x	x	x	x
Webb Hollow	2000	9.0	Zaleski			x	x	x
Kick Gate	1999	9.3	Mead/New Page		x	x	x	x
Cemetery	1996	13.4	Mead/New Page	x	x	x	x	x
Sand Hill	1996	13.8	Mead/New Page	x	x	x	x	x
Mead Gate ¹	1997	13.8	Mead/New Page	x	x			
Gomer Davis ¹	1998	14.6	Mead/New Page	x	x			
REMA	1999	15.7	Zaleski		x	x	x	x
Bobcat	1997	18.1	Mead/New Page		x	x	x	x

¹ Mined in 2004

Table 1.1. Study sites used in southeastern Ohio from June to August 2002-2006.

Species	Code	Adults	# Adults recaptured	# Juveniles
Yellow-breasted Chat (<i>Icteria virens</i>)	YBCH	528	168	283
White-eyed Vireo (<i>Vireo griseus</i>)	WEVI	339	143	290
Blue-winged Warbler (<i>Vermivora pinus</i>)	BWWA	378	113	397
Prairie Warbler (<i>Dendroica discolor</i>)	PRAW	288	69	161
Common Yellowthroat (<i>Geothlypis trichas</i>)	COYE	150	42	137
Indigo Bunting (<i>Passerina cyanea</i>)	INBU	318	81	160

Table 1.2. Banding results by species and age for six shrubland species banded in southeastern Ohio between June and August 2002-2006.

Model	K	ΔAIC_c					
		White-eyed Vireo	Blue-winged Warbler	Prairie Warbler	Common Yellowthroat	Yellow-breasted Chat	Indigo Bunting
$\Phi(.)p(.)$	2	0.00	0.00	1.71	13.21	0.59	0.00
$\Phi(T)p(.)$	3	1.41	1.93	2.06	2.20	0.39	2.09
$\Phi(\text{size})p(.)$	3	1.75	2.02	NA	NA	NA	1.28
$\Phi(.)p(t)$	5	5.65	5.41	3.30	5.94	0.00	5.48
$\Phi(TT)p(.)$	4	0.32	3.44	4.23	0.00	2.41	3.22
$\Phi(t)p(.)$	5	2.16	5.49	0.00	6.03	3.31	3.07
$\Phi(t)p(t)$	7	5.77	9.39	4.20	13.34	4.75	6.73
$\Phi(TT+\text{size})p(.)$	6	NA	NA	NA	3.28	NA	NA
$\Phi(\text{size})p(t)$	6	NA	NA	NA	NA	1.64	NA
$\Phi(t+\text{size})p(.)$	5	NA	NA	1.57	NA	NA	NA

*Min AIC_c , White-eyed Vireo = 309.37, Blue-winged Warbler = 235.67, Prairie Warbler = 170.22, Common Yellowthroat = 88.62, Yellow-breasted Chat = 684.39, Indigo Bunting = 457.05

Table 1.3. Model selection results (ΔAIC_c) for annual apparent survival rates in southeastern Ohio ranked by ΔAIC_c . T and TT represent linear and quadratic trends in Φ , respectively. Patch size was added as a covariate to the top-ranked model for each species. Bolded text represents $\Delta AIC_c \leq 2.00$.

	Site	Patch size (ha)	Effective Sample Area (ha)					
			White-eyed Vireo	Blue-winged Warbler	Prairie Warbler	Common Yellowthroat	Yellow-breasted Chat	Indigo Bunting
25	Green Gate	4.1	2.0	2.2	1.9	2.3	2.4	2.2
	Connaut Road	5.7	2.7	3.2	2.5	3.5	3.7	3.2
	Will Tract 2	5.7	2.3	2.7	2.1	3.0	3.2	2.8
	Will Tract 3	6.9	2.3	2.6	2.1	2.8	3.0	2.7
	CCC	7.7	2.3	2.6	2.1	2.8	2.9	2.6
	Webb Hollow	9.0	2.8	3.4	2.5	3.8	4.1	3.5
	Kick Gate	9.3	2.5	3.0	2.2	3.4	3.6	3.1
	Cemetery	13.4	2.6	3.2	2.3	3.1	3.8	3.2
	Sand Hill	13.8	2.6	3.1	2.3	3.5	3.8	3.2
	Mead Gate	13.8	2.7	3.3	2.4	3.7	4.0	3.4
	Gomer Davis	14.6	2.6	3.1	2.3	3.5	3.8	3.2
	REMA	15.7	2.7	3.3	2.4	3.7	4.0	3.4
Bobcat	18.1	2.6	3.3	2.3	3.6	3.9	3.3	

Table 1.4. Effective sample area for study sites in southeastern Ohio for six shrubland species. Effective sample area at each site represents the area that was effectively sampled by a mist-netting grid for each species based on the observed distance moved by individual birds.

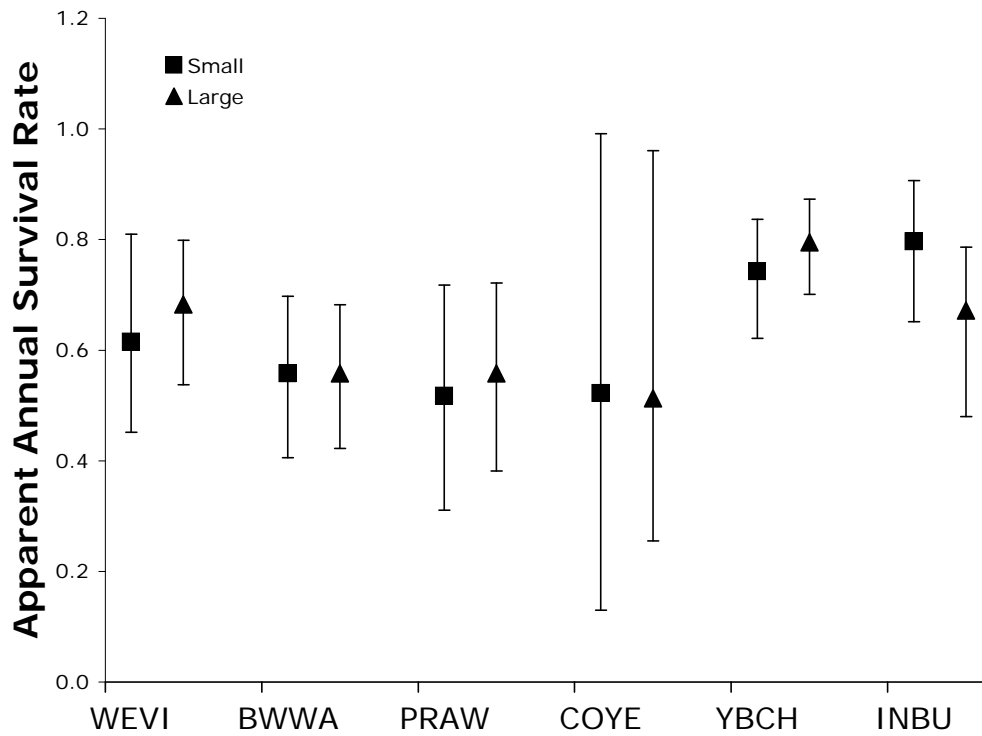


Figure 1.1 Apparent annual survival estimates based on patch size, small (4 ha) or large (16 ha), for six species of shrubland birds captured in southeastern Ohio between 2002-2006. 95% CI shown in bars. Species codes given in Table 1.2.

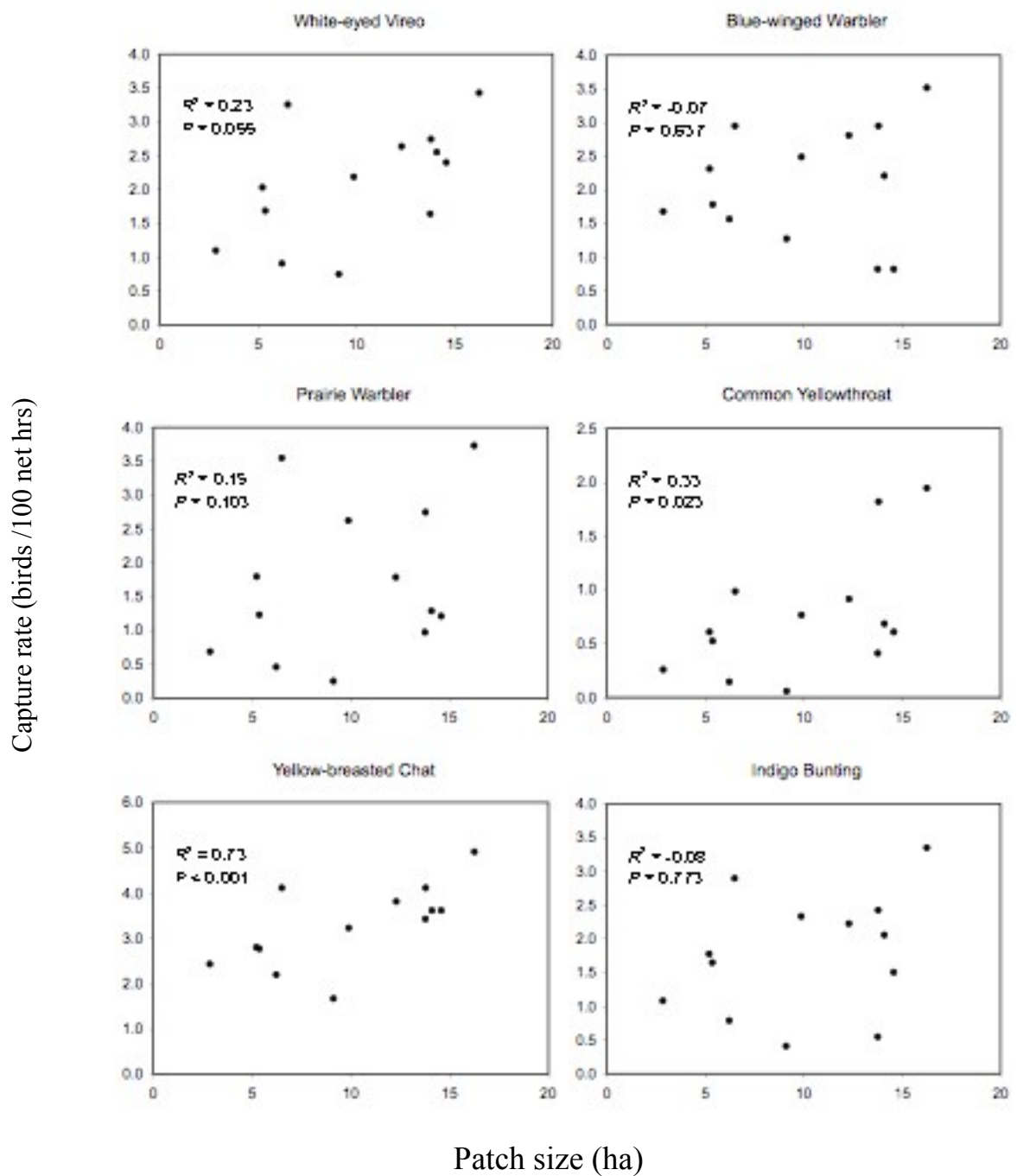


Figure 1.2. Capture rate (birds per 100 net hrs) by patch size (ha) for adults of six species of shrubland birds in southeastern Ohio during June to August 2002-2006. R^2 is the adjusted R^2 based on linear least-squares regression of patch size on capture rate.

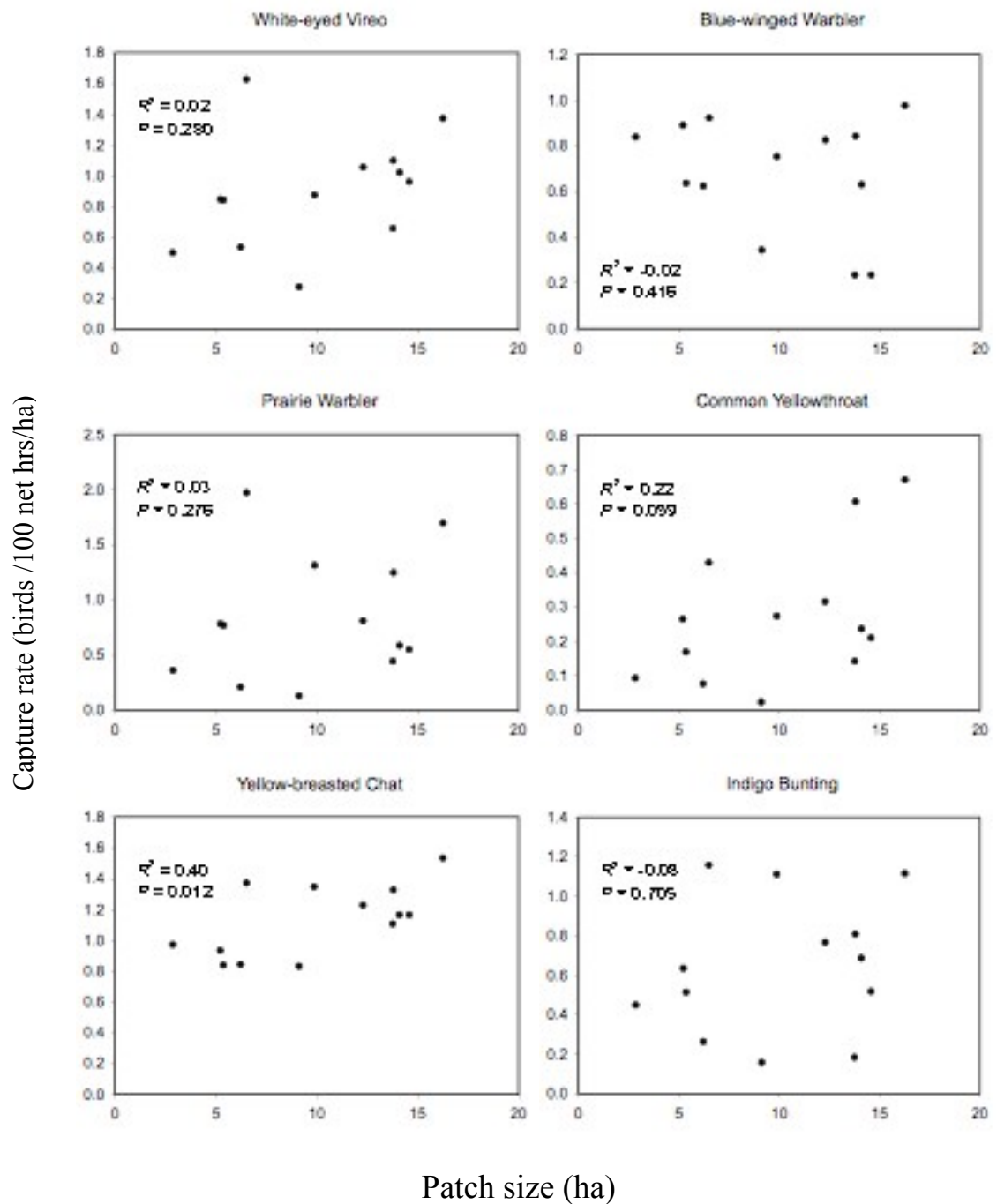


Figure 1.3. Capture rate (birds/100 net hrs/ha) adjusted for effective sample area by patch size (ha) for adults of six species of shrubland birds in southeastern Ohio during June to August 2002-2006. R^2 is the adjusted R^2 based on linear least-squares regression of patch size on capture rate.

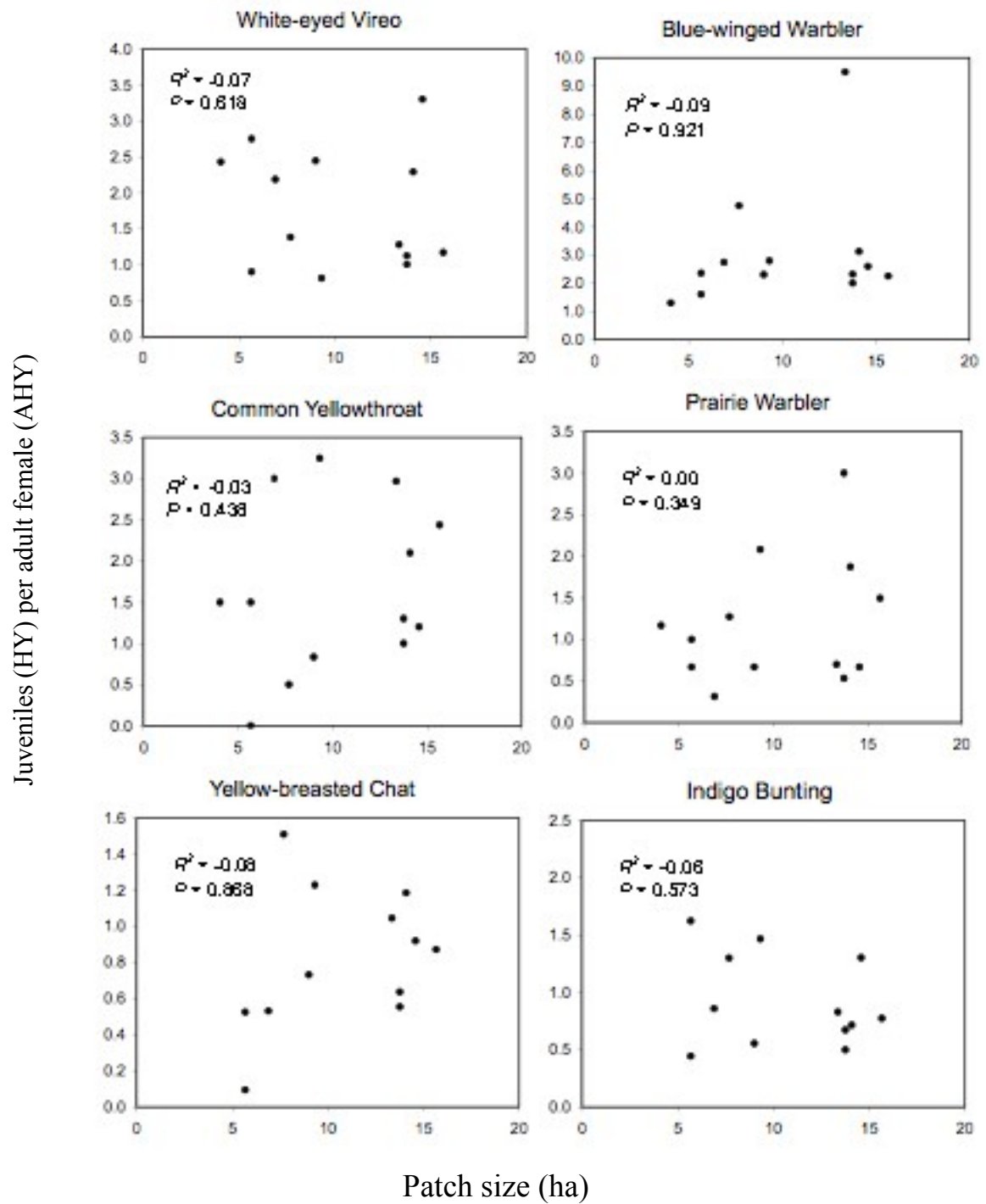


Figure 1.4. Number of juveniles captured per adult female for six species of shrubland birds by patch size (ha) in southeastern Ohio during June to August 2002-2006. R^2 is the adjusted R^2 based on linear least-squares regression of patch size on juvenile-to-adult-female ratios.

CHAPTER 2

NEST SURVIVAL, SETTLEMENT, AND TERRITORY DISTRIBUTION IN RELATION TO EDGE HABITAT IN A SHRUBLAND BIRD COMMUNITY

ABSTRACT: Shrubland bird populations have been declining since the 1960s and recent evidence suggests some shrubland species may need large tracts of habitat to maintain current population levels. Some research has also suggested lower densities and possibly higher nest predation in edge habitat within shrubland systems. We evaluated evidence for the following possible mechanisms of lower densities in edge habitat: 1) active avoidance of edge habitat resulting from higher densities of predators in edge habitat, 2) territory expansion in which territories are larger near edges, and 3) passive displacement from edge habitat in which non-inclusion of edge habitat within territories results in lower densities near edge habitat. To do this, we documented nest success, settling patterns, and territory size and placement in shrubland patches set within a mature forest matrix in southeastern Ohio, 2002-2007. Our findings provide little support for lower nest success near edge habitat or active behavioral avoidance of edges when selecting territory or nest locations. Rather, settlement patterns were consistent with predictions of the passive displacement hypothesis for both Prairie Warblers (*Dendroica discolor*) and Yellow-breasted Chats (*Icteria virens*) but not for Blue-winged Warblers (*Vermivora*

pinus). Models strongly supported the hypothesis of territory expansion for Prairie Warblers but not for Yellow-breasted Chats or Blue-winged Warblers. Because both passive displacement and territory expansion result in lower densities near edge habitat, our results suggest that creating large patches with minimum edge-to-area ratios would be the most effective strategy to supporting high densities of shrubland birds.

Key words: shrubland, nest survival, edge, settling, territory

INTRODUCTION

Populations of shrubland birds have been declining since the 1960s (Litvaitis 1993, Dessecker and McAuley 2001, Hunter et al. 2001, but see Harris and Haskell 2007) corresponding to declining amounts of shrubland habitat in the eastern United States (Litvaitis 2001). Shrubland habitat is created and maintained by disturbance regimes. However, many pre-European sources of disturbance are no longer active on the landscape. River valleys that were historically subjected to the most frequent and severe disturbances (*e.g.*, flooding and fire) have been largely developed (Noss et al. 1995, Lorimer 2001), and disturbance from river processes has been minimized by dam creation. Beavers (*Castor canadensis*) create a mosaic of wetland meadows across the landscape (Snodgrass 1997) that, as they regenerate, are used by shrubland species. However, although their numbers are increasing, beaver populations are still at a fraction of their pre-European settlement levels (Askins 2001, DeGraaf and Yamasaki 2003). These sources of natural disturbance are not likely to be reestablished because of the extent of land use change (Brooks 2003, Lorimer and White 2003). Instead, forest

harvesting, particularly even-aged practices, creates much of the early-successional habitat required by shrubland-dependent species. In light of limited and declining habitat, managers need to know to which habitat characteristics shrubland species respond at the patch level in order to best manage remaining habitat (Askins 1994).

To date, few studies have examined the influence of edge effects on shrubland species. Densities of many avian species are known to be lower in edge habitat. Observed edge avoidance can be caused by: 1) active avoidance, in which birds place territories farther from habitat edges, 2) passive displacement, in which birds are constrained by habitat edges in territory placement, leading to lower densities within about half the diameter of the average territory from the edge (Kroodsma 1984, King et al. 1997, Ortega 1999, Fletcher and Koford 2003), and 3) territory expansion, in which territories closer to edge habitat are larger resulting in lower densities near habitat edges (Ortega 1999, Fletcher and Koford 2003). For the purposes of this paper, we define territory using Wilson's (1975) definition as "an area occupied more or less exclusively by an animal or group of animals by means of repulsion through overt defense or advertisement."

Active avoidance of edge habitat may be due to higher predation risk in transitional habitat but studies have found mixed results. Researchers have documented evidence of reduced nest success near shrubland edges for Chestnut-sided Warbler (*Dendroica pensylvanica*; King and Byers 2002), Yellow-breasted Chat (*Icteria virens*; Woodward et al. 2001), Prairie Warbler (*Dendroica discolor*; Woodward et al. 2001), and Indigo Bunting (*Passerina cyanea*; Weldon and Haddad 2005). Depredation rates of artificial nests placed in clearcuts decreased with increasing distance from the edge in one

study, a pattern the authors attributed to avian predators (Vander Haegan and Degraaf 1996). Other research suggests that other potential nest predators, snakes, may have higher densities in edge habitat (Blouin-Demers and Weatherhead 2001), possibly due to higher densities of nesting birds or the thermoregulation properties of edge habitat (Carfagno et al. 2006). However, King et al. (2001) documented high nest survival in clearcuts, a finding they attributed to dense vegetation offering cover from predation.

Passive displacement results from the non-inclusion of the adjacent habitat type within an individual territory. Under the passive displacement hypothesis, individuals regard edge habitat as a border and restrict their territories to one habitat type. Passive displacement does not predict that territories are placed farther from edges than expected by random placement, but that the restriction of placement to a particular habitat type results in lower densities near habitat edges (King et al. 1997).

Territory expansion near edges can result from habitat near edges having lower food density, thus necessitating larger territories (Ortega 1999, Fletcher and Koford 2003). Empirical and observational studies of territory size and food availability have partially supported this hypothesis (Adams 2001). Of 14 studies Adams (2001) reviewed that examined the relationship between food availability and territory size in birds, seven species showed no significant relationship, five species showed a negative relationship, one species had a positive relationship, and the findings from the remaining three species produced mixed results. Other studies suggest that, rather than food, territory size is more strongly related to pressure from neighbors at territory boundaries (Peek 1972, Watson and Parr 1981, Adams 1990, Wysocki et al. 2004). Reduced pressure from

neighbors near habitat boundaries could also result in increased territory sizes in edge habitat.

According to both the ideal-free and ideal-despotic models of territory distribution, birds should occupy the territory that will maximize their fitness (Fretwell and Lucas 1970). At low densities, only high quality territories should be occupied whereas at high densities the habitat may be saturated and all territories will be occupied regardless of quality. Therefore, territory occupancy during the breeding season may be a misleading indicator of habitat preferences at high densities, when all territories are occupied regardless of quality. During the settlement period, birds should occupy the highest quality territories available meaning habitat use during settlement may reveal habitat preferences that are obscured later in the breeding season.

Objectives: Our objective was to evaluate evidence for alternate hypotheses resulting in lower densities of birds near edge habitat. To do this, we documented nest survival rates and nest placement to test for higher predation rates near edge habitat, as predicted by the active avoidance hypothesis. In addition, we also recorded habitat use during settlement and territory placement for three species: the Prairie Warbler, Blue-winged Warbler (*Vermivora pinus*), and Yellow-breasted Chat to test the hypotheses of active avoidance and passive displacement. We chose these species because they were the most common shrubland-breeding birds in our region. We assumed that during the settlement process preferred habitat would be settled first. In addition, to test the hypothesis of territory expansion, we examined territory size with respect to distance from habitat edge.

METHODS

Study area - We conducted our research at nine sites in southeast in Vinton County Ohio, USA on Zaleski State Forest and New Page (formerly Mead-Westvaco) Forest Land within the Ohio Hills Physiographic region. The region is dominated by mature oak-hickory forests (approximately 70% forest cover) and is perforated by regenerating clearcuts with small amounts of other non-forest land uses including agriculture, mining, and housing developments. Common tree species in the region include red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), red oak (*Quercus rubra*), white oak (*Quercus alba*), yellow-popular (*Liriodendron tulipifera*), and black gum (*Nyssa sylvatica*). The patches used in this study were harvested between 1997 and 2000 and were during 2005 and 2006. Dominant vegetation in the patches included saplings of the mature forest trees, predominately maple and yellow-popular, and blackberry (*Rubus* spp.), greenbrier (*Smilax* spp.), and sumac (*Rhus* spp.).

Nest monitoring - We located nests of the most common shrubland species in our system: Yellow-breasted Chat, Blue-winged Warbler, Prairie Warbler, and Field Sparrow (*Spizella pusilla*), by systematic searching through likely nest substrates. Nests of other open cup nesting species: Mourning Dove (*Zenaidura macroura*), Yellow-billed Cuckoo (*Coccyzus americanus*), Black-billed Cuckoo (*C. erthrophthalmus*), White-eyed Vireo (*Vireo griseus*), American Robin (*Turdus migratorius*), Wood Thrush (*Hylocichla mustelina*), Gray Catbird (*Dumetella carolinensis*), Hooded Warbler (*Wilsonia citrina*), Northern Cardinal (*Cardinalis cardinalis*), Indigo Bunting, and Eastern Towhee (*Pipilo erythrophthalmus*), were located during the searching process. These nests were monitored as well, though we did not actively search for nests of these species. Nests

were checked every 3-4 days or daily when nests were about to hatch or fledge young. After each nest was no longer active, we recorded its GPS coordinates (accuracy ≤ 5 m) and measured distance to nearest habitat edge using aerial photos in ArcView 3.3 (ESRI 1997). We then compared observed nest locations to an equal number of randomly generated nests locations generated in ArcView 3.3 to determine if nests were placed farther from edges than expected by chance. The distance to mature forest edge of random nest locations was compared to observed locations using Wilcoxon matched-pairs signed-ranks test (Zar 1999).

Statistical analyses – We used program MARK to model daily nest survival rate (DSR; White and Burnham 1999). Nest fate was determined as defined by Manolis et al. (2000). Initially, DSR was estimated using three models: constant, linear, and quadratic time trends. Using the top-ranked of these three time models, models were next run including the following variables: site, distance-to-edge, nest height, and year. Given the relatively small sample size and the number of parameters evaluated, we did not include interaction terms in our models. Models were evaluated using second order Akaike's information criteria (AIC_c ; Akaike 1973), which includes a small-sample bias adjustment. We considered models with $AIC_c \leq 2$ as having substantial support whereas models with $AIC_c \geq 4$ were considered to have little to no empirical support (Burnham and Anderson 2002).

Territory settling - We assumed the males that arrived first on the breeding grounds would select the territories that they perceived to be the highest quality (Bensch and Hasselquist 1991, Currie et al. 2000). Between 18-29 April during 2005 and 2006, we surveyed a 1.8 ha section (160 x 110 m) of each of nine sites in southeastern Ohio and

recorded the position for each individual located of three species: Blue-winged Warbler, Prairie Warbler and Yellow-breasted Chat on a detailed map (scale 1:2000). Each site was visited 2-3 times/year within 4.5 hours of sunrise on days without heavy rain or strong wind. We measured the distance from closest habitat edge for each observed singing male based on its position on the map. Although we could not distinguish individual males during multiple visits to the same site, we considered males to be unique individuals if they were at least 20 m (Blue-winged and Prairie Warblers) or 30 m (Yellow-breasted Chats) from previous singing male locations at the same site in the same year or if two or more males were observed counter-singing. Under either the hypothesis of active avoidance or passive displacement, we would expect the mean distance from edge of observed singing Yellow-breasted Chats and Prairie Warblers to be greater than 55 m, the halfway distance between the habitat edge and the cut off (110 m) of our map. However, under the passive displacement hypothesis Blue-winged Warblers were expected to exhibit little-to-no avoidance because this species will include the adjacent mature forest habitat within its territories (Gill et al. 2001) and inclusion of adjacent habitat reduces or eliminates passive displacement. To test for habitat preference, we compared mean distance observed to distance predicted (55 m) using a Wilcoxon signed rank test (Zar 1999) for each species.

Spot-mapping - Spot-mapping allows estimation of the density of birds within a specified area, and is based on the territorial behavior of birds (Ralph et al. 1993). At each site, individuals of the same three species (Blue-winged Warbler, Prairie Warbler, and Yellow-breasted Chat) were surveyed along parallel transects spaced at 50-m intervals using a GPS unit and flagged grid points to facilitate orientation. Each site was visited 8

times between 0600-1000 on days without rain or strong wind from 1 May - 19 June during 2005 and 2006. The location, sex (if discernable), and behavior of each bird were recorded on a detailed map (following the protocol of Ralph et al. (1993)).

Each observation was transferred to a geographic information system (ArcView 3.3, ESRI 1997) using the grid locations for reference points. To aid in territory delineation, we also incorporated locations of known nests. One observer (SEL) compiled the bird locations and delineated territories to minimize interpretation bias (Verner 1985).

Observations of an individual of a given species on at least three out of the eight survey days in the same area were designated as a territory for that individual; counter singing was used to separate adjacent territories (Robbins 1970). From the observations in each territory, we generated a minimum convex polygon (MCP) and a centroid. We determined the size in ha of the MCP for each bird's territory and measured the distance from the centroid to the nearest habitat edge. We then modeled territory size in R (R Development Core Team 2006) using the general linear model. Territory size for the Blue-winged Warbler and Prairie Warbler were log transformed to approximate normality; Yellow-breasted Chat territories approximated normality untransformed. Size of territory was the response variable and year*site, number of observations, and distance to habitat edge were the explanatory variables. We included site and year to account for differences among the sites and between years. The interaction term year*site was included to account for differences in vegetation development among the sites between years. We included the square root of the number of observations in each territory to account for increase in territory size with additional observations.

To determine if the MCPs were farther from the edge than expected based on random placement, we compared the observed distance from edge of each individual's centroid to the distance to edge of randomly generated centroids. For each species, we randomly generated 100 centroids for each site/year combination. The centroids were placed at least half the mean width of the observed MCPs for that site-year-species combination from the habitat edge and from each other to simulate exclusion of non-shrubland habitat and non-overlapping territories. The distance from edge of each observed centroid and the mean of the randomly generated centroids for that site-year-species combination were compared using a Wilcoxon matched-pairs signed-ranks test (Zar 1999) to determine whether territories were placed farther from edges than would be expected based on chance.

RESULTS

Nest monitoring and survival - We monitored 134 nests of 15 species during 2005 and 2006 (Table 2.1). The most common species were the Yellow-breasted Chat ($n=33$), Eastern Towhee ($n=23$), Blue-winged Warbler ($n=13$), and Field Sparrow ($n=11$). Nest parasitism was low; only 5% ($n=134$) of nests contained Brown-headed Cowbird (*Molothrus ater*) eggs or nestlings. The quadratic time model was the best supported but most models were under 2 Δ AIC_c (Table 2.2). The model including distance to edge received little support (AIC_c weight = 0.07); in addition the beta value was close to zero (0.0002, 95% CI -0.0067, 0.0062), which suggests this variable did little to explain variation in nest survival. For shrubland species overall, DSR was low at 0.940 (95% CI 0.927-0.951). For the two species for which we had large enough samples to estimate DSR separately, survival of Yellow-breasted Chats was best explained by a linear time

trend and nest height while no model out-performed the null for Eastern Towhees (Table 2.3). Mean nest height was 75 cm (SD 25, $n=16$) for successful nests whereas unsuccessful nests had a mean height of 122 cm (SD 45; $n = 18$). Yellow-breasted Chats had a nest success rate of 39.1% (95% CI 22.6, 55.4%) and Eastern Towhees had a nest success rate of 16.9% (95% CI 5.5, 33.8%). Placement of nests in relation to habitat edge (mean distance to edge = 42.9 m) did not differ from that of random locations (mean 39.9 m; $W^+ = 4435$, $W^- = 4610$, $n = 134$, $P = 0.847$).

Settlement - We observed 154 singing males that we considered to be unique individuals during the settlement period over the two years: 96 Blue-winged Warblers, 45 Prairie Warblers, and 13 Yellow-breasted Chats. The mean distance from habitat edge was 54.5 m (SE 4.5) for Blue-winged Warblers, 65.3 m (SE 4.4) for Prairie Warblers, and 79.6 m (SE 8.4) for Yellow-breasted Chats. These means were greater than the expected null (55 m) for Prairie Warbler ($z = 753$, $n = 45$, $P = 0.008$) and Yellow-breasted Chat ($z = 78$, $n = 13$, $P = 0.021$) but not for Blue-winged Warbler ($z = -2299$, $n = 94$, $P = 0.805$). Yellow-breasted Chats were generally located farther from habitat edges (79.6 m, SE 8.4) during settlement than Prairie Warblers (65.3 m, SE 4.4); the Yellow-breasted Chat defends larger territories than the Prairie Warbler, so we would expect the former to exhibit edge avoidance at a greater distance under the passive displacement hypothesis.

Territory expansion - Of the three species, models for territory size that included distance to edge had some support for the Prairie Warbler and little support for the Yellow-breasted Chat and Blue-winged Warbler (Table 2.4). The beta estimate for distance to edge approximated zero for the Yellow-breasted Chat (0.0001, 95% CI -0.0002, 0.0003) and Blue-winged Warbler (-0.0002, 95% CI -0.0026, 0.0022), which suggests this

variable did not explain variation in territory size. For the Prairie Warbler, the beta estimate for distance to edge was negative and not centered at zero (-0.0017, 95% CI - 0.0005, 0.0040), offering some support for larger territories near edges (Figure 2.1).

Territory placement – For all three species, distance from habitat edge of observed territories was not significantly different than that predicted by random placement. Mean distance from habitat edge was 49.5 m (SD 6.1) for observed territories versus 54.4 m for randomly generated territories ($z = -19$, $n = 6$, $P = 0.094$) for Yellow-breasted Chats, 52.5 m (SD 5.9) for observed versus 55.9 m for randomly generated territories ($z = 17$, $n = 6$, $P = 0.219$) for Blue-winged Warblers, and 59.8 m (SD 9.6) for observed territories versus 49.6 m for randomly generated territories for Prairie Warblers ($z = 17$, $n = 6$, $P = 0.219$).

DISCUSSION

Of the three hypothesized mechanisms, we observed strong support for passive displacement and some support for territory expansion. The active avoidance hypothesis was not well-supported; we did not detect lower nest survival near edge habitat or avoidance of edge habitat in nest or territory placement and Blue-winged Warblers did not avoid edges during settlement. Blue-winged Warblers are known to include edge habitat in their territories (Gill et al. 2001) and thus are not expected to avoid habitat edges under the passive displacement hypothesis, but they are expected to avoid edges under the active avoidance hypothesis. Likewise, results consistent with the passive displacement hypothesis were observed in a concurrent study on radio-marked Yellow-breasted Chats (Chapter 3). For the territory expansion hypothesis, we found strong support for the Prairie Warbler but little support for the Yellow-breasted Chat or Blue-winged Warbler (Table 2.4).

Another possible explanation for the patterns during settlement we observed for the Yellow-breasted Chat and Prairie Warbler is that interior habitat is considered higher quality habitat because of greater access to extra-pair copulations and lower foraging costs. Birds with interior territories would have shorter travel distances to both potential foraging sites and extra-pair opportunities outside their defended territories.

Our finding that distance-to-edge was not a good predictor of daily nest survival is consistent with other studies of shrubland birds. In studies examining the effect of distance to edge on nest survival only, most researchers have found only weak evidence. However, in a study comparing patches of the same area that differed only in the amount of edge habitat, Indigo Buntings had lower nest success in patches with higher edge ratios (Weldon 2006). Chandler (2006) also found evidence of lower nest success in patches with more complex shapes. These studies suggest that edge density at the landscape scale may be more relevant than distance-to-edge to nesting success (Donovan et al. 1997).

For the two species for which we had sufficient sample sizes to estimate species-specific nest survival rates, the Yellow-breasted Chat had a fairly high nest survival rate of 39.1% (95% CI 22.6-55.4%) whereas nest survival for the Eastern Towhee was quite low at 16.9% (95% CI 5.5-33.8%). Donovan and Thompson (2001) suggested a nest survival rate of 0.25-0.30 is required to balance juvenile and adult mortality. However, the Yellow-breasted Chat typically produces only one brood per season (Eckerle and Thompson 2001) while the Eastern Towhee generally raises two broods per season in the midwestern United States (Greenlaw 1996), so seasonal productivity for the Eastern Towhee may be higher than the nest survival rate suggests. At least for the Yellow-

breasted Chat, these results suggest shrubland habitat in the region provides quality habitat for the nesting stage.

Our ability to detect differences in nest survival or nest placement was limited due to small sample size. We were also not able to uniquely identify individuals during the settlement and spot mapping procedures. For spot mapping, we assumed that territories were fixed during the 7-week survey period. Other studies of territorial birds have suggested that territory boundaries are likely to be fluid (Heg et al. 2000, Adams 2001). In addition, shrubland birds may move between territories during the breeding season (Thompson and Nolan 1973, Nolan 1978). Despite these potential problems, we feel that the overall conclusions in our study regarding distance-to-edge habitat use were robust to violations of the fixed territory assumption; a preference for interior habitat should have been revealed even if territory boundaries shifted during the course of the study.

We also made the assumption that during settlement males would select habitat in an ideal manner, preferentially selecting the highest quality habitat available. This assumption remains untested for the most part but Arlt and Pärt (2007) observed evidence of nonideal habitat selection during their study on settlement patterns in the Northern Wheatear (*Oenanthe oenanthe*). Poor choices may result from imperfect knowledge of the spatial distribution of available habitats (Lima and Zollner 1996), poor correlation between the cues used to select habitats and habitat quality (Orians and Wittenberger 1991, Schlaepfer et al. 2002), or conflicting benefits such as site fidelity (Orians and Wittenberger 1991) or mate choice (Kokko and Sutherland 2001). Potentially, birds may have been making suboptimal decisions in habitat selection, which would obscure the importance of edge habitat to bird fitness.

Future studies documenting the identity of nest predators in edge habitat would help to elucidate the relationship between habitat type and the predator community. In particular, studies addressing nest success in shrubland habitat adjacent to urban and agricultural areas would help to clarify the effect of this type of edge habitat on reproductive success; only one study has compared these systems to date (Burhans and Thompson 2006). In addition, few studies have addressed postfledging success in the shrubland bird community and future research during this period of the breeding cycle would identify habitat needs critical to juvenile survival.

Although our results do not provide strong support for the hypothesis of higher nest predation in edge habitat, the observed edge avoidance in settling and territory placement for Prairie Warbler and Yellow-breasted Chat suggests that, for at least some species, larger patches support higher densities. Additional studies have suggested some degree of area-sensitivity for many species of scrub-shrub birds (King and DeGraaf 2000, King and DeGraaf 2004). Maximizing the area-to-edge ratio of patches may also help to reduce territory displacement and thereby support higher densities. Concurrently, maximizing area-to-edge ratios may also benefit birds dependent on mature forest habitat by reducing disturbance and the amount of edge. Clarifying the habitat needs of this declining suite of birds will help to focus management efforts.

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Species	2005	2006	Total
American Robin	3	0	3
Black-billed Cuckoo	5	3	8
Blue-winged Warbler	4	9	13
Eastern Towhee	6	17	23
Field Sparrow	7	4	11
Gray Catbird	0	1	1
Hooded Warbler	1	3	4
Indigo Bunting	3	5	8
Mourning Dove	3	3	6
Northern Cardinal	3	3	6
Prairie Warbler	3	2	5
White-eyed Vireo	4	3	7
Wood Thrush	3	1	4
Yellow-breasted Chat	20	13	33
Yellow-billed Cuckoo	2	0	2
Total	67	67	134

Table 2.1. Nests found in shrubland habitat in southeastern Ohio during 2005 and 2006.

Model	ΔAIC_c^*	K	w_i	Deviance
DSR _{TT}	0.00	3	0.21	466.81
DSR _{TT + site}	0.04	5	0.21	462.82
DSR _T	0.63	2	0.16	469.45
DSR _{TT + nest height}	0.85	4	0.14	465.64
DSR _{TT + year}	0.96	4	0.13	465.76
DSR _{TT + distance from edge}	2.01	4	0.08	466.81
DSR _(.)	2.29	1	0.07	473.12

*Min AIC_c = 472.83

Table 2.2. Model selection results for daily nest survival rate (DSR) for shrubland nesting birds in southeastern Ohio, 2005-2006. T indicates a linear time trend; TT indicates a quadratic time trend.

Species	Model	ΔAIC^*	K	w_i	Deviance
Yellow-breasted Chat	DSR _{T + nest height}	0.00	3	0.94	81.88
	DSR _T	7.77	2	0.02	91.69
	DSR _{T + site}	8.81	4	0.01	88.64
	DSR _{T + year}	9.49	3	0.01	91.38
	DSR _{TT}	9.69	3	0.01	91.57
	DSR _{T + distance from edge}	9.73	3	0.01	91.61
	DSR _(.)	13.95	1	0.00	99.89
Eastern Towhee	DSR _(.)	0.00	1	0.31	88.93
	DSR _T	1.60	2	0.14	88.49
	DSR _{nest height}	1.66	2	0.13	88.54
	DSR _{TT}	1.77	3	0.13	86.60
	DSR _{distance from edge}	1.77	2	0.13	88.66
	DSR _{year}	2.03	2	0.11	88.92
	DSR _{site}	3.45	3	0.05	88.28

*Min AIC_c = 87.96 Yellow-breasted Chat, 90.95 Eastern Towhee

Table 2.3. Model selection results for daily nest survival rate (DSR) for Yellow-breasted Chats and Eastern Towhees nesting birds in southeastern Ohio, 2005-2006. T indicates a linear time trend; TT indicates a quadratic time trend.

Species	Model	Δ AIC*	K	LogLik	w_i
Blue-winged Warbler	Year*Site + obs	0.00	7	-36.41	0.73
	Year*Site + obs + distance	1.97	8	-36.40	0.27
	Year*Site	17.47	6	-46.17	0.00
	Year*Site + distance	29.17	3	-55.00	0.00
	Site	29.67	1	-57.26	0.00
	null	44.37	7	-58.62	0.00
Yellow-breasted Chat	Year*Site + obs	0.00	7	175.60	0.73
	Year*Site + obs + distance	1.91	8	175.70	0.28
	Site	11.42	3	165.40	0.00
	null	15.60	1	162.40	0.00
	Year*Site	16.66	6	165.80	0.00
	Year*Site + distance	18.55	7	165.80	0.00
Prairie Warbler	Year*Site + obs + distance	0.00	8	-34.82	0.73
	Year*Site + obs	2.41	7	-35.98	0.22
	null	47.84	1	-64.15	0.00
	Site	48.65	3	-62.74	0.00
	Year*Site	54.08	6	-62.63	0.00
	Year*Site + distance	56.08	7	-62.55	0.00

* Minimum AIC, 88.83 for Blue-winged Warbler, -335.34 for Yellow-breasted Chat, 87.63 for Prairie Warbler

Table 2.4. Model results of territory size in relation to distance from habitat edge for three species of shrubland birds. Obs = square root of the number of observations for each territory, distance = distance from habitat edge.

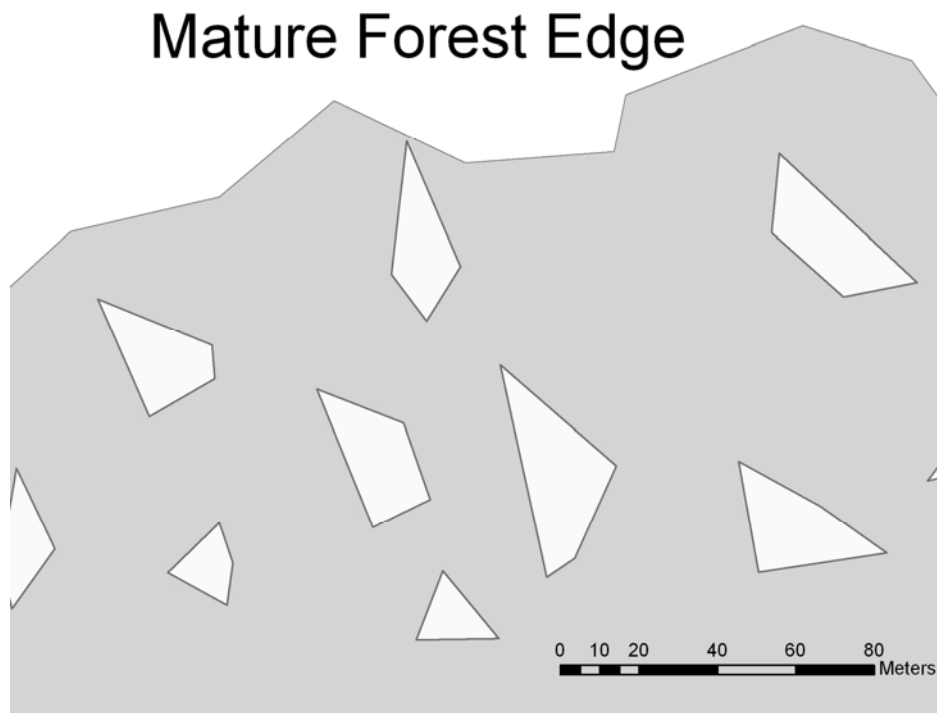


Figure 2.1. Example from the REMA site in southeastern Ohio during 2006 of Prairie Warbler territory distribution in relation to mature forest edge. Territory size of Prairie Warblers tended to decrease with distance from mature forest edge.

CHAPTER 3

DAILY AND SEASONAL MOVEMENTS OF A SHRUBLAND-OBLIGATE BREEDER IN RELATION TO MATURE FOREST EDGE HABITAT

ABSTRACT The effects of edge habitat on wildlife populations have been studied extensively in recent decades. However, most studies have focused on the observed responses of wildlife to the presence of two or more adjacent habitats rather than the mechanisms driving these responses. Based on five years of banding data showing lower capture rates of shrubland birds near habitat edges, we evaluated evidence for five hypotheses that could potentially underlie this pattern: 1) higher predation risk in edge habitat leads to lower usage of edge habitat, 2) birds direct movements towards the interior of sites for territory defense and extra-pair copulations, 3) use of edge habitat changes throughout the day, such that birds favor the interior of cuts in the cooler morning hours and favor shadier edges during warmer periods of the day, 4) due to passive displacement, sampling in the interior of the harvest is more likely to intersect multiple home ranges compared to sampling near edges, and 5) home range expansion results in larger home ranges near edge habitat. To test these hypotheses, we radio-marked 37 yellow-breasted chats (*Icteria virens*) during the summers of 2005 and 2006

and relocated each bird over an average of five weeks. We analyzed results based both on individual locations within each bird's home range and placement of the home range within the habitat patch. Yellow-breasted chats did not appear to avoid habitat edges in either home range placement or habitat usage within their home ranges, though there was some support for changing edge habitat usage over the season. Home ranges did not vary in size with distance from edge. These results support the passive displacement hypothesis and, to a lesser extent, the hypothesis that birds direct movements towards the interior of sites, possibly for territory defense and extra-pair copulations. This study suggests that although small patches and patches with high edge-to-area ratios do not appear to be actively avoided *per se* nor associated with poor habitat quality, managing for large patches that minimize edge-to-area ratios will likely yield higher densities of a sensitive shrubland specialist.

INTRODUCTION

Due to habitat fragmentation, the amount of forest edge habitat is orders of magnitude greater now in the United States than when Europeans first began settling North America. Depending on their life history and habitat requirements, individual species may be positively or negatively influenced by edge effects, which are the biotic and abiotic effects created by the juxtaposition of two or more habitat types in a landscape. One predicted edge effect is greater predator densities (Askins 1995) because edges may be used by predator species of both habitat types. Although more attention has been directed to the conservation of mature forest-dependent birds, shrubland species have been declining since the 1960s (DeGraaf and Yamasaki 2003). However, managing for

shrubland species is complex given that the creation of early-successional habitat may result in edge effects that negatively impact forest interior species.

Pronounced edge effects have been reported for forest interior species in forest adjacent to agricultural lands (Faaborg et al. 1995), but some research suggests that within a forested landscape edge effects created by even-aged management are negligible for forest interior species. DeGraaf and Yamasaki (2003) reviewed studies from the northeastern United States and found that silvicultural edges did not result in elevated nest predation rates. Conversely, Lahti (2001) summarized the results of 54 studies relating to edge effects and concluded that the hypothesis that clearcuts within a forest matrix have fewer edge effects than those in forest-agricultural edges has not been supported. Similarly, Manolis et al. (2000) reviewed and reanalyzed studies investigating edge effects associated with clearcuts in contiguous northern hardwoods and concluded that most studies with a high power of detection showed evidence of edge effects. In a study on the effects of forest-clearcut edges on a mature forest songbird, Harris and Reed (2002) found that edges were associated with both positive and negative impacts. However, Driscoll and Donovan (2004) documented lower nest survival in edge habitat in forest fragments but not contiguous forest landscapes. As Chalfoun et al. (2002) concluded, the response of nest predators to fragmentation complex, taxon specific, and context dependent. Nest predation may vary across temporal and spatial scales so the landscape context as well as the local habitat type is important to nesting success (Donovan et al. 1997, Thompson 2007).

Few studies have examined edge effects for shrubland species though what research has been conducted suggests that predation rates may be higher closer to edges.

There was evidence of reduced nest success near shrubland edges for chestnut-sided warbler (*Dendroica pensylvanica*; King and Byers 2002), yellow-breasted chat (*Icteria virens*; Woodward et al. 2001), and prairie warbler (*Dendroica discolor*; Woodward et al. 2001). Depredation rates of artificial nests placed in clearcuts decreased when farther than 75 m from the edge in one study, a pattern the authors attributed to avian predators (Vander Haegan and Degraaf 1996). However, King et al. (2001) documented high nest survival in clearcuts, a finding they attributed to dense vegetation offering cover from predation.

Some evidence has suggested that densities of shrubland birds may be lower in smaller shrubland patches or near edges within shrubland habitat. Alterman et al. (2005) found that yellow-breasted chats and prairie warblers were absent or rare in group-selection cuts (≤ 0.8 ha). Costello et al. (2000) also found lower shrubland bird densities in smaller patches and King and DeGraaf (2004) documented later nest initiation dates in smaller patches, which they suggested may mean smaller patches are regarded as lower quality habitat by birds. In shrubland patches in Ohio, Rodewald and Vitz (2005) documented lower capture rates for several shrubland species at 20 m than at 80 m from mature forest edge habitat, a finding the authors suggested might have been due to active edge avoidance.

One possible mechanism for reduced densities in edge habitat is territory expansion (Ortega 1999, Fletcher and Koford 2003). One situation that may prompt larger territories and consequently lower densities near edges is if habitat near edges having lower food density, thus necessitating larger territories. However, empirical and observational studies of birds have been equivocal (Adams 2001). Of 14 studies

summarized in Adams (2001), seven species showed no significant relationship between food availability and territory size, five species showed a negative relationship, one species had a positive relationship, and the findings from the remaining three species produced mixed results. Other studies suggest that, rather than food, territory size is more strongly related to pressure from neighbors at territory boundaries (Peek 1972, Watson and Parr 1981, Adams 1990, Wysocki et al. 2004).

Another possible cause of lower densities in edge habitat in avian populations is passive displacement (King et al. 1997, Ortega 1999, Fletcher and Koford 2003). In this situation, the geometry of packing bird home ranges into patches results in lower densities near edges. The reduced density is not based on habitat quality but rather non-use of the adjacent habitat type.

This study evaluated the following four hypothesized mechanisms of edge avoidance in shrubland birds: Hypothesis 1) predation avoidance – predator densities are higher in edge habitat, resulting in a consistent preference for interior habitat in home range placement and use. Hypothesis 2) social behavior – edge home ranges are more likely to abut neighboring home ranges on their interior borders, resulting in directional movements towards the interior of sites for social interactions (e.g. territory defense and extra-pair copulations). If true, then edge avoidance should predominate in the morning hours and early in the breeding season, when birds engage in the most territory defense and extra-territory forays. Hypothesis 3) temperature regulation – use of edges changes throughout the day, such that birds favor the sunlit interior of cuts in the cooler morning hours and favor shadier edges during warmer periods of the day. Edge avoidance should be predominantly before ~9 EST in this case, at which point most of the patch is exposed

to full sunlight. Hypothesis 4) passive displacement – non-use of adjacent mature forest habitat results in passive displacement from edge habitat. Although home range placement and habitat use within the home range does not differ from random, restriction to shrubland habitat results in lower bird densities near edge habitat. Hypothesis 5) home range expansion – home ranges are larger near habitat boarders resulting in lower densities near edge habitat. Under this hypothesis individual locations should be random with respect to edge habitat but home ranges should decrease in size with distance from edge.

STUDY AREA

We conducted our research at three sites (CC, KG, and RE) in southeast in Vinton County Ohio, USA on Zaleski State Forest and New Page (formerly Mead-Westvaco) Forest Land within the Ohio Hills Physiographic region. The region is dominated by mature oak-hickory forests (approximately 70% forest cover) and is perforated by regenerating clearcuts with small amounts of other non-forest land uses including agriculture, mining, and housing developments. Common tree species in the region include red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), red oak (*Quercus rubra*), white oak (*Quercus alba*), yellow-poplar (*Liriodendron tulipifera*), and black gum (*Nyssa sylvatica*). Patches included in this study were harvested between 1997 and 1999 and were used during 2005 and 2006. Dominant vegetation in the patches included saplings of the mature forest trees, predominately maple and yellow-popular, and blackberry (*Rubus* spp.), greenbrier (*Smilax* spp.), and sumac (*Rhus* spp.). The shrubland bird community in this region included the white-eyed vireo (*Vireo griseus*), gray catbird (*Dumetella carolinensis*), blue-winged warbler (*Vermivora pinus*), prairie warbler,

common yellowthroat (*Geothlypis trichas*), yellow-breasted chat, eastern towhee (*Pipilo erythrophthalmus*), field sparrow (*Spizella pusilla*), and indigo bunting (*Passerina cyanea*).

METHODS

Radio-telemetry

Movement in relation to edge was assessed by radio-marking 39 adult male yellow-breasted chats during 2005 and 2006 (20 and 19, respectively). We captured birds using passive netting and call-back tapes. Age of each bird (second year or after-second year) was determined (Phillips 1974), and mass (g) and wing chord (cm) were recorded.

Radios transmitters (Holohil BD-2) were attached using the figure-8 harness proposed by Rappole and Tipton (1991). We used a non-irritating cotton material to attach the transmitters in order to minimize chafing while allowing the harness to biodegrade and fall off before the start of fall migration. Adult yellow-breasted chats have a mass range of 22 to 29g (Eckerle and Thompson 2001). The transmitters had a mass of 0.90 g, which was 3.1% to 4.1% of the bird's total mass.

To allow individuals time to adjust to transmitters, we waited 24 h after transmitter attachment to begin observations. Each individual was located twice per day with sequential locations at least 30 min apart (early morning [0530-0830], afternoon [1100-1500], and evening [1700-2000]) using a handheld receiver and a three-element Yagi antenna. We located each bird 4-5 days per week, which resulted in at least 40 locations per individual as long as the bird was tracked for ≥ 5 weeks. Locations were determined using triangulation from numbered grid points set at 50 m intervals throughout the sites. To preserve the accuracy of our locations, we censored locations if

the angle of intersection of bearings was greater than 140 or less than 60 (White and Garrott 1990). Locations are most accurate when the angle of intersection is 90-120 degrees (White and Garrott 1990). To minimize the location error generated by bird activity, we recorded bearings from the second grid point within 3 min of recording the bearing from the first grid point. We also identified periods of high bird activity using signal strength and frequency; locations were not taken when birds were considered highly active.

Autocorrelation

Correlation between successive locations for an individual within a stable home range implies that the time interval separating these observations is too short to meet the statistical assumption of independence. To test for autocorrelation we calculated Schoener's ratio (Schoener 1981) for each bird's locations. Independence between consecutive locations was obtained after 37 min (SE 7 min). A proportion of the locations recorded after 30 min may therefore have not been independent. However, the majority of locations were independent and restricting sampling intervals to times that are statistically independent can result in the loss of important biological information (Reynolds and Laundre 1990).

Measuring Error

To determine the error associated with our triangulation method we tested the accuracy of locations using a beacon test with transmitters at known locations set at the study sites and located using standard procedures (White and Garrott 1990). The transmitters were attached to small plastic containers of sugar water and placed ~ 1 m from the ground to

simulate the absorption of radio signals by the bird's bodies (Larkin et al. 1996).

Transmitter locations were determined using Garmin GPS units on days when the error rate was $< 5\text{m}$. However, because these measurements were taken on stationary transmitters, they might have underestimated the error associated with tracking active birds in the field.

Kernel Home Range Estimation

The fixed kernel technique is considered the most robust of the various home range estimators (Seaman and Powell 1996, Kernohan et al. 2001). We calculated 95 and 50% (core) home-range estimators using the Home Range Extension (Rodgers and Carr 1998) in ArcView 3.2 (ESRI 1997). Home range sizes were evaluated using age of bird (second year and after-second year), year, and distance from mature forest edge using linear mixed-effects models. Because home ranges from the same site might not have been independent, we included site as a random effect in all models. The 95% and 50% fixed-kernel home range sizes were log-transformed to approximate normality. Models were run first using only birds with known ages and then for year, distance to edge, and territory density (territories/ha) using all birds of all ages. Territory density was determined based on spot mapping during 2005 and 2006 (Chapter 2). The predictor variables were age, year, distance to edge. We also determined minimum convex polygon home ranges to: 1) compare these estimates with those from other studies, and 2) estimate habitat available for use.

Behavior in Relation to Edge

We tested for behavior in relation to edge habitat within individual bird locations. Distance from habitat edge was determined for each location and each bird. We

generated 100 random locations within the minimum convex polygon of each bird to represent habitat that was available for the bird to use. We used the minimum convex polygon because we considered it likely that intraspecies interactions affected what habitat was available for use; we felt that the minimum convex polygon best represented habitat that was available to the bird. We then tested the hypothesis that distance from edge of observed locations was greater than that of random locations by comparing the means of distance from edge for each individual using a Wilcoxon matched-pairs signed-ranks test (Zar 1999).

Because we were interested in factors affecting habitat use as well as overall patterns, we then examined other variables influencing distance to edge. After verifying normality of distance to edge we used a linear mixed effects model. We included the individual bird as a random effect in this model and season (Julian day), time of day, year, and site were the explanatory variables and distance from edge was the response variable.

Home Range Placement

Because birds might still avoid edge habitat through home range placement even without showing edge avoidance within individual locations, we tested for home range placement in relation to distance from edge using observed and randomly generated home ranges. We determined the distance from the centroid of each bird's home range to the closest edge. The centroid of a bird's home range is the intersection of all hyperplanes that divide the home range into two parts of equal moment about the hyperplane. Informally, it is the "mean" of all locations in the home range. We then randomly generated 100 home ranges in each of the three habitat patches. Randomly generated home ranges were

circular, had the area of the mean of the home ranges at that site, and were constrained to be 80% contained within the habitat patch. The containment rule was used to simulate non-use of mature forest habitat while allowing for variation in home range shape. To test for edge avoidance in home range placement, we used a Wilcoxon matched-pairs signed-ranks test (Zar 1999) to compare the observed and random locations of the centroid of each bird.

RESULTS

Radio-transmitters were attached to 39 Yellow-breasted chats over the 2 years of the study, 20 in 2005 and 19 in 2006. One chat in each year was not located two days following radio-marking. Because both of these individuals were radio-tagged early in the season (12 May and 5 May, respectively) it is likely that they left the study region and settled elsewhere. One of these individuals was located in a shrubland patch 1.5 km east from its capture patch the day after marking; the following day it was not located in any patch within 3 km of the original site. Of the 37 remaining individuals, 22 were labeled after-second-year birds, 12 were second-year birds, and three were adults of unknown age. Transmitters functioned for a mean of 38 days (range 11-48), allowing us to record a mean of 52 locations per individual (range 16-69). In all, 1885 locations were recorded for the 37 chats. Based on tests of location error, recorded locations were within 13.6 m (4.3 SD) of the actual locations.

Movement in Relation to Edge

We observed little evidence of active edge avoidance. The difference between mean distance from edge for the observed 43.3 m (SD 27.2) versus random 45.7 m locations

was not significant ($z = 378$, $n = 37$, $P = 0.485$). For the linear fixed effects models, there was little support for models containing time of day, site, or year. Only season (Julian day) performed better than the null model in explaining distance to edge (Table 3.1). Mean distance from edge peaked at about 11 June, which corresponded with the peak of the breeding season (Figure 3.1). Time of day had no observable influence on distance from edge (Figure 3.2).

Home Range Placement

There was no observable edge avoidance in placement of observed home ranges (mean 49.8 m, SD 4.3) and random observed home ranges (mean 46.3 m, SD 15.3). Home ranges were not significantly farther from edge habitat than predicted based on random placement ($z = 346$, $n = 32$, $P = 0.128$).

Home Range Size

The mean home range estimate was 3.7 ha (SD 1.9) for the 95% kernel and 0.64 ha (SD 0.86) for the 50% kernel. Home range size for both kernel types reached an asymptote after about 30 locations so only the 34 individuals with more than 30 locations were included for the analyses of home range size. There was little support for age or distance from edge in explaining variation in home range sizes but weak support for year and strong support for territory density (Table 3.2). The fixed-kernel 95% home range estimates were larger in 2006 (mean 4.7 ha SD 5.4) than in 2005 (mean 2.5 ha SD 2.4; Figure 3.3). Kernel home range size also differed by site (Figure 3.3). The mean MCP was 1.7 ha (SE 0.20; range 0.4-5.0 ha).

DISCUSSION

Results from this study provide the strongest support for the passive displacement hypothesis in explaining lower densities near edge habitat for yellow-breasted chats. Passive displacement results from non-use of the adjacent habitat type, resulting in lower densities near edge habitat. We observed little evidence of active edge avoidance by the individuals in our study in either home range placement or in habitat usage within home ranges. Although there was some seasonal change in use of edge habitat over the season, habitat use did not vary with time of day. These results provide only weak support for the social behavior hypothesis, which predicted edge avoidance early in the morning and during the peak breeding season (mid May to mid June), when birds engage in the most territory defense and extra-territory forays. In addition, although the home ranges may have been regularly spaced throughout the patch, nets in the interior of the harvest were more likely to intersect multiple home ranges compared to nets at edges, and hence catch more individuals.

These findings illustrate that patterns showing apparent edge effects may not always result from active edge avoidance. In particular, the results of Rodewald and Vitz (2005) suggested that densities of many shrubland species were lower close to the mature forest edge. By evaluating potential mechanisms driving this pattern, we concluded that this pattern was being driven primarily by passive displacement due to non-use of mature forest habitat. Although both passive displacement and active avoidance suggest densities will be lower near edges, passive displacement does not imply that small or irregularly shaped patches will be detrimental to nesting success or survival. Thus, these two hypotheses have different management implications.

Studies of avian ecology have frequently relied on early morning detections of individuals early in the breeding season. Many studies on avian biology rely on the detection of singing males during the four hours following sunrise and during the peak breeding season when these birds are most vocal. However, habitat use during this period may not be reflective of habitat use throughout the day and season or habitat use by both sexes. Mazerole and Hobson (2003) documented male ovenbirds (*Seiurus aurocapilla*) preferentially using edge habitat during the late morning and early afternoon while during the early morning periods these birds avoided habitat near edges. This study compared habitat usage on both a daily and seasonal basis to achieve a full picture of habitat use during the breeding season. Although we did not detect habitat use changes by time of day, we did detect a seasonal pattern of lower edge habitat use during the peak breeding season.

There have been recent efforts to tease out the relative importance and influence of edge and area effects (Fletcher et al. 2007). In general, studies where edge and area were not confounded have most frequently supported edge effects, and Fletcher et al. (2007) suggest that some observed area effects could be explained by edge effects. As shown in our study, passive displacement can lead to lower densities in smaller patches, hence, area sensitivity in the yellow-breasted chat could be at least partially attributed to this mechanism rather than preference for larger patches.

This study was restricted to a subset of shrubland birds; we only examined movements of the male of one species in our region. Males and females may have different patterns of edge habitat usage. In addition, other studies have found edge effects to vary by region (Johnson and Igl 2001). However, the lack of active edge

avoidance observed with yellow-breasted chats was consistent with data for blue-winged and prairie warblers (Chapter 2).

Our work suggests that studies examining habitat use only during the early morning may reflect habitat use patterns for the yellow-breasted chat during the peak breeding season but habitat usage may vary seasonally. In addition, recent studies have found that habitat use during the post-fledging period may differ from usage during the breeding season (Marshall et al. 2003, King et al. 2006, Vitz and Rodewald 2006). Research conducted during the morning hours during the peak breeding season only accurately identifies habitat use of singing adult males during this period; additional research would elucidate if habitat use during this period is typical of that of all age and sex classes and if habitat use varies on a daily or seasonal basis.

MANAGEMENT IMPLICATIONS

Overall, these results suggest that although minimizing the edge-to-area ratios of habitat patches may support higher densities of these birds by minimizing passive displacement, smaller patches and patches with higher edge-to-area ratios still may provide quality habitat. Reducing the amount of disturbance to mature forest habitat through the creation of larger and more regularly shaped shrubland patches may benefit mature forest dependent species as well.

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Model	Δ AIC*	K	w_i
Day	0.00	4	0.72
Null	2.60	2	0.20
Time + day + year + site	5.43	7	0.05
Time	6.58	4	0.03
Time + day + site*year	8.78	10	0.01
Site*year	11.78	8	0.00

*Min AIC=15542.09

Table 3.1. Results of model fitting and selection for distance from edge habitat for male yellow-breasted chats in southeastern Ohio, USA, during 2005-2006. Time indicates time of day and day indicates Julian day (season).

Data set	Model	50% Kernel				95% Kernel		
		K	AIC_c	ΔAIC_c	w_i	AIC_c	ΔAIC_c	w_i
Known-age only ($n=31$)	null	2	97.11	0.00	0.72	82.46	0.00	0.77
	Age	3	99.00	1.89	0.28	84.86	2.40	0.23
all ($n=34$)	Density	4	102.70	0.00	0.52	87.72	0.00	0.41
	null	2	103.80	1.10	0.30	88.3	0.58	0.31
	Year	3	104.90	2.20	0.17	88.76	1.04	0.24
	Distance to edge	3	111.20	8.50	0.01	93.2	5.48	0.03
	Distance to edge + Year	5	112.80	10.10	0.00	94.74	7.02	0.01

Table 3.2. Linear mixed-effects models for the effect of bird age, year, and distance to edge on estimates of 50% and 95% fixed-kernel home range size for male yellow-breasted chats in southeastern Ohio during 2005 and 2006.

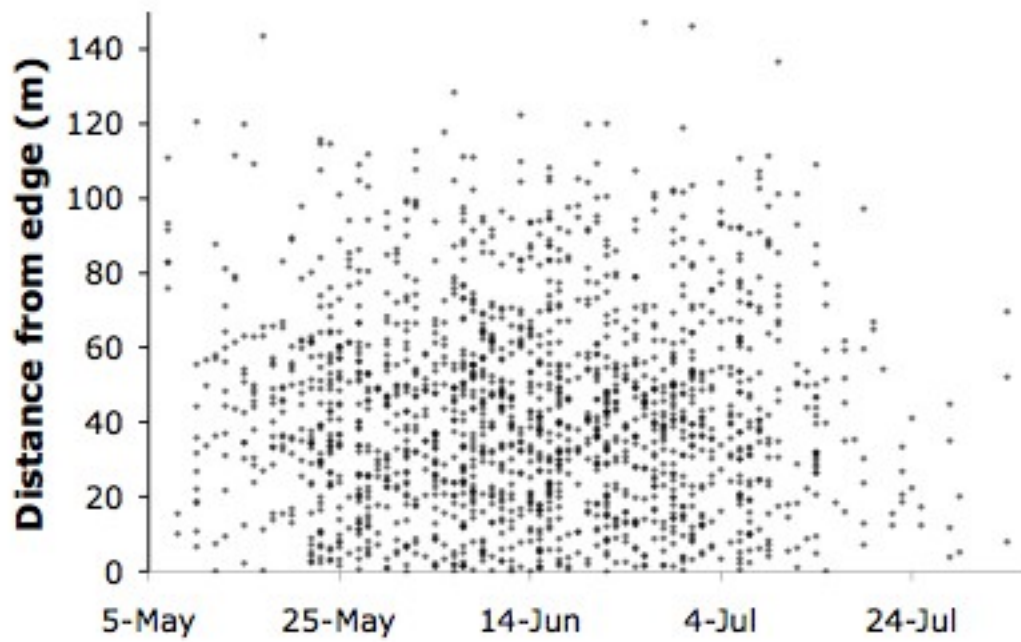


Figure 3.1. Distance from mature forest habitat edge by season (5 May to 3 August) for male yellow-breasted chats in southeastern Ohio, USA, during 2005-2006.

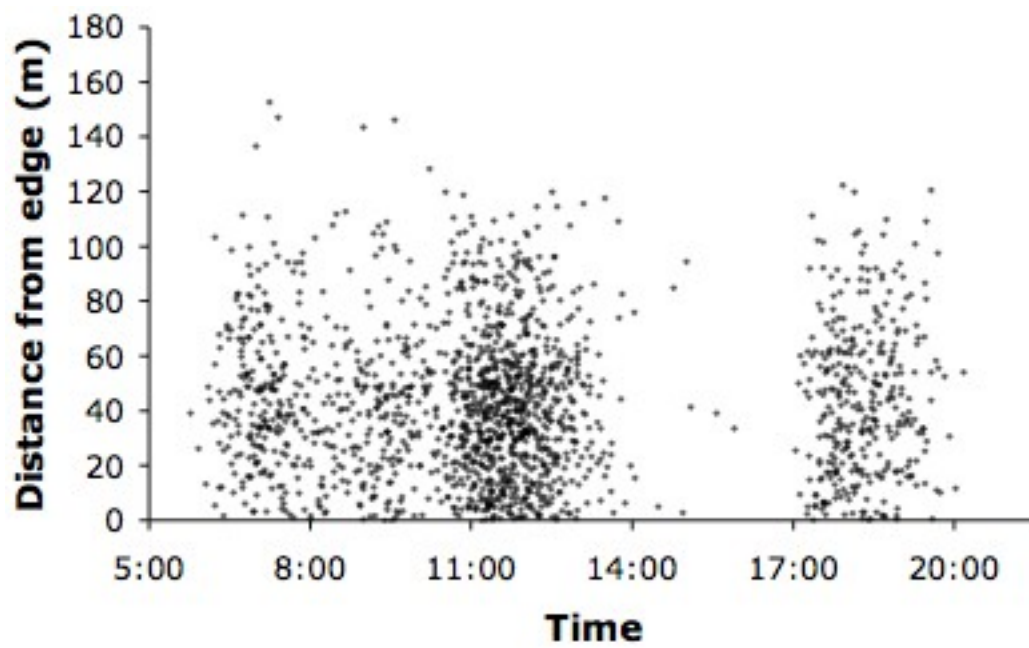


Figure 3.2. Distance from habitat edge by time of day (05:00 to 20:00) for male yellow-breasted chats in southeastern Ohio, USA, during 2005-2006.

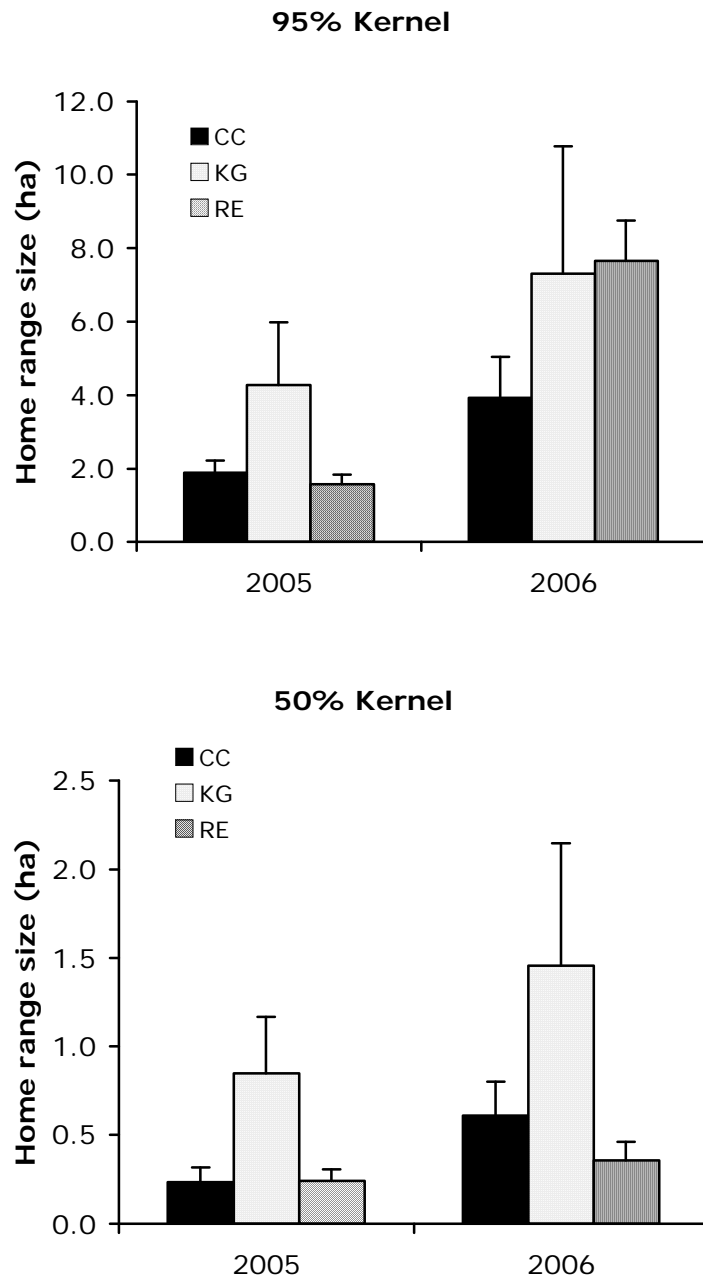


Figure 3.3. Fixed-kernel (95% and 50%) home range size (ha) by site (CC, KG, and RE) and year for male yellow-breasted chats during 2005 and 2006 in southeastern Ohio. SE shown in error bars.

CHAPTER 4

EFFECT OF FOREST SUCCESSION AND SPATIAL SCALE ON AVIAN ABUNDANCE IN A SHRUBLAND SYSTEM DURING BREEDING AND POST- BREEDING PERIODS

Abstract: The influence of spatial scale on avian use of shrubland habitat during the late- and post-breeding season is poorly known. In particular, the importance of landscape connectivity to this group of species is unclear. We collected mist-netting data over a 5-year period to examine the effect of spatial scale on capture rates using characteristics at the plot (20 m), patch, and landscape (2 km) level. In addition, we evaluated avian community structure by harvest age. Between 2002 and 2006, we banded 2,890 shrubland specialists, 2,912 shrubland generalists, and 3,493 forest specialists in 13 shrubland patches in southeastern Ohio, USA. Generalized linear mixed-effects models including variables at the plot and landscape levels received the most support. In general, shrubland specialists and generalists increased with the amount of shrubland habitat in the landscape though captures of shrubland generalists also increased with the amount of mature forest in the landscape. As a whole, patch level variables (harvest age, area, and perimeter-to-area ratio) received little support; and captures also increased at the plot level with increases in stem density, Japanese honeysuckle (*Lonicera japonica*), and

distance from mature forest edge. For forest specialists, captures were best explained by plot level variables and amount of mature forest in the landscape. Capture rates of forest specialists were independent of harvest age, whereas capture rates for shrubland specialists and generalists declined from a peak at 4 years post-harvest (minimum harvest age in the study) to a low at 10 years post-harvest (maximum harvest age in the study). Similarly, conservation value indices, a value similar to species richness but weighted for the conservation value of a species, and species richness peaked at 4-5 years post-harvest. These results suggest that because greater landscape connectivity increases habitat use of shrubland species and shrubland habitat created by forest management had the highest conservation value soon after harvesting, a short harvest rotation schedule concentrated in one region might most benefit this group of shrubland species.

Introduction

Shrubland-breeding songbirds have been declining over much of the eastern United States since the 1960s due to the regeneration of forest on abandoned farm fields and the suppression of natural disturbances that once provided appropriate habitat (Litvaitis 1993; Dessecker and McAuley 2001; Hunter et al. 2001; DeGraaf and Yamasaki 2003). These species rely upon disturbance of forest habitat, such as flooding, fire, windstorm, insect outbreaks, or logging, to create the low, woody vegetative structure they require (Askins 2002). Numerous studies have documented that recent clearcuts provide the structure required by shrubland specialist songbirds (Webb et al. 1977; Crawford et al. 1981; Hagan et al. 1997; Yahner 1997). We define shrubland specialists as those species requiring the low, dense vegetative structure of shrubland habitat for breeding whereas

shrubland generalists are those species that use other types of habitat during the breeding season as well.

Because shrubland habitat is ephemeral, use by birds changes over time. Keller et al. (2003) found a sharp increase in species diversity from years 2-6 post-cutting followed by a steep decline until 25 years post-cutting. The authors speculated that the decline after year 7 was due to loss of foraging and nesting sites near ground level as the canopy closed. In addition to temporal changes, spatial scale also may influence the habitat use of birds. Askins et al. (2007) found that bird abundance was best explained using plot-level variables, and to a lesser extent patch-level variables, rather than landscape-level variables.

Most studies in shrubland systems have been conducted during the breeding season and much less attention has been paid to the post-breeding period, the 2-3 month span after nesting or fledging and before the onset of migration (Pagen et al. 2000). Several studies have documented heavy use of shrubland habitat during the post-breeding period by young and adults of forest specialist songbirds (Anders et al. 1998; Vega Rivera et al. 1998; Vega Rivera et al. 1999; Pagen et al. 2000; Marshall et al. 2003; Vitz and Rodewald 2006). This habitat use is often attributed to juveniles and post-breeding adults seeking out denser habitat for cover and/or food resources (King et al. 2006; Vitz and Rodewald 2006). Vitz and Rodewald (2007) found density of low vegetation and canopy height best explained variation in capture rates of forest specialists utilizing shrubland habitat. In the one study to date on postfledging use of habitat by shrubland species, Maxted (2001) documented a preference for higher stem densities by gray catbird (*Dumetella carolinensis*) and yellow-breasted chat (*Icteria virens*) fledglings

compared to nesting locations. Given the potential importance of the post-breeding period to songbird population viability (Anders and Marshall 2005), more research is needed on songbird use of shrubland habitat during this period.

We wanted to determine the influence of forest succession at multiple spatial scales (e.g. plot, patch, landscape) on avian use of shrubland habitat during the breeding and post-breeding periods. We were particularly interested in the effect of harvest age on capture rates for each species group. In addition, we evaluated the effects of harvest age on the avian community using five metrics of community structure: species richness, two indices of species diversity, and two indices of conservation value.

Methods

Study area

Study sites were located in southeast Ohio, USA on Zaleski State Forest (Athens and Vinton Counties) and New Page (formerly Mead-Westvaco) Forest Land (Athens, Vinton, and Jackson Counties) within the Ohio Hills Physiographic region. The region is dominated by mature oak-hickory forests (approximately 70% forest cover) and is perforated by regenerating clearcuts with small amounts of other non-forest land uses. Common tree species in the region include red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), red oak (*Quercus rubra*), white oak (*Quercus alba*), yellow-poplar (*Liriodendron tulipifera*), and black gum (*Nyssa sylvatica*). Dominant vegetation in clearcut patches included saplings of the mature forest trees, predominately maple and yellow-poplar, and blackberry (*Rubus* spp.), greenbrier (*Smilax* spp.), and sumac (*Rhus* spp.). Thirteen clearcut patches were used between 2002 and 2006 although not all sites

were used during all years. Two sites were dropped in 2004 due to strip mining activity and two additional sites were not used after 2003 and 2004, respectively, due to low capture rates. The sites were 4-6 years postharvest the first year they were included in the study and up to 10 years postharvest by the last year of the study. Sites ranged from 3-16 ha in size and all sites were separated by ≥ 2 km.

Common shrubland specialist species in our region included the white-eyed vireo (*Vireo griseus*), blue-winged warbler (*Vermivora pinus*), prairie warbler (*Dendroica discolor*), and yellow-breasted chat; generalist shrubland species included the common yellowthroat (*Geothlypis trichas*), field sparrow (*Spizella pusilla*), indigo bunting (*Passerina cyanea*), eastern towhee (*Pipilo erythrophthalmus*), and gray catbird. Common forest specialist species in our region included the ovenbird (*Seiurus aurocapillus*), worm-eating warbler (*Helmitheros vermivorum*), red-eyed vireo (*Vireo olivaceus*), scarlet tanager (*Piranga olivacea*), wood thrush (*Hylocichla mustelina*), and Kentucky warbler (*Oporornis formosus*). These birds may be secretive and non-vocal during the late- and post-breeding periods. Mist nets do not depend on auditory or visual detection and so may better sample secretive species (Karr 1981).

Banding data

We conducted our banding operation from June to mid-August 2002-2006 at 9-12 sites/year in southeastern Ohio. To standardize captures among sites, each site had nine nets set in identical 3 x 3 grids. Nets (12 x 2.6 m, 30-mm mesh) were placed at 20, 50, and 80 m from the mature forest edge along three transects. Each site was visited once per week for 9 weeks (June 15 - August 15) during 2002 and 2003, and once per week for 11 weeks (1 June - August 15) during 2004 - 2006. However, for this analysis we only

used banding data collected during the late- and post-breeding period 15 June - 17 August. We opened mist nets 30 minutes before sunrise (~0540 EST) and closed nets 4.5 hours later. Burton and DeSante (2004) found that as few as 3-10 stations may be sufficient to produce representational regional results so we believe that this sample was sufficient for making inferences about the southeastern Ohio region.

Each individual captured was classified as either an after-hatch-year (AHY) or hatch-year (HY) according to plumage, feather shape and wear, and skull ossification. All birds were banded with a numbered USGS aluminum band. We also recorded the date, time of capture, wing chord, body mass, breeding condition, fat score (Helms and Drury 1960), and net of capture for each bird. Only the initial capture of an individual bird was included in the analysis for any given year. After the initial year of the study, we included birds banded in previous years the first time they were captured after 14 June. Had we excluded recaptures of birds from previous years, we would have artificially lowered our capture rates over the duration of the study.

Vegetation Monitoring

We sampled vegetation at each mist net using a modified James and Shugart (1970) method. A 0.04 ha circular plot was established at the center of each net resulting in 9 plots per site. Vegetation structure was measured along two 10-m transects at each net by recording the number of total stem hits (i.e., number of times stems touched a pole) from 0.5-3.0 m off the ground in 0.5 m increments using a telescoping pole. We identified the three dominant sapling and shrub species within the plot. We tallied the number of small (12-23 cm diameter at breast height, dbh), medium (23-38 cm dbh) and large (>38 cm dbh) snags, residual trees, and logs longer than 1.0 m with diameter >7.5 cm. We also

estimated the average height of woody vegetation within the 0.04 ha circular plot using the telescoping pole. Finally, we recorded the presence or absence of Japanese honeysuckle vines (*Lonicera japonica*) within each vegetation plot. Japanese honeysuckle is an introduced vine that slows succession by preventing trees from becoming established (Schierenbeck 2004). Askins (2002) noted that a dense covering of Japanese honeysuckle can delay forest succession in shrubland patches and thus provide habitat for shrubland-breeding birds for a longer period.

Patch and landscape characteristics

We used aerial photos (2004-2006; USDA FSA Aerial Photography Field Office) to calculate patch (area and perimeter) and landscape characteristics, which included the percentage of mature forest, shrubland, agriculture, and residential (developed) land within a 1 km radius centered on the mist net grid in each patch. We used a 1 km radius because this distance approximated the maximum distance moved by radio-tagged yellow-breasted chats in our system as part of a concurrent study (Chapter 3) and thus this distance seemed a reasonable approximation of the landscape as viewed by an individual bird. Habitat type was delineated using harvest information obtained from Zaleaski State Forest and New Page Corporation and visual assessment of National Agriculture Imagery Program digital images in ArcGIS (ESRI 1997).

Principal component analysis

We used separate principal component analyses (PCA) at each of the three spatial scales: plot, patch, and landscape levels. Four variables were used at the plot level: woody vegetation height, average number of stem hits, Japanese honeysuckle (present or not present), and distance to habitat edge. At the patch level, we included three variables:

harvest age, patch area, and patch-area-to-edge ratio. For the landscape level we included four variables: percent mature forest, shrubland, developed, and agricultural habitat within 1 km. Data for each variable were checked for normality using Q-Q plots in R (version 2.4.1) and transformed if necessary to approximate normality. Data for vegetation height and stem density were transformed using the natural log (\ln); all other variables approximated normal distributions and remained untransformed.

Model building

Because some of the same sites were studied over the five-year period, we accounted for possible dependence in data among years by using a nested mixed effects model approach with site as a random effect. The mixed effects models treat data from the same sites as repeated measures, which allows for direct modeling of temporally correlated observations by modeling the covariance structure of the data (Gutzwiller and Riffell 2007). Net (plot) was nested within site. Before considering the covariance structure of the data, we fit the fixed effects portion of the data set using a linear model. Factor scores from the three principal component analyses were used as independent variables and captures were used as the response variable. We ran linear mixed effects models separately for each species and also for three species groups: shrubland specialists, shrubland generalists, and forest specialist species.

Although many covariance structures are possible, we ran models for only those we considered to be biologically plausible. In our model set, we included an autoregressive covariance structure, which considers observations closer together in time to be more highly correlated than those observations spaced farther apart in time and a compound symmetry covariance structure, which considers all observations from the

same site to be equally correlated, regardless of their separation in time. We ran the models for covariance selection using the restricted maximum likelihood approach fit to the fixed effects model for each species group. The covariance structure was selected using AIC_c rankings (Burnham and Anderson 2002) in program R (R Development Core Team 2006).

After selecting the covariance structure, we ran 11 candidate models for each species and species group. Candidate models were additive combinations of plot, patch, and landscape variables we considered to be biologically likely. We ran models using the maximum likelihood approach and specifying a Poisson distribution. Initially, models were run separately for adults and juveniles of each group. If the top models were the same for both age groups, the models were run again after pooling captures by age. To the top-ranked model in each group we added time (year) both as a linear trend and as a factor; the best-supported time variable was included in the top model(s). Models were ranked using AIC_c .

Effect of harvest age on capture rate

We were also interested in the effect of harvest age on the capture rates of each species group. We modeled capture rate by harvest age, again using the mixed-effects approach to account for possible dependence of observations from the same sites. Models were run by species habitat group to determine overall trends by guilds.

Temporal patterns in the avian community

We evaluated the avian community over time using five metrics: species richness, Simpson and Shannon indices of species diversity, and two conservation value indices – one based on abundance and another based on detection. Species richness was calculated

as the number of species observed per site/year due to problems with bootstrap and jackknife estimates of species richness. In addition, Evans et al. (2008) found that using observed species richness rather than nonparametric estimators of species richness did not alter their results or conclusions. Shannon index of species diversity (H' ; Shannon 1948) was calculated as:

$$H' = -\sum_{i=1}^n p_i \ln p_i, \quad (1)$$

where n is the number of species detected, n_i is the number of individuals detected for species i , and p_i is the ratio of individuals of species i to the total number of individuals detected. The Simpson's index of species diversity (λ ; Simpson 1949) was calculated as:

$$\lambda = \frac{\sum_{i=1}^n n_i(n_i - 1)}{N(N - 1)}, \quad (2)$$

where the parameters are the same as for the Shannon index with the addition that N is the total number of individuals detected. Because diversity indices have been criticized for assuming more diverse systems are preferable regardless of species composition (Nuttall et al. 2003), we also calculated conservation value indices to better reflect the conservation importance. For the conservation value index, we used the Partners in Flight conservation priority species assessment scores (Carter et al. 2000; Rocky Mountain Bird Observatory 2002) from the Appalachian Mountains region to derive a categorical rank for each species. The rank was assigned using the categorical ranking algorithm developed by Beissinger et al. (2000) and modified in Nuttall et al. (2003).

Each species we banded was assigned to one of five categories: 0 = not native to region, 1 = not at risk, 2 = species of low concern, 3 = species of moderate concern, and 4 =

species of high concern. The ranks were then used in determining the conservation value index for each site-year combination using the formula:

$$CV = \sum_{i=1}^S (a_i w_i), \quad (3)$$

where S is the number of species in the community, a_i is the number of individuals of species i detected, and w_i is the weighting factor (rank) for species i (Nuttall et al. 2003).

With this method, we assumed that detection rates were constant across sites and years but not that detection rates were uniform across species. Because this method was sensitive to abundance and capture rates differed among species, we also calculated a conservation value index using only detection and non-detection. Using this method, a_i in equation 3 was substituted with a 1 if a species was detected at a site in a given year and a 0 if it was not detected. We called this method “conservation value index - detection” and the former method “conservation value – abundance.”

To test for relationships between harvest age in metrics of community diversity and value, we used linear mixed effects model with site as the random effect, each of the community metrics as the response variable, and harvest age as the explanatory variable. Models were ranked using AIC adjusted for small sample size (AIC_c ; Akaike 1973).

Results

Banding

Between 2002 and 2006, we banded 2890 shrubland specialists (1143 HY, 1747 AHY), 2912 shrubland generalists (1385 HY, 1527 AHY), and 3493 forest specialists (1701 HY, 1792 AHY) over 17,496 net hours (Table 4.1). The most commonly captured shrubland specialist species were the yellow-breasted chat, blue-winged warbler, and prairie

warbler; the most common shrubland generalists were the gray catbird, hooded warbler, and indigo bunting. For forest specialists, the most commonly captured species were the ovenbird, worm-eating warbler, red-eyed vireo, scarlet tanager, and wood thrush.

Principal component analyses

Using the three principal component analyses, we reduced the number of habitat variables from 11 to seven. The first three principal components for the four plot-level variables accounted for 85% of the variance in the habitat variables, the first two principal components for the three patch-level variables accounted for 80% of the variance, and the first two principal components for four landscape-level variables accounted for 96% for the variance (Table 4.2). Overall, these results indicate low-to-modest correlations among the plot and patch level variables and strong correlations among the landscape level variables. Because the landscape variables were percentages of land cover type within a 1 km radius, they were expected to be highly correlated.

Two pairs of variables recorded at the plot level (stem density and woody vegetation height and stem density and Japanese honeysuckle) were weakly correlated with one another. Stem density was inversely related to canopy height ($r = -0.26$) and positively related to the presence of Japanese honeysuckle ($r = 0.15$).

Spatial modeling

The covariance structure selection suggested capture rates for shrubland generalists and specialists were correlated across years and by site whereas capture rates for forest specialists were correlated only by site (e.g. for forest specialists, capture rates in year $t + 1$ were not correlated with capture rates in year t). Models using an autoregressive covariance structure received more support for both shrubland specialists

and shrubland generalists whereas the compound symmetry covariance structure received more support for forest specialists.

For shrubland specialists and generalists overall, both plot and landscape variables received strong support (Table 4.3, Table 4.4). Captures for specialists increased with higher stem density, the presence of Japanese honeysuckle, increased distance from habitat edge, and more shrubland habitat in the landscape. Captures for shrubland generalists increased with higher stem densities, presence of Japanese honeysuckle, increased distance from edge, and more shrubland and mature forest habitat in the landscape. For forest specialists, variables at all scales were important (Table 4.5). Capture rates for forest specialists increased with higher stem densities, presence of Japanese honeysuckle, increased distance from edge, increased harvest age, greater perimeter-to-area ratio, and higher % shrubland and mature forest in the landscape. Due to the number of models run, only models within $2 \Delta AIC_c$ of the top model for each species or group are presented in the tables.

Temporal patterns in the avian community

Capture rates by time-since-harvest varied by species habitat group. For forest specialists, capture rates were similar across harvest ages (Figure 4.1). The capture rates for shrubland specialists and generalists both declined with time since harvest but shrubland specialists declined at a higher rate than shrubland specialists. Compared to 4-year-old harvests, shrubland generalists had 60% lower capture rates in 10-year-old harvests while shrubland specialists had 71% lower capture rates in 10-year-old compared to 4-year-old harvests.

Harvest age was a strong predictor of species richness, both abundance and detection conservation value indices, and was a weak predictor for Simpson's and Shannon diversity indices as well (Table 4.6). Conservation value indices were greatest four-to-five years after harvest; both conservation value indices declined from six-to-ten years following harvest (Figure 4.2). The conservation value index based on detection was less sensitive to harvest age than conservation value based on abundance.

Discussion

Our results suggest that landscape composition and local vegetation characteristics, rather than patch size, have the strongest influence on bird communities in regenerating clearcuts. For shrubland specialists and generalists, capture rates were positively associated with local vegetation density, including the invasive Japanese honeysuckle, interior areas of harvests, and amount of shrubland habitat within the surrounding landscape. Shrubland generalists also seemed to respond positively to high percentage of mature forest in the landscape, most likely because some of these species also breed in mature forest habitat. Associations for mature-forest specialists were more variable among species, but, like the shrubland species, they also tended to respond positively to vegetation density and distance from mature forest edge. Forest specialists did not appear to be influenced by harvest age as were shrubland specialists and generalists, both of which declined after a peak at 4 years post-harvest.

For shrubland specialists and generalists (with the exceptions of northern cardinals and adult hooded warblers), capture rates were higher farther from habitat edge. Additional research in this system (Chapters 2 and 3) indicates lower densities in edge

habitat can be explained by passive displacement, a mechanism whereby non-use of adjacent habitat results in displacement from edge borders leading to lower densities near edges (King et al. 1997, Fletcher and Koford. 2003). Hooded warblers and northern cardinals both nest in edge habitat, making it likely that these species preferentially used habitat close to the mature forest edge.

In general, capture rates were highest for both shrubland specialists and generalists at plots with high stem density, colonization by Japanese honeysuckle, and low woody vegetation. However, stem density was weakly correlated with both the presence of Japanese honeysuckle ($r = 0.15$) and vegetation height ($r = -0.26$). High stem density and low woody vegetation are characteristics associated with the shrubland bird community (Askins et al. 2007), so it is not surprising that capture rates were higher in these areas.

Forest specialists varied in their responses to plot variables. Some species appeared insensitive to all plot level variables (ovenbird and Kentucky warbler) or had ambiguous relationships (wood thrush and worm-eating warbler). Whereas as shrubland species had the highest capture rates at plots with vegetative characteristics commonly associated with known shrubland bird habitat needs, the habitat associations of mature forest species in shrubland habitat during the post-breeding period are less well-known. Some evidence suggests these species are seeking low, dense vegetative cover during the post breeding season, possibly for food resources and/or concealment from predators (Pagen et al. 2000, Yahner 2003). Possibly, for some mature forest species, all plots in the patch provided sufficient low, dense cover, resulting in these species being less responsive to plot-level variables. Mature forest bird capture rates were constant across

harvest ages, which suggests mature forest species are not as sensitive to changes in vegetative structure. Interestingly, the red-eyed vireo and scarlet tanager also had higher capture rates with increased distance from forest edge. Given that these species do not breed in shrubland habitat, passive displacement is unlikely to be a mechanism driving this relationship. Potentially, these species perceived higher risk in edge habitat or were tracking a resource more abundant in the interior.

Capture rates of shrubland-breeding species increased with the amount of shrubland habitat in the landscape whereas patch level variables, including harvest area, received little support in explaining capture rates. Additional research in the same system documented fairly frequent movement among patches (Chapter 5). Potentially, these movements could lead to higher capture rates in landscapes with numerous patches. Another, non-exclusive possibility is that bird densities were higher in patches with high connectivity. Nesting in landscapes with high percentages of shrubland habitat may be beneficial for shrubland birds because the additional shrubland habitat provides cover for fledglings, which have documented making long-distance movements during the post-fledging period (Maxted 2001).

Capture rates for all species groups may have been affected by landscape context. Our patches were located in a heavily forested region. Mature forest accounted for the majority of the landuse (range 53-95%) within a 1 km radius of the banding sites. Most species in our study declined with the amount of agricultural and developed habitat in the landscape, with the exceptions of the wood thrush, northern cardinal, and white-eyed vireo. Some shrubland-breeding species (e.g. field sparrow; Carey et al. 1994) are

known to be sensitive to urban development, so relationships with landscape-level variables may be different in a more urbanized or agricultural settings.

Few studies to date have examined the effect of scale on metrics of shrubland bird abundance. Askins et al. (2007) found that point count abundances of most shrubland specialists and generalists in Connecticut were best explained by plot level (low vegetation, few trees, and a high density of shrubs) variables. Patch characteristics (opening size) and landscape variables (amount of urban land use within 1 km) did receive some support but only for the eastern towhee and gray catbird, respectively. The importance of plot characteristics is consistent with our study but we had more support for landscape characteristics. Askins et al. (2007) did not find any variables that adequately explained variation in point count abundances of forest specialists. However, our study differed from theirs in that we sampled during the late and post-breeding period, and used capture rates rather than point count observations. Mature forest birds were uncommon in our sites until early to mid June (Lehnen, unpublished data), when mature forest species begin to fledge young.

We assumed detection probability was constant across sites and years and thus declines in capture rates were the result of lower usage of habitat rather than lower capture probabilities. Ballard et al. (2004) found that capture rates of the breeding community decreased after the initial year. If this were the case in our system, we would have expected to observe a decrease in the capture rates of both shrubland specialists and generalists, which had high site fidelities (minimum of 0.4-0.8 for most species, Chapter 1), but we would not have expected capture rates to decrease over years for mature forest specialists because we captured primarily new individuals each year. However, our

observed declines in capture rates of shrubland specialists and generalists are consistent with observed declines in spot mapping in a concurrent study (Chapter 2). These declines are also consistent with expected decreases in shrubland avian densities as the vegetation matured; Keller et al. (2003) found that species richness in the northeast peaked six years post-harvesting. Although a proportion of the decreased capture rates over years may have been due to net avoidance by individual birds, the decreased capture rates are consistent with predicted decreased use by birds as the vegetation in the sites matured.

As illustrated in this and other studies, habitat use by shrubland-breeding songbirds declines rapidly in the years following harvest. Our study also supports the importance of landscape connectivity to shrubland species; capture rates for both shrubland specialists and shrubland generalists were highest in landscapes with more shrubland habitat. Given a system in which the majority of shrubland habitat is created by forest harvesting, harvests should occur at intervals frequent enough to insure adequate habitat is available during all time periods. A rapidly shifting mosaic of clustered early-successional habitat patches within a mature forest matrix may be the best management scenario for shrubland species.

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Species	Species Code	Breeding habitat group	Mean # individuals/100 net hours	SD
Ovenbird	OVEN	Forest specialist	5.3	4.0
Yellow-breasted chat	YBCH	Shrubland specialist	5.1	5.2
Blue-winged warbler	BWWA	Shrubland specialist	4.6	5.1
Worm-eating warbler	WEWA	Forest specialist	4.4	4.0
Red-eyed vireo	REVI	Forest specialist	4.1	4.8
White-eyed vireo	WEVI	Shrubland specialist	4.0	4.0
Gray catbird	GRCA	Shrubland generalist	3.2	4.4
Hooded warbler	HOWA	Shrubland generalist	3.2	3.7
Indigo bunting	INBU	Shrubland generalist	3.0	3.8
Prairie warbler	PRAW	Shrubland specialist	2.8	4.3
Scarlet tanager	SCTA	Forest specialist	2.2	3.7
Wood thrush	WOTH	Forest specialist	2.1	3.0
Kentucky warbler	KEWA	Forest specialist	2.0	2.6
Common yellowthroat	COYE	Shrubland generalist	1.7	3.1
Eastern towhee	EATO	Shrubland generalist	1.7	2.4
Northern cardinal	NOCA	Shrubland generalist	1.4	2.0
Field sparrow	FISP	Shrubland generalist	1.3	2.9
American goldfinch	AMGO	Shrubland generalist	1.1	2.7

Table 4.1. Capture rates for songbird species in 13 shrubland patches in Ohio during the late- and post-breeding period (15 June to 17 August). Species were grouped according to breeding habitat associations: open shrubland (“shrubland specialist”), shrub habitat both with and without a tree canopy (“shrubland generalist”), and closed-canopy forest (“forest specialist”).

	Plot 1	Plot 2	Plot 3	Patch 1	Patch 2	Landscape 1	Landscape 2
Percent of variance explained	0.357	0.255	0.235	0.515	0.286	0.671	0.294
Plot PCA							
Stem density	-0.633	-0.367					
Vegetation height	0.603	0.122	0.508				
Japanese honeysuckle	-0.434	0.267	0.806				
Distance from edge	-0.215	0.822	-0.301				
Patch PCA							
Harvest age				0.623	-0.367		
Clearcut area				-0.636	0.276		
Perimeter-to-area ratio				0.455	0.888		
Landscape PCA							
% shrubland						0.237	0.848
% mature forest						0.501	-0.524
% development						-0.582	
% agricultural						-0.595	

Table 4.2. Results of principal component analyses for variables measured in 13 shrubland patches in southeastern Ohio. Variables were recorded at three spatial scales: plot scale (variables sampled within 20 m diameter survey plot), patch scale (variables associated with the forest opening), and landscape scale (variables associated with the area within 1 km of the banding site). Factor scores are shown for each independent variable for principal components that explained a high percentage of the variance.

Model	Species	AIC _c	Δ AIC _c	K	w _i	Captures increase with
-Plot1+Landscape1+y	PRAW	627.8	0.00	8	0.53	Stem density, JH, distance to edge, % shrubland and forest
-Plot1+ Landscape1+ Landscape2+y		628.2	0.40	9	0.43	Stem density, JH, distance to edge, % shrubland
-Plot1- Landscape1+ Landscape2+y	WEVI	623.3	0.00	9	0.69	Stem density, JH, distance to edge, % agricultural, development, and shrubland
-Landscape1+ Landscape2+y		625.0	1.70	8	0.30	% agricultural, development, and shrubland
-Plot1+ Landscape1+ Landscape2-Y	YBCH	603.9	0.00	6	1.00	Stem density, JH, distance to edge, % shrubland
-Plot1+ Landscape1+ Landscape2-Y	BWWA HY	583.6	0.00	6	0.52	Stem density, JH, distance to edge, clearcut area, % shrubland and forest
-Plot1+ Landscape1-Y		584.7	1.14	5	0.30	Stem density, JH, distance to edge, % shrubland and forest
-Plot1+ Landscape1-Y	BWWA AHY	588.1	0.00	5	0.51	Stem density, JH, distance to edge, % shrubland and forest
-Plot1+ Landscape1+ Landscape2-Y		588.2	0.06	6	0.49	Stem density, JH, distance to edge, % shrubland
-Plot1+ Landscape1+ Landscape2-Y	Group overall	919.4	0.00	6	1.00	Stem density, JH, distance to edge, % shrubland

Table 4.3. Generalized linear mixed-effects models for the effect of plot, patch, and landscape variables on capture rates of shrubland specialist songbirds in 13 shrubland patches in Ohio during 2002-2006. Y = linear year effect, y = captures vary by year, HY = juvenile, AHY = adult, JH = presence of Japanese honeysuckle. Species codes given in Table 4.1.

Model	Species	AIC _c	Δ AIC _c	K	w _i	Captures increase with
-Plot1+Landscape1+Landscape2-Y	AMGO	447.2	0.00	5	0.52	Stem density, JH, distance to edge, % shrubland
-Plot1+Landscape1-Y		447.6	0.40	4	0.42	Stem density, JH, distance to edge, % shrubland and forest
-Plot1+Landscape1+Landscape2-Y	COYE	509.1	0.00	6	0.85	Stem density, JH, distance to edge, % shrubland
-Plot1+Landscape1-Landscape2-Y	EATO	504.3	0.00	6	0.59	Stem density, JH, distance to edge, % forest
Landscape1- Landscape2-Y		505.1	0.80	5	0.39	% forest
-Plot1+Landscape1+Landscape2-Y	FISP	437.9	0.00	6	0.98	Stem density, J. honeysuckle, distance to edge, % shrubland
-Plot1-Y	GRCA	641.3	0.00	4	0.39	Stem density, JH, increased distance to edge
-Plot1+Plot2-Y		642.3	1.00	5	0.23	JH, distance to edge
-Plot1+Landscape1-Y		643.2	1.90	5	0.15	Stem density, JH, distance to edge, % shrubland and forest
-Plot1+Landscape1+Landscape2-Y	INBU	624.8	0.00	6	0.89	Stem density, JH, distance to edge, % shrubland habitat
Plot1	NOCA	489.6	0.00	6	0.41	Vegetation height
Plot1-Landscape1		490.1	0.50	7	0.32	Vegetation height, % development and
Plot1+Plot2		491.2	1.60	8	0.18	Vegetation height

Table 4.4. Generalized linear mixed-effects models for the effect of plot, patch, and landscape variables on capture rates of shrubland generalist songbirds in 13 shrubland patches in Ohio during 2002-2006. Y = linear year effect, y = captures varied by year, HY=juvenile, AHY=adult, species codes given in Table 4.1. (Continued)

Table 4.4 continued

Model	Species	AIC _c	Δ AIC _c	K	w _i	Captures increase with
Plot1+Landscape1-Landscape2	HOWA	499.9	0.00	5	0.56	Vegetation height, % forest
Landscape1-Landscape2	AHY	500.7	0.75	4	0.39	% forest
Landscape1-Landscape2	HOWA	534.3	0.00	4	0.61	% forest
-Plot1+Landscape1- Landscape2	HY	535.3	1.05	5	0.36	Stem density, JH distance to edge, % forest
-Plot1+Landscape1-Y	Group overall	823.5	0.00	5	0.60	Stem density, JH, distance to edge, % shrubland and forest
-Plot1+Landscape1+Landscape2 -Y		825.2	1.70	6	0.26	Stem density, JH, distance to edge, % shrubland

Model	Species	AIC _c	Δ AIC _c	K	w _i	Captures increase with
Null	KEWA	553.9	0.00	2	0.32	
Landscape1		555.4	1.50	3	0.15	% shrubland and forest
Plot1		555.5	1.60	3	0.14	Vegetation height
Landscape1+ Landscape2		555.6	1.70	4	0.14	% shrubland
Landscape1- Landscape2+Y	OVEN	544.8	0.00	7	0.90	% forest
-Plot1+Landscape1	REVI	794.2	0.00	4	0.68	Stem density, JH, distance to edge, % shrubland and forest
-Plot1+ Landscape1- Landscape2+y	SCTA	608.1	0.00	8	0.98	Stem density, JH, distance to edge, % forest
-Landscape1- Landscape2+y	WOTH	569.3	0.00	8	0.57	% development and agriculture
Plot1- Landscape1- Landscape2+y		569.9	0.60	7	0.43	Vegetation height, % development and
Plot1+ Plot2+ Plot3+y	WEWA	552.8	0.00	9	0.54	Vegetation height, JH
-Plot1+ Patch1+ Landscape1+y	HY	554.8	2.00	9	0.20	Stem density, JH, distance to edge, harvest age, perimeter-to-area, % shrubland and forest
Landscape1+ Landscape2+Y	WEWA	504.7	0.00	5	0.64	% shrubland
Plot1+ Landscape1+ Landscape2+Y	AHY	506.0	1.26	6	0.34	Vegetation height, % shrubland
-Plot1+ Landscape1- Landscape2+y	Group	684.7	0.00	9	0.69	Stem density, JH, distance to edge, % forest
-Plot1+ Patch1+ Landscape1+y	overall	686.4	1.70	9	0.29	% forest

Table 4.5. Generalized linear mixed-effects models for the effect of plot, patch, and landscape variables on capture rates of forest specialist songbirds in 13 shrubland patches in southeastern Ohio during 2002-2006. Y = linear year effect, y = captures varied by year, HY=juvenile, AHY=adult, JH = presence of Japanese honeysuckle. Species codes given in Table 4.1.

Index	Model	AIC _c	Δ AIC _c	<i>K</i>	<i>w_i</i>	$\beta_{\text{harvest age}}$ (SE)
Richness	Harvest age	267.26	0.00	2	0.98	-1.395 (0.291)
	null	275.56	8.30	1	0.02	NA
Simpson	null	-276.23	0.00	1	0.67	NA
	Harvest age	-274.81	1.41	2	0.33	-0.001 (0.001)
Shannon	null	-48.57	0.00	1	0.55	NA
	Harvest age	-48.19	0.39	2	0.45	-0.016 (0.012)
CVI-a	Harvest age	650.04	0.00	2	1	-171.508 (18.867)
	null	677.61	27.57	1	0	NA
CVI-d	Harvest age	388.8	0.00	2	0.99	-4.795 (1.001)
	null	398.43	9.63	1	0.01	NA

Table 4.6. Mixed-effects models for the effect of harvest age of metrics of species richness, species diversity, and conservation value. Richness = observed species richness, Simpson = Simpson's species diversity, Shannon = Shannon diversity index, CVI-d = Conservation value index - density, CVI-a = Conservation value index - abundance. Beta estimates for harvest age (SE) shown for each model including harvest age. Metrics calculated from banding data collected in 13 shrubland patches in southeastern Ohio during 2002-2006.

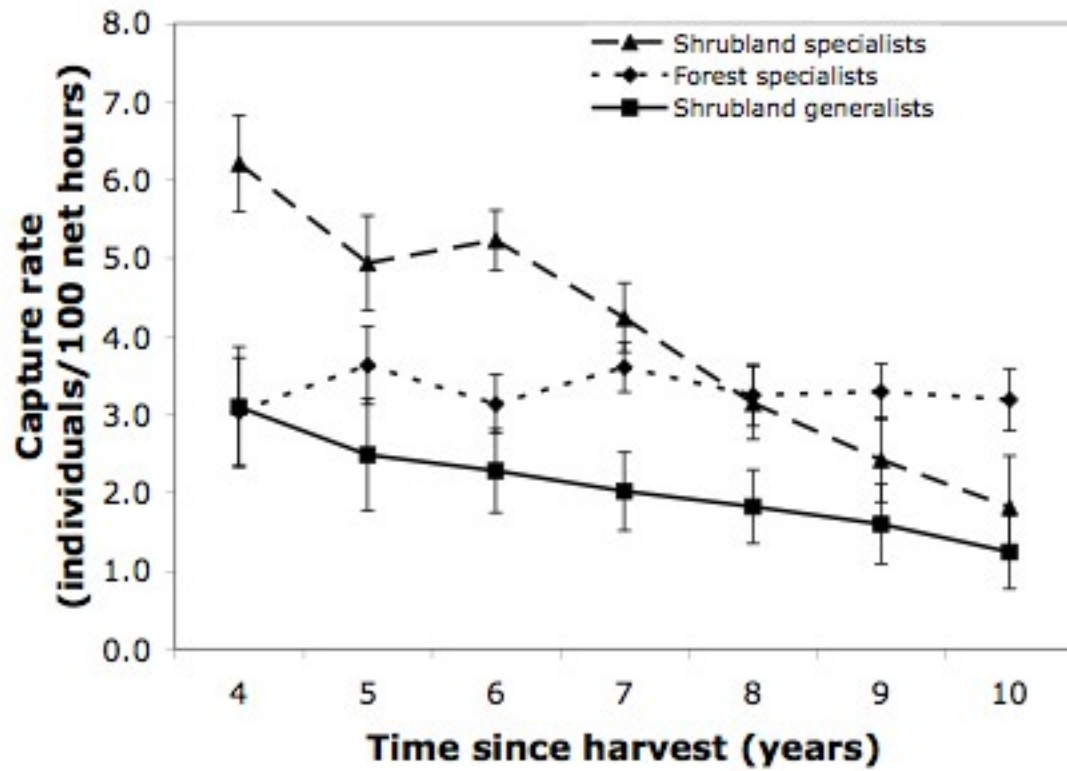


Figure 4.1. Capture rates by harvest age for songbird species in 13 shrubland patches in Ohio during the late- and post-breeding period (15 June to 17 August). Songbirds classified into for three categories: shrubland specialists, forest specialists, and shrubland generalists. Bars show ± 1 standard error.

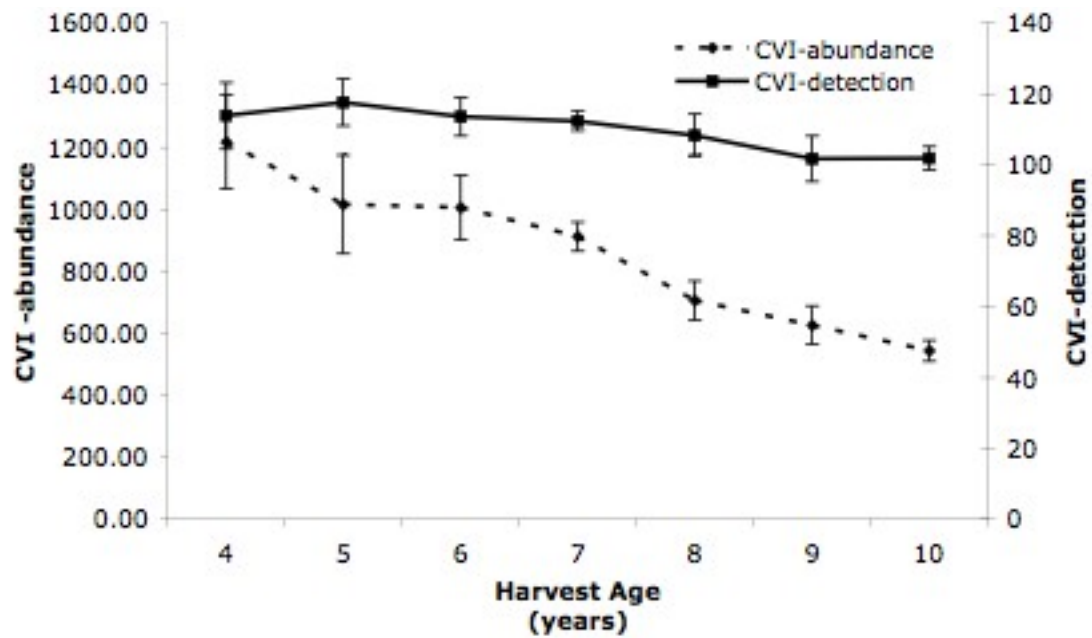


Figure 4.2. The effect of harvest age on two conservation value indices for a songbird community in a shrubland system. Metrics calculated from banding data collected measured between 2002-2006 in 13 shrubland patches in southeastern Ohio. Bars show ± 1 standard error.

CHAPTER 5

DISPERSAL, INTER-PATCH MOVEMENTS, AND SURVIVAL IN A SHRUBLAND BREEDING BIRD COMMUNITY ABSTRACT.

ABSTRACT. Dispersal events can affect the distribution, abundance, population structure, and gene flow of animal populations, but few studies have collected empirical data on long-distance movements due to the inherent difficulty of tracking individuals across space. We documented natal and breeding dispersal of shrubland birds among 13 study sites in a 1000 km² area in southeast Ohio, USA. In addition, we radio-marked and tracked 37 adult males of one shrubland specialist, the Yellow-breasted Chat (*Icteria virens*). We banded 1925 juveniles and 2112 adults of nine shrubland species between 2002 and 2005. Of these, 33 (1.7%) juveniles were encountered in subsequent years (2003-2006) as adults (natal dispersal) and 442 (20.9%) birds initially banded as breeding adults were reencountered in subsequent years (breeding dispersal). Apparent survival of juvenile shrubland birds on their natal patches was 0.024 (95% CI 0.016-0.036). When survival rates were adjusted for the probability of detection, 21% of juveniles returned to their natal patches compared to 78% of adult birds showing fidelity to the patch in which they were originally captured. We also used our estimates of natal dispersal and annual

apparent survival to estimate true survival of 0.11 (95% CI 0.07-0.18) for juveniles in their first year; however, this estimate was only applicable for birds dispersing within 7 km of their natal patches. Inter-patch movements of radio-marked Yellow-breasted Chats were not uncommon, with 13 of the 37 males located in more than one habitat patch. Considering the frequency of short-distance (<875 m) movements observed clustering of patches might facilitate usage of shrubland habitat.

Key words: breeding dispersal, Icteria virens, natal dispersal, Ohio, shrubland

Optimal management of declining species requires knowledge of the demographic parameters that affect the long-term viability of these populations. Animal movements at large spatial scales can affect the distribution, abundance, extinction and colonization rates, population structure, and gene flow of populations (Colbert et al. 2001, Bowne and Bowers 2004, Dale et al. 2006). However, few empirical data have been collected on long distance movements due to the practical constraints involved in tracking individuals across space (Dale et al. 2006, Hosner and Winkler 2007). Natal dispersal is the movement of juvenile birds from their natal patches to their first breeding territories whereas breeding dispersal is the movement of adult birds between breeding territories either in sequential years or within a breeding season. Natal and breeding dispersal distances of birds have been reported to range from several hundred meters to a few kilometers (Greenwood and Harvey 1982, Paradis et al. 1998) but much larger movements have also been documented (Marzluff and Balda 1989, Moore and Dolbeer

1989, Veit 2000). Baker et al. (1995) developed a method to correct for biased dispersal estimates by incorporating habitat area and sampling design.

Dispersal rates and distances will depend on the perceptual range of each species (Zollner 2000, Olden et al. 2004) and its locomotory patterns (Dale et al. 2006).

Individuals are expected to minimize the time spent searching for new habitat and so minimize costs incurred. The timing of these dispersal movements for habitat selection remains unclear. Although there is some evidence that individuals use environmental and social cues encountered early in the breeding season to select that season's territory (Eadie and Gauthier 1985, Reed and Oring 1992, Mönkkönen et al. 1999), studies also suggest post-breeding movements during the previous year play an important role in habitat selection. Under this "prospecting" scenario, juvenile and adult birds explore patches during the period between the end of the breeding season and migration to assess habitat quality for next year's territory selection (Brewer and Harrison 1975, Adams and Brewer 1981, Morton et al. 1991, Reed et al. 1999, Pärt and Doilgez 2003, Nocera et al. 2006, Parejo et al. 2007).

Our objective in this study was to document natal and breeding dispersal of shrubland-breeding birds, populations of which have been declining since the 1960s (Hunter et al. 2001, DeGraaf and Yamasaki 2003). We also documented the movements of one shrubland specialist, the Yellow-breasted Chat (*Icteria virens*), to determine the frequency of inter-patch movements during the breeding season. In addition, we used our data on breeding dispersal to estimate patch fidelity of adult birds and philopatry of juveniles. We also wanted to document patch characteristics associated with dispersal to make management recommendations for habitat creation. Knowledge of movement

rates, dispersal distances, and habitat preferences for this suite of declining species will help to determine the habitat types and spatial arrangements of patches that will maximize population viability.

METHODS

Study Area. our study sites were located in a 1000 ha (28×44 km) area in southeast Ohio, USA on Zaleski State Forest (Athens and Vinton Counties) and New Page (formerly Mead-Westvaco) Forest Land (Athens, Vinton, and Jackson Counties) within the Ohio Hills Physiographic region (Fig. 1). The region is dominated by mature oak-hickory forests (~70% forest cover) and is perforated by regenerating clearcuts with small amounts of other non-forest land uses including agriculture, mining, and housing developments. Thirteen 4-10 year-old clearcut patches ranging from 4 to 18 ha were used between 2002 and 2006, although not all sites were used during all years. Two sites were dropped in 2004 due to mining activities and two additional sites were not used after 2003 and 2004, respectively, due to low capture rates. Dominant vegetation in the sites included saplings of the mature forest trees, predominately maple and yellow-popular, and blackberry (*Rubus* spp.), greenbrier (*Smilax* spp.), and sumac (*Rhus* spp.). We studied nine species of shrubland-breeding songbirds: White-eyed Vireo (*Vireo griseus*), Gray Catbird (*Dumetella carolinensis*), Blue-winged Warbler (*Vermivora pinus*), Prairie Warbler (*Dendroica discolor*), Common Yellowthroat (*Geothlypis trichas*), Yellow-breasted Chat (*Icteria virens*), Eastern Towhee (*Pipilo erythrophthalmus*), Field Sparrow (*Spizella pusilla*), and Indigo Bunting (*Passerina cyanea*).

Banding. We conducted mist-netting from June to mid-August 2002-2006 at 9-12 sites/year. At each site, nets were arranged in a 3 x 3 grid with nets at 20, 50, and 80 m from the mature forest edge and net lanes separated by 50 m. Sites were visited once per week for 9 weeks (15 June - 15 August) during 2002 and 2003, and once per week for 11 weeks (1 June – 15 August) during 2004 - 2006. We opened mist nets 30 minutes before sunrise (~0540 EST) and closed them 4.5 hours later. Age of birds captured (juvenile or adult) was determined as described by Pyle (1997). We assumed that juvenile birds were captured in their natal patches.

Radio-telemetry. To examine within-season movements of a shrubland specialist, we radio-marked 37 male Yellow-breasted Chats in 2005 and 2006 (19 and 18, respectively). We captured birds using passive netting and call-back tapes at three of the patches used in the constant-effort mist-netting. Radios transmitters (Holohil BD-2) were attached to adult male Yellow-breasted Chats using a figure-8 harness (Rappole and Tipton 1991) made of a non-irritating, biodegradable cotton material. Adult Yellow-breasted Chats range in mass from 22 to 29 g (Eckerle and Thompson 2001) and the transmitters weighed 0.90 g, which was 3.1-4.1% of the chat's total mass. To allow individuals time to adjust to transmitters, we waited 24 h after transmitter attachment to begin observations. Each individual was located twice per day and tracked with sequential locations at least 20 min apart during three time periods (morning [0530-0900], afternoon [1100-1500], and evening [1700-2000]) using a handheld receiver and a three-element Yagi antenna. We located each individual 3-4 days each week, which resulted in at least 40-50 locations per individual. Because the patches were located in heavily harvested regions, the three patches were separated from the closest edge of the nearest neighboring

shrubland patch by a swath of mature forest ranging in width from 70-100 m. We estimated distance moved as the distance from the center of a bird's home range (centroid) to the all extra-patch locations and calculated a mean distance moved over all extra-patch visits for each bird. We also tested for the effect of time of day (morning, afternoon, evening) on extra-patch visits using a chi-square test of the number of extra-patch locations to total locations for each time period.

Return rate and annual apparent survival. Natal return rate was determined as the number of adults captured during 2003-2006 that were originally banded as juveniles divided by the total number of juveniles banded during 2002-2005. However, the return rate itself is a conservative estimate of the number of individuals returning to their natal patch because it does not account for birds that returned but were overlooked (Sandercock 2006). To account for these individuals, we estimated annual apparent survival (ϕ) of juveniles in the year after capture for all shrubland birds captured between 2002 and 2005 using program MARK (White and Burnham 1999). Estimates of detectability (p) in all years and ϕ in all but the first year were estimated as species-specific parameters using data from shrubland birds initially banded as adults. The global model included effects of age, time, and species on ϕ . Age estimated ϕ separately for juveniles during their first year. Due to both lower survival and lower patch fidelity in juveniles compared to adults, we expected ϕ to be lower during a bird's first year than in subsequent years. We included models estimating first year ϕ of juveniles as both species-specific parameters and pooled across species. We estimated ϕ by year separately for each species for adult birds; we included year to account for differences among years and to account for lowered patch fidelity as the vegetation matured.

Adjusting dispersal for probability of encounter. We expected the probability of detecting an individual to decrease with distance from the original patch. This expectation was due to increasing habitat area with increased distance and the limited range of the study region. We followed the methodology of Baker et al. (1995) to correct for underestimation of dispersal events by weighting each dispersal event by the inverse of the probability of observing that event. We weighted the dispersal events in each category by dividing the observable dispersal events in that distance category by all possible dispersal events at that distance. To accomplish this, we delineated all shrubland habitat within a 7 km radius of each study site, which was the maximum observed dispersal distance in our study. Habitat was delineated using harvesting information obtained from Zaleaski State Forest and New Page Corporation and visual assessment of National Agriculture Imagery Program digital images. We then summed the total area of shrubland habitat from the center of each site in each of four distance categories (0-499 m, 500-2999 m, 3000 – 4999 m, and 5000-7000 m), and counted the number of mist-netting occasions (e.g., one site mist-netted for two years was two occasions) that fell within each of these categories for each site. We used the average ratio of sampling occasions to habitat area in each of the four distance categories to weight observations within that category.

Using this method and the estimate of annual apparent survival, we were also able to estimate survival of shrubland birds during their first year. To do this, we assumed that survival was constant, regardless of the dispersal distance from the natal patch. We estimated survival as $S = \phi/r$, where S = true survival of juveniles during their first year, ϕ = apparent survival of juveniles in their first year, and r = the percentage of surviving

birds returning to the same site or site fidelity. Site fidelity was the percentage of surviving juveniles that returned to their natal patches as estimated by the percentage of birds in the 0-499 m category corrected for probability of encounter. We report 95% confidence intervals around our adjusted estimates of survival.

Patch characteristics associated with dispersal. Because we were interested in patch characteristics and landscape context associated with movement to new patches, we compared age of patch and amount of shrubland habitat available within 500 m between initial and dispersal patches. We made two predictions regarding the role of patch characteristics in likelihood of occupancy. First, we predicted that birds would disperse from older to younger patches and, second, we predicted that birds would disperse from patches with less to more shrubland habitat available. We compared the amount of shrubland habitat available within a 500 m radius of a patch. We chose 500 m because the vast majority of movements we observed were within this distance. Due to our small sample size, we pooled natal and breeding dispersers across species and used a Wilcoxon matched-pairs signed-ranks test to compare initial and dispersal patches. Although we expected that natal and breeding dispersers might differ in dispersal distances and frequency, we expected the habitat selection between the two groups would be similar so we feel this pooling was justified. We also examined patch characteristics between initial patch and visited patch(es) for radio-marked Yellow-breasted Chats.

RESULTS

Return rates. Of the nine species commonly encountered during mist-netting and documented nesting in our patches, we banded 1925 juveniles (Table 5.1) and 2112

adults (Table 5.2) between 2002 and 2005. Thirty-three of these juveniles were encountered in subsequent years as adults (natal dispersal). Of these natal dispersers, 25 were recaptured in their presumed natal patch and eight were encountered as adults in a different patch. Twelve birds initially banded as breeding adults were recaptured in a patch other than their original capture patch (breeding dispersal) and an additional 430 individuals were encountered on the same site in subsequent years. All 12 of these breeding dispersers were captured as part of our standardized mist netting operations, five within the same season and seven in different years.

Movements of radio-tagged birds. Of the 37 birds monitored, we documented a mean of 1.4 patches used per bird with 13 individuals located in at least two habitat patches. Of these 13, three established territories in patches other than their original capture patch. Two of these three established their territories within 3 days of radio-marking, the third established a territory in a new patch 28 days after radio-marking, following the presumed failure of its nest. The mean distance moved by the 13 birds was 502 m (median = 531 m; Fig. 2) and the mean number of patches visited was 2.2. Time of day did not affect the frequency of extra-patch visits ($P = 0.79$), which occurred throughout the season with a median visit day of 2 June.

Natal and breeding dispersal. Natal birds appeared to disperse farther than breeding adults (Figs. 3 and 4). We observed 79% of the natal dispersers on their natal patches. However, after correcting for encounter probability, only 21% of second year birds returned to their natal patches. Similarly, 98% of adults encountered were recaptured in their initial patches but, correcting for probability of detection, only an estimated 78% of adults returned to their original patch. Because the probability of detection decreased

with increasing distance, observations farther from the original site were weighted more heavily than observations at or close to the original site.

Natal return rates and juvenile survival. The best model for natal return rates pooled return rates across species, though there was weak support for species-specific estimates (Table 5.3). The apparent annual survival rate for juvenile shrubland species, averaged across models, was 0.02 (95% CI 0.01-0.04). To estimate true survival for juveniles during their first year, we used the equation $S = \phi/r$ and obtained an estimate of 0.11 (95% CI 0.07-0.18). However, this estimate is applicable only for juveniles dispersing within 7 km of the study sites. Our probability of encountering individuals farther than 7 km was extremely low due to the limited of our study region.

Patch characteristics associated with dispersal. There was some evidence that natal and breeding dispersers tended to move from older to younger patches and much weaker evidence that birds dispersed to patches with more shrubland habitat available within a 500 m radius than in their natal patches. The average age of initial capture patches was 6.6 (SE 0.4) years versus 5.6 (SE 0.5) years for dispersal patches, showing some support for the prediction that birds tended to move to younger patches (One-sided test, $V = 55$, $df = 18$, $P = 0.057$). Likewise, we found evidence of a preference for younger patches by Yellow-breasted Chats during extra-patch visits. Patches visited by radio-marked male Yellow-breasted Chats were, on average, 5.5 years old versus 7.3 years for the home range patch ($z = 28$, $n = 12$, $P = 0.016$). The evidence for movements by dispersing birds to larger patches was weaker; initial patches contained an average of 12.9 (SE 2.2) ha of shrubland habitat within 500 m versus 14.1 (SE 1.9) ha of habitat available in dispersal patches ($z = 50.5$, $n = 18$, $P = 0.23$). Patches visited by radio-marked Yellow-breasted

Chats were of similar size (8.2 ha) to the home range patch (9.0 ha) ($z = 54$, $n = 12$, $P = 0.266$).

DISCUSSION

Within-season movement among patches was relatively common. We documented 35% (13 of 37) of male Yellow-breasted Chats making interpatch movements and movements might have been common among other shrubland species as well. Although we observed only five cases of shrubland-nesting birds moving between sites in the same season, the extremely low probability of capture suggests that within-season movement rates of individuals between patches might have been higher than documented. For example, one individual moved over 4 km in the same season. In addition, with two exceptions, sampling sites were separated by a minimum of 2 km, meaning that short-distance movements were likely to go undetected. Natal dispersers in our study appeared to move much farther than breeding dispersers, corresponding with the traditional view that long distance movements to new habitat patches occur during natal dispersal whereas breeding dispersal among adults is much more restricted (Greenwood and Harvey 1982, Paradis et al. 1998, but see Dale et al. 2006).

Our estimate of juvenile survival ($\phi = 0.11$ (95% CI 0.07-0.18)) was lower than reported in other studies (Anders and Marshall 2005, Fletcher et al. 2006), though there are few direct estimates of juvenile survival rates for songbirds. We suspect that our estimate is biased downward because it did not account for birds dispersing farther than 7 km, a distance beyond which we had very low probabilities of detection due to the limited range of our study. The corrected distribution of natal dispersal distances in our

study suggests that many juveniles might have settled more than 7 km from their natal sites. Based on estimates of adult apparent annual survival from our study system (Chapter 1) and assuming juvenile survival was 50% of adult survival (Greenberg 1980), juvenile annual survival could be in the range of 0.20 to 0.41. However, it may be that juvenile survival in our study system was actually extremely low. Maxted (2001) observed a survival rate of 0.39 for Yellow-breasted Chats in just the two months following fledging. Assuming this rate of survival for the first two months and a high, constant monthly survival rate (0.88) for the following 10 months results in 11.7% of juveniles surviving their first year (calculated as $0.39 * \exp[-0.12t]$, where $t = 1, 2, \dots, 10$ months). Additional post-fledging studies have found survival to vary widely; Powell et al. (2000) documented survival of 0.75 for Wood Thrush (*Hylocichla mustelina*) in Georgia through 14 weeks postfledging whereas Sullivan (1989) observed a survival rate of 0.32 for Yellow-eyed Juncos (*Junco phaeotus*) through 3 weeks postfledging. Given the range of survival estimates for just the 2-3 month postfledging period, a survival rate of 0.11 for a bird's first year may not be unlikely. our estimate of natal philopatry was extremely low (0.02 (95% CI 0.01-0.04)). However, Payne (1991) observed low (0.02-0.09) return rates for Indigo Buntings in southern Michigan so these rates may be typical for this group of species.

Although we documented intra-seasonal movements in Yellow-breasted Chats and suspect other species may make intra-seasonal movements among patches as well, we do not know the purpose of these movements. These movements may have been for the purpose of assessing patches for territory selection either within the same season or in future years. Jackson et al. (1989) found evidence consistent with the prediction that

within-season dispersal is based on nest predation avoidance in Prairie Warblers. If birds are likely to disperse between nesting attempts, periodically assessing neighboring territory quality may provide them with information needed to make a decision following nest failure. Alternatively, rather than evaluate habitat quality directly, birds could use the presence of conspecifics as an indication of territory quality (Ahlering and Faaborg 2006). The one individual observed defending territories in two different patches during the course of the same season visited the second patch over a period of several days before relocating. The tendency for birds to visit patches younger than their current patch also suggests that birds may have been evaluating patches for future territory suitability.

Another option is that these birds were seeking other resources, either food or extra-pair copulations. However, the expense involved in moving long distances would likely make foraging unprofitable. Mays and Ritchison (2004) found that it was female radio-marked Yellow-breasted Chats who left their territories to seek extra-pair copulations rather than the males. Conversely, for passerine species overall, both males and females have been documented making extra-territory forays for the sake of obtaining extra-pair copulations (Westneat and Stewart 2003). For Common Yellowthroats, Pedersen et al. (2006) found that both males and females forayed but that most (80%) extra-pair sires had territories adjacent to the social male. Similarly, both male and female Hooded Warblers (*Wilsonia citrina*) made extra-territorial forays (Neudorf et al. 1997, Stutchbury 1998), but territorial neighbors accounted for most of the extra-pair fertilizations (Stutchbury et al. 1994). Paternity studies of territorial passerines overall have found extra-pair fertilization by neighbors to be a consistent pattern (e.g. Black-throated Blue Warblers, *Dendroica carulescens*; Webster et al. 2001,

Yellow Warbler, *Dendroica petechia*, Yezerinac et al. 1995) the exception being Acadian Flycatchers (*Empidonax vireescens*) in a system where bird pairs were widely dispersed with few adjacent neighbors (Woolfenden et al. 2005). Although we cannot exclude the possibility that long distance extra-territorial forays were for the purpose of extra-pair copulations, the majority of research to date suggests that most extra-pair copulations in territory-dense systems like ours would be among neighbors. Given this evidence, we postulate that the inter-patch movements we observed by adult Yellow-breasted Chats were for the purpose of prospecting habitat for future territories.

Based on banding data from a subset of the study sites (Lehnen, unpublished data) and other studies (Dale et al. 2006), second-year birds arrive on the breeding grounds after older adults. It may be that second-year birds, by arriving later, use the presence of conspecifics as a gauge of habitat quality (Ward and Schlossberg 2004). Dale et al. (2006) suggested that Ortolan Buntings (*Emberiza hortulana*) often start their first year as adults by returning to their natal area to establish a territory. The authors also found that second-year males were frequently unsuccessful in attracting a mate to their first territory (94%) and would often change territories, settling in nearby patches.

Our observed rates of intra-patch movements are conservative. Given that each Yellow-breasted Chat was located only 10-12 times/week it is plausible that more than 13 of the 37 birds we tracked left their patch on occasion. Recall that our probability of reencountering a bird once it left its initial patch was extremely low. Although we were able to account for this low probability of detection within the study region, at distances greater than 7 km from our study sites we had almost no chance of encountering dispersing individuals. Because some birds will disperse beyond the limits of the study

area, it is understood that estimates of dispersal and survival calculated within the study area are underestimates (Baker et al. 1995). We also assumed that juveniles were originally captured in their natal patches. Maxted (2001) found that two shrubland species, the Yellow-breasted Chat and Gray Catbird, traveled a mean of 297 and 221 m, respectively, from their nests six weeks after fledging. Based on these movement rates and the size and distribution of patches in this study, the vast majority of juveniles captured during banding would have been captured in their natal patches.

Because dispersal can affect estimates of survival and reproductive rates, studies should be performed at scales large enough to capture dispersal movements (Clark et al. 2004). Future radio-telemetry studies would help to determine the frequency and distance associated with inter-patch movements. From our results, it did appear that birds readily moved among nearby patches (< 400 m). Clustering patches of shrubland habitat may reduce risks posed by movement among patches and also minimize disturbance to mature forest habitat.

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Species	# juveniles banded 2002- 2005	% (<i>n</i>) encountered as adults	% (<i>n</i>) encountered as adults at natal site
White-eyed Vireo	273	2.8 (7)	2.2 (6)
Gray Catbird	304	1.1 (3)	1.0 (3)
Blue-winged Warbler	353	3.4 (11)	2.3 (8)
Prairie Warbler	166	1.2 (2)	0.6 (1)
Common Yellowthroat	131	2.3 (3)	2.3 (3)
Yellow-breasted Chat	270	0.8 (2)	0.4 (1)
Eastern Towhee	170	1.8 (3)	1.2 (2)
Field Sparrow	103	0.9 (1)	0.0 (0)
Indigo Bunting	155	1.3 (2)	0.6 (1)
Total	1925	1.7 (33)	1.3 (25)

Table 5.1. Natal returns of shrubland birds initially banded between June and August 2002-2005 in southeastern Ohio.

Species	# adults banded 2002-2005	% (n) encountered 2003-2006	% (n) encountered at same site
White-eyed Vireo	285	23.5% (67)	23.2% (66)
Gray Catbird	189	4.2% (8)	4.2% (8)
Blue-winged Warbler	323	18.9% (62)	18.9% (61)
Prairie Warbler	269	14.1% (38)	13.0% (35)
Common Yellowthroat	128	32.0% (41)	32.0% (41)
Yellow-breasted Chat	464	19.8% (92)	19.2% (89)
Eastern Towhee	77	15.6% (12)	14.3% (11)
Field Sparrow	97	40.2% (39)	39.2% (38)
Indigo Bunting	280	29.3% (82)	28.9% (81)
Total	2112	20.9% (442)	20.4% (430)

Table 5.2. Adult returns of shrubland birds banded from June to August 2002-2005 in southeastern Ohio.

Model	ΔAIC_c^*	K	w_i
ϕ (juvenile (.) adult (species, (Common Yellowthroat and Prairie Warbler by t))) p (species)	0.00	25	0.93
ϕ (juvenile (species) adult (species, (Common Yellowthroat and Prairie Warbler by t))) p (species)	5.91	33	0.05
ϕ (juvenile (.) adult (species)) p (species)	8.32	19	0.01
ϕ (juvenile (.) adult (species, (Common Yellowthroat, Prairie Warbler, and Indigo Bunting by t))) p (species)	11.59	28	0.00
ϕ (juvenile (.) adult (species, (Common Yellowthroat, Prairie Warbler, Indigo Bunting, Yellow-breasted Chat by t))) p (species)	15.67	31	0.00

* $\text{Min } AIC_c = 2687.52$

Table 5.3. Model selection results for annual apparent survival of juvenile shrubland birds in southeastern Ohio ranked by ΔAIC_c

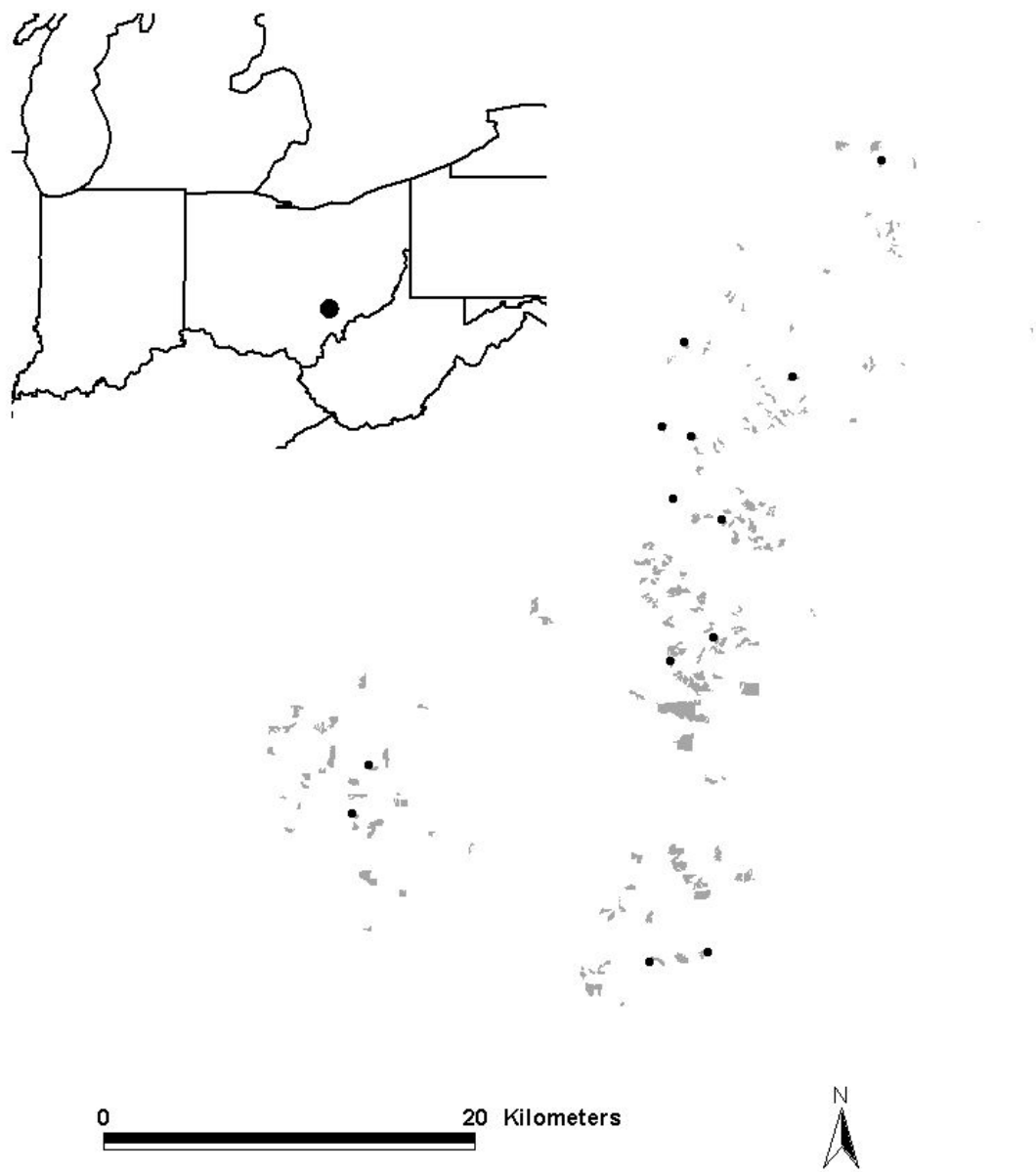


Figure 5.1. Map of study area showing study sites (dark circles) that were used between 2002-2006 and shrubland habitat (gray patches) in the region. Location of the study area in Ohio is indicated by the dark circle in the top left corner.

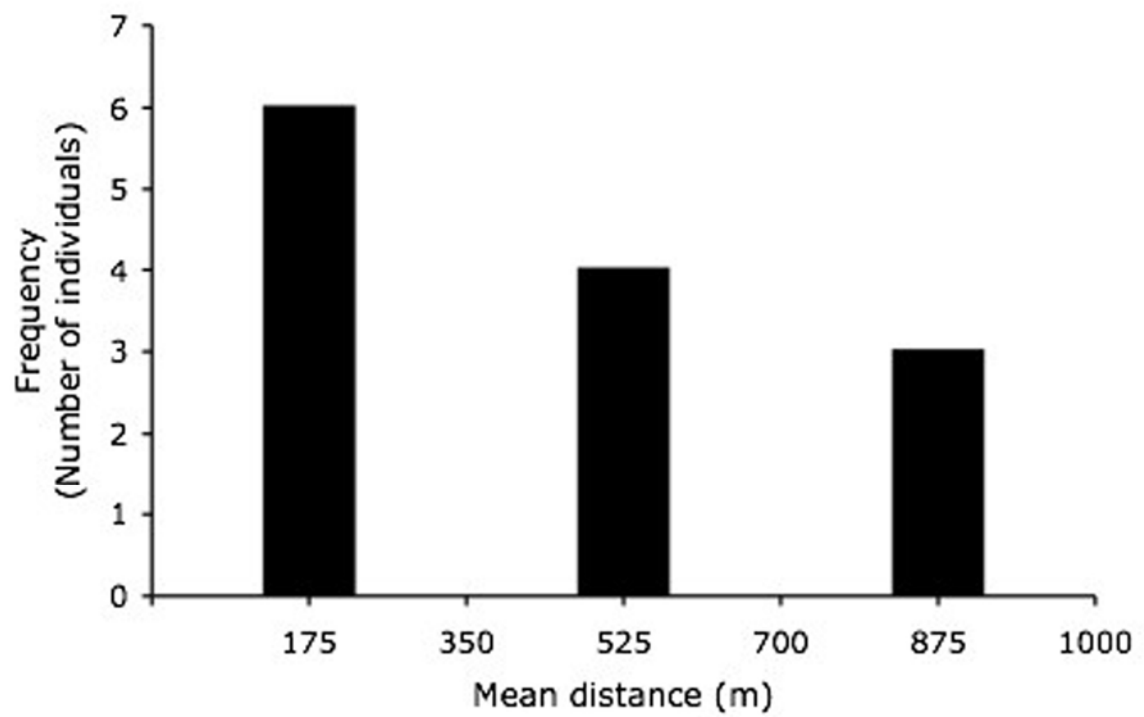


Figure 5.2. Mean distance traveled by radio-marked male Yellow-breasted Chats making inter-patch movements in Ohio during summer 2005-2006.

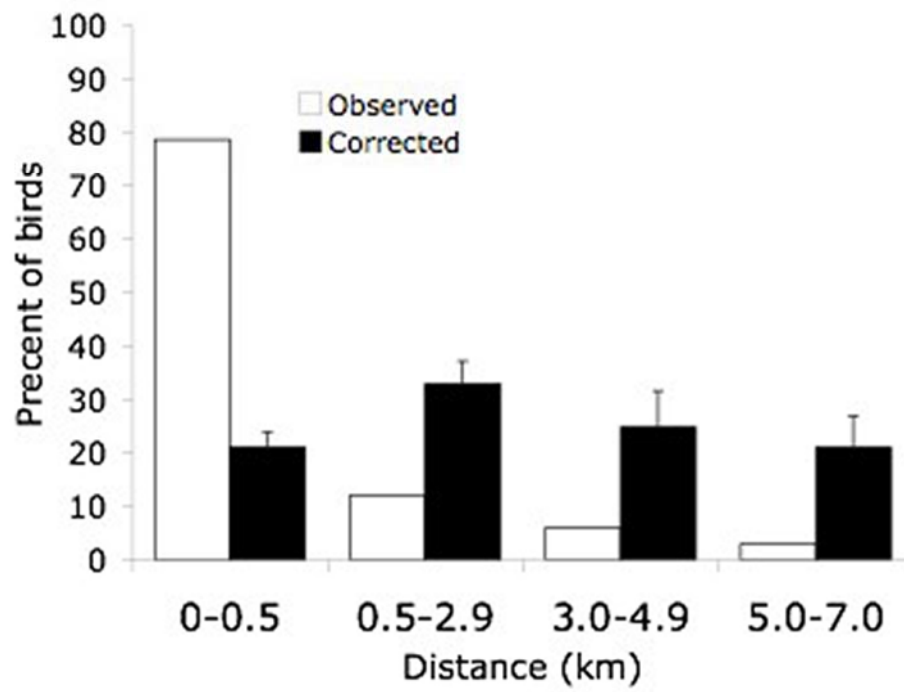


Figure 5.3. Natal dispersal of shrubland breeding birds in southeastern Ohio 2002-2006.

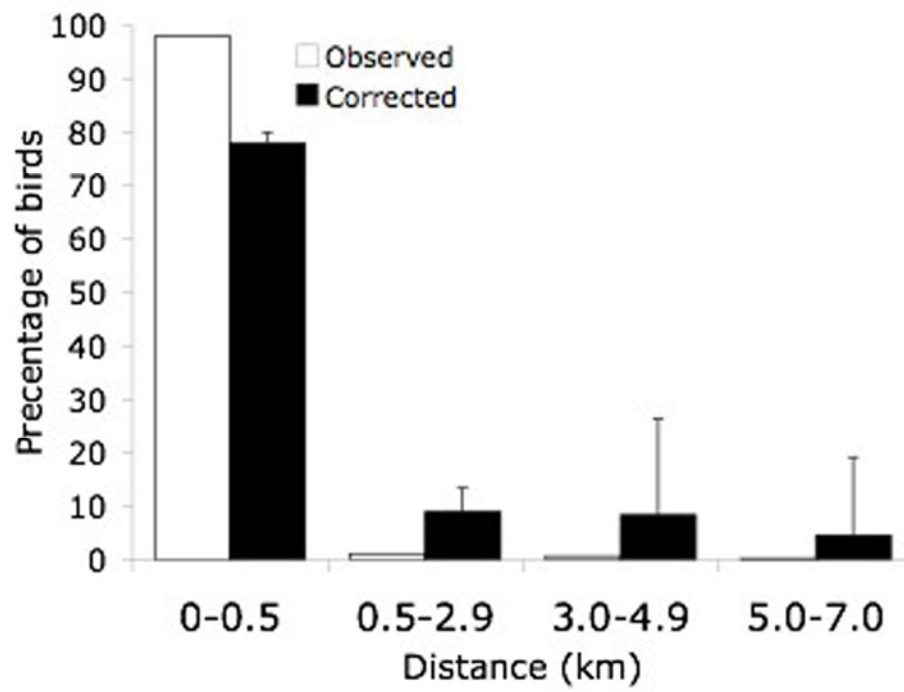


Figure 5.4. Breeding dispersal of shrubland-breeding birds in southeastern Ohio 2002-2006.

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APPENDIX A
ADDITIONAL INFORMATION

Site	Site Code	Study years		County	Ownership	Latitude	Size (ha)	Year Harvested	DI
		First	Last						
Bobcat	BO	2003	2006	Vinton	PI	39°08'N	16.1	1997	1.89
CCC	CC	2002	2006	Vinton	State	39°17'N	6.2	1997	1.63
Cemetery	CM	2002	2006	Jackson	PI	39°04'N	13.8	1996	1.18
Connaut Rd	CA	2002	2004	Athens	PI	39°23'N	6.5	1996	1.44
Gomer Davis	GD	2002	2003	Jackson	PI	38°59'N	14.6	1998	1.52
Green Gate	GG	2002	2006	Vinton	PI	39°13'N	2.9	1996	1.13
Kick Gate	KG	2003	2006	Vinton	PI	39°12'N	9.9	1999	1.49
Mead Gate	MG	2002	2003	Gallia	PI	38°59'N	13.8	1997	1.12
REMA	RE	2003	2006	Vinton	State	39°09'N	16.3	1999	1.13
Sand Hill	SA	2002	2006	Jackson	PI	39°05'N	12.3	1996	1.71
Webb Hollow	WH	2004	2006	Vinton	State	39°15'N	9.1	2000	1.31
Will Tract 2	W2	2002	2003	Vinton	State	39°15'N	5.4	1996	1.66
Will Tract 3	W3	2003	2006	Vinton	State	39°15'N	5.2	1996	1.47

TABLE A.1. Study site information. Ownership: PI = Private industrial forest, State = State-owned forestland, DI = ratio of perimeter to area, defined as $\text{perimeter} / 2\sqrt{(\text{area} * \pi)}$.

Species	i	R_i	$j = 2$	m_{ij}		
				3	4	5
Common Yellowthroat	1	13	3	2	0	0
	2	26		10	2	0
	3	18			3	0
	$k = 4$	8				0
Prairie Warbler	1	24	13	1	0	0
	2	31		8	2	0
	3	27			13	2
	$k = 4$	21				5
White-eyed Vireo	1	20	10	3	1	0
	2	60		17	6	1
	3	56			17	5
	$k = 4$	39				17
Yellow-breasted Chat	1	90	44	3	5	1
	2	119		45	5	6
	3	101			37	14
	$k = 4$	65				18
Blue-winged Warbler	1	17	6	2	0	0
	2	40		14	2	1
	3	40			15	2
	$k = 4$	42				19
Indigo Bunting	1	26	6	2	0	0
	2	48		13	7	1
	3	38			9	4
	$k = 4$	24				8

Table A. 2. Capture-recapture matrices for six species of shrubland birds. Capture histories are for adult individuals considered “residents” – those individuals captured at least twice a week or more apart – between 2002-2006 in southeastern Ohio. R_i is the number of birds banded and released at each occasion $i = 1, \dots, k$. The triangular matrix indicates how many birds banded at each occasion i were reported in recovery interval j .

ID	Site	Year	Age	Start date	End date	<i>n</i>	MCP		Kernel Home Range				# of patches visited	# of locations outside of main patch
							Area (ha)	Perimeter (m)	95% area (ha)	50% area (ha)	Distance from edge (m)	Shape of kernel		
1	CC	2005	AHY	22-May	26-Jun	48	1.4	454	2.6	0.4	43	U	0	0
2	CC	2005	ASY	26-Jun	10-Jul	24	0.8	337	1.3	0.5	56	U	0	0
3	CC	2005	ASY	6-Jun	14-Jul	30	0.9	378	2.3	0.3	39	B	1	4
4	CC	2005	ASY	27-May	3-Jul	57	1.7	536	1.4	0.1	40	U	0	0
5	CC	2005	ASY	22-May	3-Jul	59	0.9	391	1.2	0.1	28	B	0	0
6	CC	2005	SY	27-May	7-Jun	16	0.4	299	0.7	0.1	34	B	0	0
7	CC	2005	SY	26-Jun	16-Jul	23	1.6	548	6.6	1.3	39	U	1	2
8	CC	2006	ASY	16-May	28-Jun	51	3.0	707	4.8	1.0	43	B	1	2
9	CC	2006	ASY	16-May	28-Jun	57	2.4	687	3.9	0.6	36	B	1	2
10	CC	2006	ASY	8-May	17-Jun	61	1.5	496	2.0	0.3	30	U	0	0
11	CC	2006	ASY	16-May	21-Jun	63	5.0	986	7.6	1.1	72	B	1	4
12	CC	2006	SY	8-May	17-Jun	61	1.5	480	1.4	0.1	64	U	0	0
13	KG	2005	ASY	20-May	25-Jun	32	1.0	383	10.8	2.0	75	U	1	6
14	KG	2005	ASY	24-May	1-Jul	45	0.8	352	1.6	0.3	14	U	0	0
15	KG	2005	ASY	4-Jun	8-Jul	51	0.7	362	3.3	0.9	30	U	0	0
16	KG	2005	SY	4-Jun	14-Jul	51	0.9	359	1.6	0.2	57	B	0	0
17	KG	2005	SY	24-May	4-Jul	51	1.0	406	4.1	0.9	55	U	1	2

Table A.3. Data on individual radio-marked Yellow-breasted Chats. Birds were adult males radio-marked May-June of 2005 and 2006 in southeastern Ohio. MCP = Minimum convex polygon, shape of kernel: U = unimodal, B = bimodal.

(Continued)

Table A.3 (continued).

18	KG	2006	AHY	28-May	8-Jul	69	1.3	423	3.5	0.9	52	U	1	2
19	KG	2006	ASY	12-May	11-Jun	47	1.6	529	1.9	0.5	53	U	0	0
20	KG	2006	ASY	11-Jun	25-Jul	53	1.6	478	14.8	3.1	60	U	0	0
21	KG	2006	ASY	12-May	21-Jun	60	1.8	528	1.1	0.1	27	U	0	0
22	KG	2006	SY	3-Jun	17-Jul	49	1.2	526	1.5	0.1	25	U	2	2
23	KG	2006	SY	28-May	11-Jul	57	5.2	887	21.0	4.0	44	U	1	2
24	RE	2005	AHY	24-May	8-Jul	63	5.2	271	0.8	0.1	43	U	0	0
25	RE	2005	ASY	17-May	27-Jun	57	5.8	292	0.7	0.1	28	B	0	0
26	RE	2005	ASY	4-Jun	15-Jul	62	1.5	462	1.9	0.3	70	B	0	0
27	RE	2005	ASY	17-May	27-Jun	65	1.3	434	2.4	0.4	17	U	0	0
28	RE	2005	ASY	23-May	6-Jul	68	1.1	430	1.1	0.1	30	U	0	0
29	RE	2005	SY	14-Jun	21-Jul	52	1.3	462	2.2	0.5	30	B	0	0
30	RE	2005	SY	23-May	30-Jun	57	1.1	452	1.8	0.2	96	B	0	0
31	RE	2006	ASY	29-Jun	3-Aug	48	1.2	449	2.2	0.3	22	U	0	0
32	RE	2006	ASY	7-May	16-Jun	60	1.6	551	0.6	0.1	63	U	0	0
33	RE	2006	ASY	22-May	7-Jul	61	1.9	551	3.1	0.4	31	U	2	5
34	RE	2006	ASY	7-May	16-Jun	63	7.8	1068	9.3	0.9	128	B	0	0
35	RE	2006	SY	2-Jun	10-Jul	39	1.6	556	3.1	0.5	89	U	0	0
36	RE	2006	SY	27-May	14-Jul	59	1.9	584	2.1	0.3	37	U	1	1
37	RE	2006	SY	6-Jun	19-Jul	61	1.0	392	1.1	0.1	67	U	0	0