

MINIMUM PATCH SIZE THRESHOLDS OF REPRODUCTIVE SUCCESS OF
SONGBIRDS

A Dissertation

by

JERROD ANTHONY BUTCHER

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

May 2008

Major Subject: Wildlife and Fisheries Sciences

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ABSTRACT

Minimum Patch Size Thresholds of Reproductive Success of Songbirds.

(May 2008)

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Arlington

Co-Chairs of Advisory Committee: Dr. R. Dean Ransom
Dr. Michael L. Morrison

Preservation of large tracts of habitat is often recommended for long-term population viability of area-sensitive species. Large tracts may not always be available. Smaller patches, though not able to contain a viable population individually, may contribute to overall regional population viability if within the small patches pairs could successfully reproduce. By definition, area-sensitive species should have a minimum patch size threshold of habitat below which they will not likely reproduce. Two potential causes for positive relationships between patch size and production are inverse relationships between patch size and brood parasitism and patch size and food availability. My objectives were (1) to determine the minimum patch size thresholds of reproductive success for golden-cheeked warblers (*Dendroica chrysoparia*), black-and-white warblers (*Mniotilta varia*), and white-eyed vireos (*Vireo griseus*); (2) to determine whether thresholds for occupancy, territory establishment by males, or pairing success were indicative of thresholds of reproduction; (3) to determine whether the proportion of pairs fledging brown-headed cowbird (*Molothrus ater*) young was related to patch size,

and (4) to determine the affects of patch size on food availability (i.e., arthropod abundance). The Vickery index of reproductive activity was used to determine reproductive activity of each male or pair and to quantify parasitism occurrences. I collected arthropods using branch clipping to assess the relationship between patch size and arthropod abundance. I found minimum patch size thresholds of reproductive success for golden-cheeked and black-and-white warblers, but not for white-eyed vireos. Minimum patch size of reproductive success was between 15 and 20.1 ha. Minimum patch size thresholds for occupancy, territory establishment by males, and pair formation were not consistent with thresholds for reproductive success. I found no relationships between patch size and cowbird parasitism or patch size and arthropod biomass. Conservation practices for target species based on thresholds of occupancy, territory establishment, or pair formation may not address issues of reproduction. The ability to identify thresholds of reproductive success for target species could be useful in conservation and management in multiple ways including setting goals for retention and restoration of a target species' habitat patch size.

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INTRODUCTION

It is often recommended that large tracts of habitat be preserved for long-term population viability of area-sensitive species (e.g., Wahl et al. 1990, Donovan et al. 1995, Beardmore et al. 1996). Large tracts may not always be available for preservation particularly in regions where most of the area is privately owned (e.g., Texas, where 94% of land is privately owned [Texas Parks and Wildlife Department 2007]). Smaller patches, though not able to maintain a viable population without emigration from outside sources, may contribute to overall regional population viability if within the small patches pairs could successfully reproduce. The question then is how large of a patch is required for successful breeding by an area-sensitive species. That is, what is the minimum patch size threshold above which reproduction will likely occur?

The concept of thresholds has pervaded ecology in various forms (e.g., Liebig's law of the minimum, Shelford's law of tolerance, carrying capacity, Hutchinsonian niche). Huggett (2005) defined ecological thresholds as points or zones at which relatively rapid change occurs from one condition to another. Due to the prevalence of habitat loss and habitat fragmentation throughout the world, researchers have been studying thresholds in landscape structure (e.g., With and Crist 1995, Jansson and Angelstam 1999, Huggett 2005, Denoël and Ficetola 2007).

Although the usefulness of identifying thresholds within landscapes for biodiversity and species assemblages is debatable (Lindenmayer and Luck 2005, Denoël and Ficetola 2007), identifying thresholds for target species appears to be practical and useful in conservation and management (Jansson and Angelstam 1999, van der Ree et al. 2003, Radford and Bennett 2004, Denoël and Ficetola 2004, Denoël and Ficetola 2007). The ability to identify thresholds for target species could be useful in conservation and management in multiple ways including setting goals for retention and restoration of the target species' habitat patch size (Huggett 2005).

Most studies searching for ecological thresholds within landscapes have focused on occupancy, which, like density, may not be indicative of productivity (Van Horne 1983). Arnold et al. (1996) reported that golden-cheeked warblers (*Dendroica chrysoparia*) did not occupy patches <10 ha and speculated that 23 ha represented a threshold for consistent production of young. The difference in threshold for occupancy and consistent production of young reveals a potential bias in looking only at occupancy. The danger of this bias could be expressed in conservation and management. For example, in the case of the golden-cheeked warblers, managers may allow a 30-ha patch to be divided into 2 14-ha patches. The remaining patches may allow for occupancy, but may be too small for reproduction. Although there would only be a loss of 2 ha of habitat, there would be a complete loss of production.

Many authors have reported positive correlations between patch size and nest success (Paton 1994, Burke and Nol 2000, Stephens et al. 2003, Rodewald and Vitz 2005). Hypotheses proposed for the positive relationship between patch size and

reproductive success includes reduced brood parasitism and predation (Andrén and Angelstam 1988, Wilcove 1985, Robinson et al. 1995) and increased food availability (Burke and Nol 1998, Zanette et al. 2000). Brood parasitism and nest predation are 2 of the leading causes of reproductive failure (Martin 1995). The associations between patch size and brood parasitism and between patch size and predation are uncertain and vary with species and location (Tewksberry et al. 1998). Scientists often attribute such relations to edge effects and the fact that smaller patches of similar shape have higher edge-to-area ratios than larger patches (Andrén and Angelstam 1988, Wilcove 1985). Some researchers found that brood parasitism and nest predation were higher at edges than in interiors of patches (Andrén and Angelstam 1988, Wilcove 1985, Robinson et al. 1995) although others did not (Tewksberry et al. 1998).

Burke and Nol (1998) found correlations between patch size, arthropod densities, and pairing success in ovenbirds (*Seiurus aurocapillus*). Burke and Nol (2000) later concluded that food availability affected reproductive success of ovenbirds. Zanette et al. (2000) observed similar patterns of patch effects on arthropod abundance and reproductive success. They found that arthropod biomass in small patches was about half that of larger patches, females in small patches received 40% less food from mates while on the nests, and females left their nests more often to forage on their own. They also found a shorter breeding season, lower egg weights, and smaller chicks in smaller patches.

The positive relationship between arthropod biomass and patch size may be attributed to edge effects. Microclimate variables influence arthropod abundance (Helle and Muona 1985, Didham et al. 1996). Van Wilgenburg et al. (2001) found that edge-induced changes in microclimate caused a negative response in soil arthropods, but did not affect foliage arthropods.

My objectives were (1) to determine the minimum patch size thresholds of reproductive success for three Neotropical migratory songbirds; (2) to determine whether thresholds for occupancy, territory establishment by males, or pairing success were indicative of thresholds of reproduction; (3) to determine whether the proportion of pairs fledging brown-headed cowbird (*Molothrus ater*) young was related to patch size, and (4) to determine the affects of patch size on food availability (i.e., arthropod abundance). Meeting these objectives could enable natural resource managers to make judicious decisions about where vegetation clearing should be conducted and where to focus future research and conservation efforts.

STUDY SPECIES

I studied the golden-cheeked warbler, black-and-white warbler (*Mniotilta varia*), and white-eyed vireo (*Vireo griseus*). I chose to study these 3 migratory songbirds because they represent varying degrees of sensitivity to forest patch area. Coldren (1998) concluded that golden-cheeked warblers were an area-sensitive species based on observations of positive relationships between reproductive success and patch size and pairing success and patch size. Black-and-white warblers are sensitive to forest area (Hannon 1993, Kricher 1995). Hannon (1993) reported that black-and-white warblers only occupied forest patches >10 ha. White-eyed vireos are not area-sensitive, are habitat generalist, and are known to breed in the interior, exterior, and at the edges of forest stands (Hopp et al. 1995). I included white-eyed vireos, because they are not area-sensitive, which allowed me to observe reproductive activity of an insectivorous migratory species in the full range of patches sizes studied.

All three songbirds are susceptible to cowbird parasitism (Pulich 1976, Hopp et al. 1995, Kricher 1995), are insectivorous (Pulich 1976, Hopp et al. 1995, Kricher 1995), and breed in juniper-oak (*Juniperus-Quercus*) forests (Pulich 1976, personal observation). Golden-cheeked warblers and black-and-white warblers usually rear only a single brood per season, though circumstantial evidence suggests that golden-cheeked warblers occasionally double brood (Ladd and Gass 1999) and black-and-white warblers are suspected of occasionally double brooding (Kricher 1995). Golden-cheeked warblers and black-and-white warblers will attempt to re-nest if their nest is destroyed

(Kircher 1995, Ladd and Gass 1999). Number of broods reared per season by white-eyed vireos is uncertain. White-eyed vireos will also re-nest if nest is destroyed or depredated (person observation). Golden-cheeked warblers require mature stands of juniper-oak (*Juniperus ashei*) forests for breeding, and were listed as endangered in 1990 due to loss of habitat (U.S. Fish and Wildlife Service 1990).

Based on research showing that golden-cheeked warblers and black-and-white warblers are sensitive to patch area and white-eyed vireos are habitat-generalists, I predicted that I would find thresholds of reproductive success for both warblers, but not for white-eyed vireos.

STUDY AREA

I conducted my study on private lands in the Cross Timbers and Prairies and Lampasas Cut Plains plant life areas in east-central Texas (Hatch 2008: 106). The study area consisted of canyons, mesas, and bottomlands composed of alkaline soils and limestone bedrock. The major ecological sites were steep adobe, low stony hill, loamy bottomland, and clay loam (National Cartography and Geospatial Center 2002). Total precipitation between February and May was 43 cm and 61 cm in 2006 and 2007, respectively (National Oceanic and Atmospheric Administration 2006, 2007). Prevalent tree species included Ashe juniper, Texas oak (*Quercus buckleyi*), live oak (*Q. virginiana*), shin oak (*Q. sinuata*), post oak (*Q. stellata*), blackjack oak (*Q. marilandica*), Texas ash (*Fraxinus texensis*), cedar elm (*Ulmus crassifolia*), American elm (*U. americana*), redbud (*Cercis canadensis*), hackberry (*Celtis laevigata*), and pecan (*Carya illinoensis*). About 13% of the study area is composed of patches of mixed juniper-oak forests. The remainder of the area is composed of a mosaic of cropland, rangeland, and developed land. Twenty-five percent of the patches of juniper-oak forest are <3.3 ha, 50% are <6.2, and 75% are <17.7 ha. Patches >17.7 ha make up 81% of the total area of mixed juniper-oak forest. Patches of various sizes are mostly interspersed (Figure 1). Canyons and steep slopes supported most of the mature juniper-oak forests; though, mesa tops and bottomlands contained some forest patches, as well.

In much of east-central Texas, land managers view Ashe juniper (*Juniperus ashei*) as an invasive species (Owens 1996). The removal of juniper surrounding juniper-oak (*Juniperus-Quercus*) forests invariably leaves smaller patches.

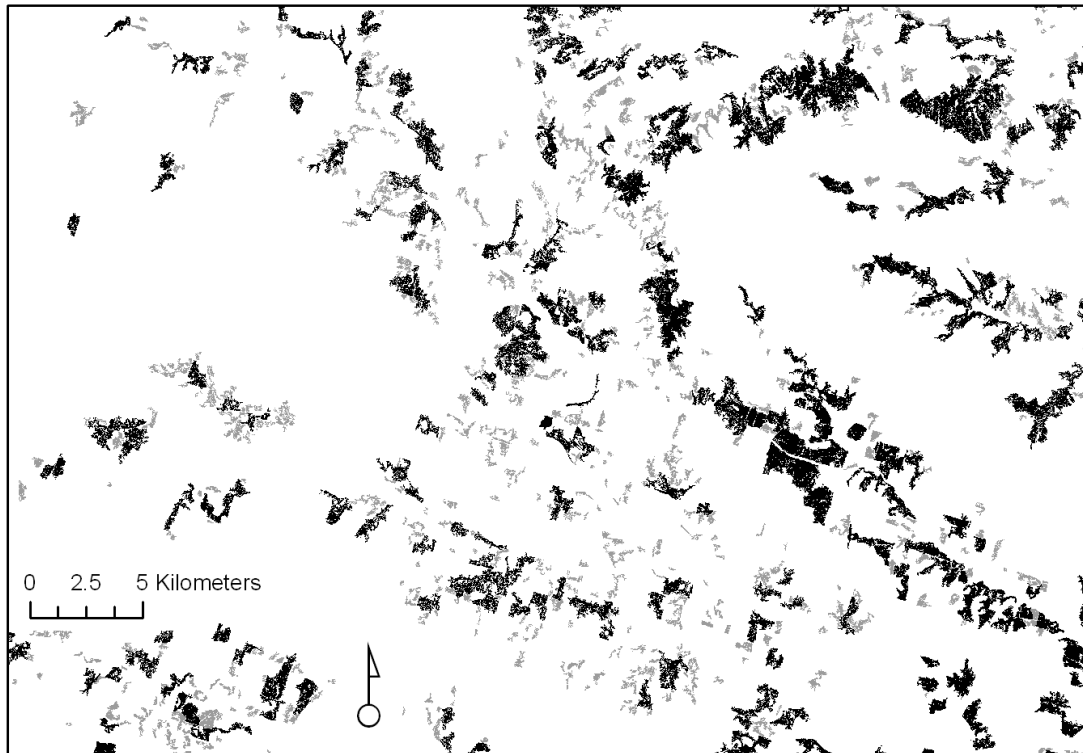


Figure 1. Map showing the interspersed distribution of patch sizes of mature juniper-oak forests. Patches <20 ha are grey and patches >20 are black.

METHODS

Patch size thresholds and reproductive activity

I used a method developed by Vickery et al. (1992), referred to here as the Vickery method, to estimate reproductive activity of birds within patches. The Vickery method allows researchers to predict the reproductive stage of a male or pair based on behavioral observations, observations of host-species fledglings, and observations of cowbird fledglings without the time constraints of locating and monitoring nests (Vickery et al. 1992, Christoferson and Morrison 2001). Using the method proposed by Vickery et al. (1992), Christoferson and Morrison (2001) correctly predicted the outcome of 80 to 92% of nests for 3 songbirds.

The Vickery method includes assigning ranks to males or pairs that represent the most advanced stage of reproductive activity reached during the season. I used a modified version of Vickery et al's (1992) ranking system to meet my objectives. Ranks included occupancy (rank 1; Table 1), territory formation (rank 2; Table 1), pair formation and fledging cowbird young (rank 3; Table 1), and fledgling host-species young (rank 4; Table 1). I identified territorial males and pairs within the patches using a 3-step process. First, to cover all patches quickly and thoroughly, I systematically placed transects throughout patches and walked each transect twice, recording locations of each individual of the target species. I placed transects ~100 m apart in the patches so that no area in the patch was >100 m from a transect. Second, beginning on 1 April, I used spot-mapping to delineate territories. Based on preliminary data collection in the

Table 1. Description of ranks of reproductive activity assigned to each golden-cheeked warbler, black-and-white warbler, and white-eyed vireo. Ranks were based on individuals' behaviors and other evidence of breeding activity and modified from Vickery et al. (1992).

Rank	Description
1	Present
2	Male present >4 weeks (considered territorial)
3	Male and female present >4 weeks (considered paired) Evidence of nest building, male carrying food to presumed female on nest, or the female laying or incubating eggs Female carrying food to presumed nestlings Cowbird parasitized nest
4	Host-species fledgling with pair (considered successful)

study region (J. A. Butcher, Texas A&M University, unpublished data) most males establish territories and formed pairs by 1 April. I recorded an average of 41 points per territory over an average of 12 visits per territory (i.e., ~3 registration points per territory per visit), which exceeded recommendations by International Bird Census Committee (1970). I recorded the distance and direction to other individuals and locations where intraspecific interactions occurred. I entered all locations and interactions into a geographical information system (GIS) to delineate territory boundaries for males and pairs. Because I attributed reproductive success to the entire patch, exact delineation of breeding territories was not imperative to the study. That is, if, within a patch, ≥ 1 pair successfully fledged ≥ 1 host-species young I considered the patch to be above the threshold of patch size in which reproduction would likely occur. Third, during the third week in April, around the approximate date chicks begin to fledge in the region (J. A. Butcher, unpublished data, Kricher 1995, Ladd and Gass 1999) I conducted searches for fledglings within each territory. I searched each territory for fledglings an average of 12

times. I spent an average of 32 (SE = 0.5) min within each territory each time I searched for fledglings. During all 3 steps I recorded GPS points on males, females, and fledglings and recorded observations for the Vickery method.

I defined a patch as a stand of juniper-oak forest that was at least 8 m from other such stands (Rich et al. 1994, Horne 2000). Rich et al. (1994) found that corridors as narrow as 8 m contributed to negative edge effects on local breeding songbirds by attracting avian nest predators and cowbirds. Horne (2000) found that openings as narrow as 10 to 20 m might result in the loss of breeding habitat for golden-cheeked warblers. Patches met criteria for vegetation characteristics set forth by the Texas Parks and Wildlife (2005) for suitable habitat for golden-cheeked warblers. I included the criteria that Texas oak must be present in every patch, because of its importance as foraging substrate for golden-cheeked warbler (Kroll 1980), black-and-white warbler, and white-eyed vireo in my study area (personal observation). I chose to base the definition of a patch on habitat of golden-cheeked warblers because of their endangered status. Black-and-white warblers and white-eyed vireos, however, are known to breed within patches of habitat suitable for golden-cheeked warblers (personal observation). The definition of a patch for white-eyed vireos would likely encompass a greater area because of their ability to breed outside of the area included in the definition of a patch for golden-cheeked warblers. The reason for including them in the study is because they are not sensitive to patch area as defined for golden-cheeked warblers and black-and-white warblers.

I searched for thresholds in patches that ranged from 2.9 to 27.7 ha. The minimum size selected represented the approximate mean territory size of golden-cheeked warblers (Pulich 1976, Weinberg et al. 1996). I based the maximum size on knowledge that golden-cheeked warblers are successful in patches of >23 ha (Arnold et al. 1996). I exceeded the 23 ha patch size reported by Arnold et al. to ensure that the range contained the threshold of reproductive success. All available patches of mature juniper-oak forests that existed entirely on accessible private property in Bosque, Coryell, and Hamilton counties made up the sampling frame. I used 2004 digital orthoquads (DOQQ) and a geographical information system (GIS) to delineated and calculated area of potential patches. I drew polygons around forest patches that were visible on the DOQQs and then visited the patches to ensure that they met the above criteria.

I recorded locations, sex, age (adult or fledgling), and Vickery rank values of all individuals of the target species in 12 patches over 2 seasons. I observed 5 patches from 15 March to 6 July 2006 and 7 patches from 16 March to 22 June 2007. I visited each patch an average of 24 (SE = 2.6) days during each season. I attempted to visit each breeding territory every 3 days. The 12 patches represent a census of accessible patches in the 4-county study area.

Arthropod biomass

I collected branch clippings from 22 April to 10 May 2006 and from 24 April to 7 May 2007 to assess the relationship between patch size and arthropod abundance (Cooper and Whitmore 1990, Keane and Morrison 1999). Johnson (2000) found that branch clipping is an effective way of sampling food availability for foliage-gleaning species. Branch clipping included quickly placing a plastic bag over a branch, clipping the branch from the tree, freezing the sample to kill the arthropods, drying the samples at 60 °C for ~6 days, separating the arthropods from the leaves, and weighing both the leaves and the arthropods (Johnson 2000, Rodewald and Vitz 2005). I randomly placed sampling stations by overlaying each patch with a 100 × 100 m-cell grid that had a random origin, assigning each intersection a number, and using a random number table to select stations. The number of sampling stations was proportional to patch size, although I took more samples per patch during 2007 than in 2006.

I used 3 techniques to minimize variability in arthropod samples. First, I collected branch samples during the period of the breeding season when most golden-cheeked warblers, black-and-white warblers, and white-eyed vireos have nestlings and fledglings in the study region (personal observation). Limited food availability during the nestling and fledgling stages can negatively affect survival of young (Simons and Martin 1990). Wharton et al. (1996) found that arthropods in juniper-oak forests increased in abundance from March through the end of April, followed by a small decrease in May, and then remained stable through June. Second, I set the height above ground where I took samples to 2 m. Collecting samples at 2 m allowed for consistency

in placing the bag over the branch so that few arthropods would escape. Sampling at 2 m was also justifiable based on arthropod distribution and feeding behavior of the birds. Wharton et al. (1996) found that the arthropod species that they collected in large numbers in juniper-oak forests tended to show no preference for any particular height on the tree. Beardmore (1994) reported male golden-cheeked warblers spent more time foraging below 3 m while female golden-cheeked warblers spent more time foraging above 5 m. I combined Beardmore's (1994) categories of male and female foraging times and found that male and female golden-cheeked warblers spend 27% of the time foraging below 3 m, 28% foraging between 3 and 5 m, and 45% foraging above 5 m.

Third, I collected samples from 2 tree species. I chose to collect from Ashe juniper and Texas oak trees, because Wharton et al. (1996) found that most species of arthropods showed preferences for particular tree species. Ashe juniper and Texas oak comprise 2 of the 4 species that Beardmore (1994) reported that golden-cheeked warblers foraged in the most, the other 2 tree species were live oak and cedar elm, neither of which are as abundant as Ashe juniper and Texas oak in my study area (Juarez Berrios 2005). Wharton et al. (1996) stated that several insect species in all of the major orders of arthropods preferred oak, specifically Texas oak. Based on preliminary work in the study region, black-and-white warblers and white-eyed vireos forage at 2 m and in both Ashe juniper and Texas oak (personal observation). All 3 songbird species feed on a large array of arthropod species and forage to some extent on leaves and branches (Morse 1970, Pulich 1976, Hopp et al. 1995).

Data analysis

The criteria described above and the fact that my work was on private land limited my sample size. I had too few samples (patches) to analyze the reproductive activity with multinomial logistic regression; therefore, I used descriptive statistics and presented data in tables and figures.

I tabulated the relationship between patch size and the 4 ranks of reproductive activity for each target species. The 4 ranks of reproductive activity included (1) occupancy, (2) territory establishment, (3) pairing success, and (4) reproductive success. To determine whether occupancy, territory establishment, or pairing success could be used as an indicator of reproductive success I compared the thresholds of each rank to the threshold of reproductive success. I determined that the threshold of a given rank of reproductive activity (e.g., occupancy) was a good indicator of the threshold of reproductive success if the minimum patch size threshold of a given activity (e.g., occupancy) was equal to the minimum patch size threshold for reproductive success.

I calculated the mean and corresponding 95% confidence intervals for biomass of arthropods >1 mm in length for each tree species in each patch. To determine whether there was evidence of an edge effect I analyzed the relationship between arthropod biomass and distance from edge by presenting a scatterplot and calculating Pearson's correlation coefficients. To determine whether patch size influenced arthropod biomass I analyzed the relationship between patch size and arthropod biomass by calculating Pearson's correlation coefficients. To compare food availability in patches where success occurred to food availability in patches where success did not occur, I calculated

mean and standard error of arthropod biomass in patches above and below the thresholds of reproductive success for each species. I was unable to run further statistics because the number of patches where success occurred was too small for the songbirds exhibiting thresholds of reproductive success.

RESULTS

Thresholds of reproductive success

During the 2 seasons I delineated 24 golden-cheeked warbler territories, 9 black-and-white warbler territories, and 47 white-eyed vireo territories. I observed golden-cheeked warblers in 11 of 12 (92%) patches including the smallest patch studied (Table 2). Male golden-cheeked warblers established territories in all 11 patches in which they occupied and established pairs in 7 (64%) of the patches where they established territories. Pairs fledged ≥ 1 young only in patches >15 ha, and no more than 1 pair formed in any patch ≤ 15 ha. In patches >15 ha 15 of 17 (88%) males were paired and 13 of 15 pairs (86%) fledged ≥ 1 young. In patches ≤ 15 ha 3 of 7 (42%) males were paired. Despite the presence of brown-headed cowbirds in the patches, I observed no evidence of cowbird parasitism on golden-cheeked warblers.

I observed black-and-white warblers in 7 of 12 (58%) patches including the smallest patch studied (Table 2). Males established territories in 2 patches; both patches were >15 ha. Seven of 9 (78%) territorial males paired and all pairs fledged ≥ 1 young. A cowbird parasitized one pair; however, the pair fledged their own young as well. The incident of cowbird parasitism occurred in the largest patch studied.

I observed white-eyed vireos in 11 of 12 (91%) patches including the smallest patch studied (Table 2). Males established territories in all patches in which I observed them. Ten of 12 (83%) patches contained pairs. Pairs fledged ≥ 1 young in patches >4.1 ha. In patches >4.1 ha

Table 2. Occupancy (Y = yes) and number of golden-cheeked warblers, black-and-white warblers and white-eyed vireos males that reached each level of reproductive activity based on measurements using the Vickery method (Vickery et al. 1992). I made observations in 12 patches ranging from 2.9 to 27.7 ha. Threshold of reproductive success observed for golden-cheeked warbler (dashed line) and black-and-white warbler (dot-dashed line).

Patch size (ha)	Golden-cheeked warbler				Black-and-white warbler				White-eyed vireo			
	Occupancy ¹	Territorial ²	Paired ³	Successful ⁴	Occupancy ¹	Territorial ²	Paired ³	Successful ⁴	Occupancy ¹	Territorial ²	Paired ³	Successful ⁴
27.7	Y	6	5	5	Y	5	5	5	Y	9	9	6
22.2	Y	3	3	3	Y				Y	6	6	4
21.1	Y	4	3	2	Y				Y	10	9	6
20.1	Y	4	4	3	Y	4	2	2	Y	7	5	3
15.0									Y	2	1	
11.9	Y	1							Y	4	4	4
10.8	Y	1	1		Y				Y	2	1	
8.9	Y	1							Y	3	3	2
4.4	Y	1	1						Y	2	2	2
4.1	Y	1	1		Y							
3.2	Y	1							Y	1	1	
2.9	Y	1			Y				Y	1		

¹Observed individual in the patch during the breeding season

²Number of males that established and defended a territory for >4 weeks

³Number of males observed with a female for >4 weeks

⁴Number of pairs that successfully fledged ≥ 1 offspring

40 of 45 (88%) males were paired and 27 of 40 (68%) pairs fledged ≥ 1 young. In patches ≤ 4.1 ha only 1 of 2 territorial males paired. Two white-eyed vireo pairs fledged cowbird young. One pair was in the 2.9-ha patch and the other was in the 15-ha patch. The number of pairs that fledged young was linearly related to patch size (Figure 2).

Golden-cheeked warblers and black-and-white warblers were not detected in the 15.0 ha patch (Table 2). The reason is uncertain, but was not likely caused by a landscape configuration. The 15.0 ha patch was within 10 m of 2 neighboring patches, and mixed juniper-oak forest made up 13% of the area that fell within a 400 m buffer

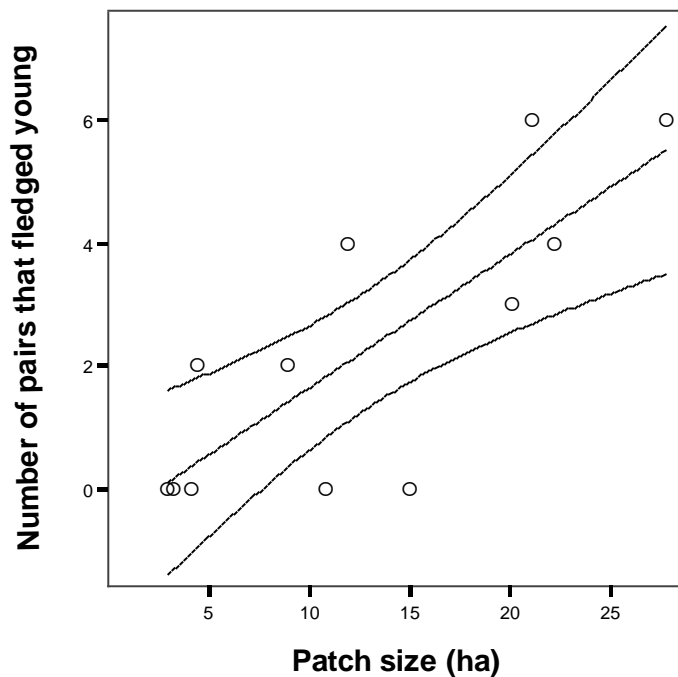


Figure 2. The number of white-eyed vireo pairs that fledged young was linearly related to patch size ($r^2 = 0.63$). Lines show mean and 95% prediction interval.

around the patch. The average area of juniper-oak forest surrounding patches was 24.3 ha ($n = 12$, $SE = 3.4$). Two patches with less juniper-oak forest surrounding the patch were occupied by golden-cheeked warblers (4.4 and 21.1 ha patches) and 1 patch was occupied by the black-and-white warbler (21.1 ha patch).

Arthropod biomass

I collected 209 branch clippings each from juniper and oak trees (Table 3). Arthropod biomass in Ashe juniper and Texas oak did not correlate with patch size ($r = 0.13$, $r = 0.12$, respectively; Fig. 3 *a, b*) or distance from edge ($r = 0.03$, $r = 0.11$, respectively; Fig. 4 *a, b*). The mean arthropod biomass above the observed minimum patch size threshold of reproductive success for golden-cheeked warblers and black-and-white warblers was 0.16 mg/g ($n = 4$, $SE = 0.04$) and 0.50 mg/g ($n = 4$, $SE = 0.26$) in juniper and oak trees, respectively. Below the observed minimum patch size threshold of reproductive success the mean arthropod biomass was 0.14 mg/g of leaves ($n = 8$, $SE = 0.03$) and 0.45 mg/g of leaves ($n = 8$, $SE = 0.15$) in juniper and oak trees, respectively.

Table 3. Arthropod biomass (mg/g of leaves) collected from branch clippings taken in 12 patches of juniper-oak (*Juniperus-Quercus*) forest in east-central Texas. I collected branch clippings 2 m above ground from Ashe juniper (*Juniperus ashei*) and Texas oak (*Quercus buckleyi*) from 22 April 2006 to 10 May 2006 and from 24 April 2007 to 7 May 2007 to assess the relationship between patch size and arthropod biomass.

Patch size (ha)	Ashe juniper		Texas oak	
	N	Mean (SE)	N	Mean (SE)
27.7	31	0.21 (0.05)	30	0.41 (0.12)
22.2	21	0.18 (0.04)	21	2.39 (0.43)
21.1	29	0.05 (0.01)	27	0.41 (0.11)
20.1	25	0.19 (0.06)	25	0.21 (0.08)
15.0	21	0.09 (0.03)	21	0.36 (0.13)
11.9	18	0.31 (0.12)	17	2.42 (0.43)
10.8	15	0.09 (0.02)	16	0.42 (0.30)
8.9	14	0.11 (0.05)	14	0.55 (0.33)
4.4	9	0.05 (0.01)	9	0.57 (0.37)
4.1	10	0.18 (0.09)	10	1.42 (0.48)
3.2	10	0.15 (0.07)	10	0.33 (0.19)
2.9	9	0.17 (0.09)	9	0.06 (0.05)

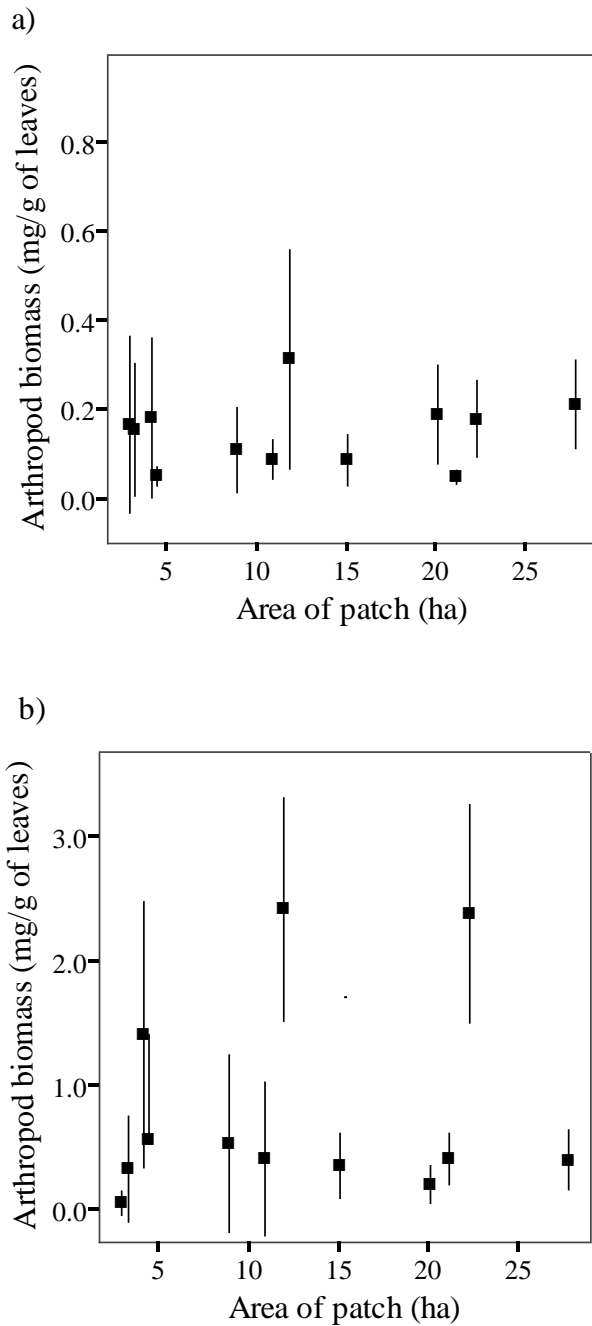


Figure 3. Arthropod biomass in each patch obtained from branch clippings of Ashe juniper (a) and Texas oak (b) during the average nestling and fledgling stages of golden-cheeked warblers, black-and-white warblers, and white-eyed vireos in east-central Texas. Squares represent mean arthropod biomass and lines represent 95% confidence intervals. Notice that the ordinates are of different scales due to the greater arthropod biomass on Texas oak than on Ashe juniper.

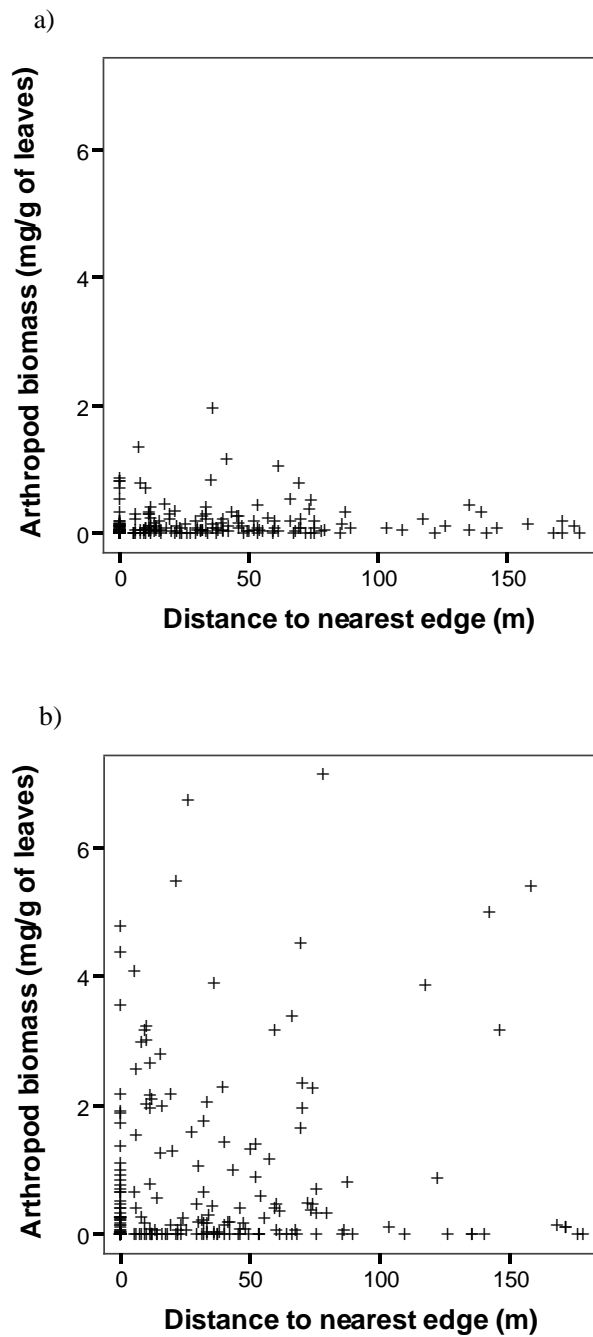


Figure 4. Arthropod biomass relative to distance from edge obtained from branch clippings of Ashe juniper (a) and Texas oak (b) during the average nestling and fledgling stages of golden-cheeked warblers, black-and-white warblers, and white-eyed vireos in east-central Texas.

DISCUSSION AND CONCLUSIONS

I found minimum patch size thresholds of reproductive success for golden-cheeked warblers and black-and-white warblers. Minimum patch size thresholds of occupancy, territory establishment, and pairing were not indicative of minimum patch size thresholds of reproduction. The observed minimum patch size threshold of reproductive success for golden-cheeked warblers and black-and-white warblers was between 15 and 20.1 ha. In a study conducted south of my study area, Arnold et al. (1996) observed a similar trend for golden-cheeked warblers. They reported that golden-cheeked warblers reliably produced young in patches >23 ha in size. To my knowledge no study has been published relating productivity of black-and-white warblers to patch size. Hannon (1993), however, found that black-and-white warblers were sensitive to patch size; she detected black-and-white warblers only in patches >10 ha.

As expected, I did not find a minimum patch size threshold of reproductive success for white-eyed vireos. The fact that there was no success in the 3 smallest patches can be explained by natural variation regardless of patch size. Territory establishment and pairing success increased linearly with patch size. Bender et al. (1998) predicted that population changes in generalist species that use both edges and interiors of forest patches would be accounted for by habitat loss alone, regardless of fragmentation.

Although research shows that birds nesting in smaller patches experience higher predation and parasitism (Hoover et al. 1995), neither appeared to be a proximate cause for the thresholds I observed. Parasitism within the patches was low and was not related

to patch size in the range of patches that I studied. Low parasitism frequency was surprising because of the ubiquity of brown-headed cowbirds in the study area.

Cowbirds were observed at 88% of survey stations within the study area (Juarez Berrios 2005), and >80% of black-capped vireo and white-eyed vireo nests in shrubs and trees surrounding my study patches were parasitized by brown-headed cowbirds (S. L. Farrell, Texas A&M University, unpublished data). Although the relationship between forest cover and parasitism is highly variable (see Tewksberry et al. 2006), the high magnitude of difference between parasitism inside and outside of the juniper-oak forest patches in my study area suggest a relationship that should be studied.

Although I did not study predation, I would expect that more white-eyed vireos would have failed in the patches below the thresholds of the warblers if predator activity caused the observed thresholds. Ultimately, adaptations by the warblers could have caused them to select larger patches because of the influence of predation in small patches in the historic past. Fontaine and Martin (2006) found that some migratory songbirds have the ability to assess predator activity and adjust breeding location accordingly.

High success above the threshold suggests that predation and parasitism were not limiting factors within larger patches. Success of golden-cheeked warbler pairs above the threshold (86% of pairs fledged young) was similar to populations at Fort Hood, Texas, (87.8% of pairs fledged young; Anders and Marshall 2005) where intensive cowbird control has been in effect since 1991 (Eckrich et al. 1999). I observed 100% of black-and-white warbler pairs fledged young.

I found no relationship between patch size and arthropod biomass. Nour et al. (1998) found that neither evidence of caterpillars (frass fall) nor provisioning rates for young great tits (*Parus major*) and blue tits (*P. caeruleus*) were correlated with patch size. Similarly, Buehler et al. (2002) found that food availability and provisioning rates of hooded warblers (*Wilsonia citrina*) did not relate to patch size. My findings, along with Nour et al. (1998) and Buehler et al. (2002), are contradictory to Burke and Nol (1998, 2000) and Zanette et al. (2000) who found that food availability was correlated with patch size and ultimately reproductive success. The differences can be explained by sampling objectives and thus sampling protocols. The 3 focal species of my study along with hooded warblers studied by Buehler et al. and the 2 species of tits studied by Nour et al. all feed above ground, therefore arthropod sampling was conducted above ground. Burke and Nol (1998) studied ovenbirds (*Seiurus aurocapillus*) and Zanette et al. (2000) studied eastern yellow robins (*Eopsaltria australis*) both of which are ground-foragers and, thus, sampling occurred at the ground level. Van Wilgenburg et al. (2001) reported that soil-dwelling arthropods responded negatively to edge effects whereas canopy-dwelling arthropods in the same forests showed no response to edge.

I did not differentiate patch size affects on specific groups of arthropods. It is possible that particular arthropod families, orders, or species are important to each bird species, and that patch size affected those arthropod groups. Although Lepidoptera

larvae comprised the greatest percentage of any one order of arthropods in stomach contents for all 3 songbird species, the contents, along with observational studies, revealed that all 3 species feed on a large variety of arthropods (Nolan and Wooldridge 1962, Pulich 1976, Kricher 1995).

Because there was no relationship between patch size and arthropod biomass, there was little reason to believe that food availability was the cause of the observed thresholds. The patterns related to the thresholds may offer some insight to possible causes for the thresholds of reproductive success. Besides fledging young, an obvious difference between reproductive activity above and below the threshold of reproductive success was number of territories established and number of pairs formed; for all 3 species success occurred only in patches where >1 pair was formed. Researchers have noticed that some territorial species aggregate their territories even when surrounding unoccupied habitat exists (Svårdson 1949, Hildén 1965, Stamps 1988). Two theoretical reasons for aggregation of territories are (1) conspecifics may act as cues for settling individuals and (2) there might be some type of benefit in living within an aggregation (e.g., predator protection, access to mates; Muller et al. 1997). My results showed what appeared to be clumping for golden-cheeked warblers and black-and-white warblers. The aggregation of black-and-white warblers into 2 patches despite occupying multiple patches suggests conspecific attraction, defined as aggregation of territories caused by apparent attraction to neighbors (Stamps 1988, Ahlering and Faaborg 2006, Campomizzi et al. 2008). Campomizzi et al. (2008) reported evidence of conspecific attraction in golden-cheeked warblers in the same study area. Without experiments controlling for

habitat quality, predator activity, and other variables that influence habitat selection, conspecific attraction as a means of habitat selection is difficult to discern from other habitat cues (e.g., predator activity, food availability; Stamps 1988).

Although determining success by searching territories may express season-long productivity more accurately than nest monitoring (Anders and Marshall 2005), fledging young does not necessarily culminate in higher fitness (number of offspring that successfully reproduce). I relocated fledglings throughout the season, but at the end of the season I was unable to determine whether juveniles that fledged in the patches were depredated, starved, or survived to migrate south. Further research on survival of juveniles, recruitment, and offspring breeding success could help address relationships between patch size and fitness.

To date, most researchers used occupancy of the target species as the response variable for thresholds. My research showed that minimum patch size thresholds for occupancy were not indicative of the thresholds of reproductive success, and minimum patch size thresholds for territory establishment and pair formation were not indicative of patch size thresholds for reproductive success. Management and conservation practices for target species based on thresholds of occupancy, territory establishment, or pair formation could be dangerous. Some may argue, and rightly so, that preserving patches based on occupancy, territory establishment, or pair formation will include patches where reproduction could occur. However, the danger comes not when managers attempt to conserve all patches above the threshold of occupancy or pair

formation (that would be ideal), but when managers use the minimum patch size threshold of occupancy as a basis for allowing larger patches to be fragmented into patches that may fall below the patch size threshold of reproductive success.

Thresholds are an integral part of ecological theory (e.g., Shelford's law of tolerance, Hutchinsonian niche). Studies show that thresholds of habitat distribution, amount, and configuration of a species' habitat in a landscape influence population dynamics (Fahrig and Merriam 1994, Morrison et al. 1998: 48–49, Hokit and Branch 2003, Denoël and Ficetola 2007). The ability to identify thresholds of reproductive success for target species could be useful in conservation and management in multiple ways including setting goals for retention and restoration of target species' habitat patch size (Huggett 2005).

Management implications

Because both warblers have relatively uniform habitat requirements across their distribution ranges (Kricher 1995, Ladd and Gass 1999), patch size relationships observed in this study should hold across much of their ranges. Managers involved in juniper clearing in east-central Texas particularly, and in forest removal in general, should be cautious not to decrease patches below 20 ha. Because patches below the threshold of reproductive success were occupied by golden-cheeked warblers, research is needed to determine the role that such patches play in population dynamics of golden-cheeked warblers.

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