

**Effects of Forest Fragmentation on the Physiology and Health Status of  
Wood Thrush (*Hylocichla mustelina*) in the Upper Midwest**

By

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## Abstract

Recent population declines of neotropical migrant songbirds breeding in the eastern deciduous forests have been attributed to forest fragmentation. Although some research has been conducted on the demographic processes occurring in forest songbirds subjected to habitat fragmentation, little is known about the physiological and health-related ramifications of forest degradation. I used Wood Thrushes (*Hylocichla mustelina*) to investigate whether forest fragmentation has an impact on immunological condition and infection with ectoparasites and blood-borne pathogens. I compared Wood Thrushes occurring in small, fragmented forest patches to others living in unfragmented areas for differences in morphology, immunological and body condition, behavior, and infection with hemoparasites and ectoparasites. Wood Thrushes in unfragmented sites exhibited more aggressive behaviors against standardized experimental challenges, and were in better physiological condition, as evidenced by higher hematocrits, than those from fragmented sites. Tail and wing length were negatively correlated to Julian date while total fat deposits were positively correlated to Julian date, suggesting that birds in the late summer had abraded plumage but higher energetic reserves. Total parasitemia (intensity of hemoparasite infections) positively correlated to heterophil-lymphocyte ratio (H/L) indicating heavy infections precipitated a skew in normal immunological profiles. Ectoparasite burden decreased over the course of the summer, and was negatively correlated to fat deposits, suggesting a negative impact of ectoparasites on the energetic balance of the host. Fragmentation did not appear to have an effect on either ectoparasite or hemoparasite infections. My results suggest that fragmentation has impacts on some aspects of Wood Thrushes' behavior physiology but that such effects may not be immediately observable. Furthermore, any studies should consider timing of measurements in addition to habitat condition as important factors shaping the physiological condition and infection status of forest migrants.

## **Acknowledgments**

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## **Introduction**

Habitat change and loss are the main drivers of the ongoing extinction of plant and animal species (Pimm et al. 1995, Arroyo-Rodriguez and Mandujano 2006). When habitats are being lost, not only is the overall area reduced, but the remaining habitat also becomes fragmented. Isolation of surviving populations on small patches exacerbates habitat loss and may ultimately cause species extinctions, even if patches of suitable habitat still persist (Andren 1994; Bender et al. 1998).

A substantial body of literature has accumulated as the result of recent research on how habitat fragmentation affects passerine birds (see Table 1. and Table 2.) Habitat fragmentation affects reproduction, population density, and the distribution of many temperate forest-breeding birds (Billard et al. 1998; Donovan and Flather 2002). For example, fragmentation can lead to changes in predator identities or numbers, and has been shown to increase predation pressure on forest birds and their nests (Andren 1992, 1995; Bayne and Hobson 1997). A substantial number of studies have indicated that nest predation and brood parasitism were the highest near the fragmented forest edge, and that they decreased with increasing distance from the edge (e.g., Hoover et al. 2006). Furthermore, habitat fragmentation also appears to affect the availability of food resources which in turn can reduce the bird fecundity (Zanette et al. 2000, Lampila et al. 2005). Habitat fragmentation can therefore dramatically impact avian reproduction success, either directly through reduced food availability, or indirectly through increases in predation pressure.

Most investigations into the impacts of fragmentation have focused primarily on nest predators, brood parasites, source-sink population dynamics or food availability for area-sensitive birds. New evidence, however, suggests that various aspects of avian physiology, such

as immunological condition, can also be affected by fragmentation. Research on Spotted Owls, (*Strix occidentalis*), an area-sensitive species, demonstrates that individuals in fragmented habitat had higher levels of circulating stress hormones, most likely because they live under conditions that were not ideal for them (Wasser et al. 1997). Birds that are more stressed may also be in poorer condition and thus more likely to be susceptible to infection with pathogens. Because the immune system plays such a central role in animal well-being, various hematological immune assays can be used to evaluate the impact of fragmentation on wildlife (Moreno et al. 2002). Heterophil-lymphocyte ratios (H/L) have been shown to be both sensitive to increased plasma corticosterone levels (Morici et al. 1997; Post et al. 2003) and a reliable physiological indicator of condition in wild bird populations (Horak et al. 1998; Ots et al. 1998). Suorsa et al. (2004) found that in Eurasian Treecreepers (*Certhia familiaris*), an area-sensitive passerine species, H/L ratios in nestlings were negatively related to forest patch area, thus indicating that fragmented forests have negative impacts on bird reproductive performance and survival.

Forest disturbance and fragmentation have implications for wildlife health not only because they may render hosts more susceptible to existing parasites but also because they may increase the presence of exotic pathogens. For example, West Nile Virus (WNV), which was first detected in the United States in 1999, is a mosquito-borne disease for which wild birds serve as the primary reservoir hosts (Hayes 1989). Wildlife epizootics can then also affect human health. Human WNV infections occur when conditions promote virus amplification within avian and mosquito populations. Recent research has demonstrated that bird diversity is negatively correlated with both mosquito and human infection rates (Ezenwa et al. 2006), thus indicating that forest fragmentation may increase the prevalence of mosquito-transmitted disease.

The Wood Thrush (*Hylocichla mustelina*) is a neotropical migrant, breeding in eastern North America. The species winters in Central America from Mexico to Panama (James et al. 1984). Because Wood Thrushes strongly prefer interior habitat in moist, deciduous forests, and are very area-sensitive; they are now a species of conservation concern, and have become a symbol of the decline of Neotropical songbirds in the forests of eastern North America (Birds in Forested Landscapes Species Account 2002). Fragmentation of breeding habitat in North American forests is considered a major factor contributing to the apparent decline in Wood Thrush abundance (Robbins 1979, Robinson 1992). Forest fragmentation can result in both increased nest predation and increased Brown-headed Cowbird (a brood-parasite) parasitism for birds nesting in fragmented forest (Brittingham and Temple 1983), thereby significantly reducing their reproductive success. Some other studies also indicate that the density of Wood Thrush is negatively related to area of forest fragment, thus suggesting that small fragments may be part of a regional population sink for the species (Weinberg and Roth 1998; Fauth 2000).

A substantial body of research has documented the adverse effects of forest fragmentation on breeding Wood Thrush populations (Fauth 2000). However, most of these studies have focused on the effects of nest predation and brood parasitism on Wood Thrush reproductive success (Hoover and Brittingham 1993; Schmidt and Whelan 2005). No research has been published investigating immunological condition and infection with hemoparasites on Wood Thrush health. Here I report on the results of a two-year study on physiological condition and infection studies between birds occurring in fragmented and unfragmented forest habitats in South East Michigan.

The goals of this study are to:

- 1) compare life history characteristics and behavioral tracts of Wood Thrush in suburban forest fragments versus unfragmented forest
- 2) evaluate prevalence of the hemoparasite genera *Leucocytozoon*, *Haemoproteus* and *Plasmodium* in Wood Thrushes occurring in fragmented versus unfragmented forest
- 3) evaluate hematological parameters related to host condition and immunity between birds in fragmented versus unfragmented habitats



## Material and Methods

### *Study Sites*

During the summers of 2005 and 2006, I compared fragmented and unfragmented forest sites from Washtenaw County in Michigan's Lower Peninsula ([Figure 1.](#)). All 14 unfragmented study sites were located in the Waterloo-Pinckney Recreation Area (WPRA), which covers 83 km<sup>2</sup> in northwest Washtenaw County (geographic coordinates of WPRA center: 42°21' N 84°05' W). Forested land covered 74% of the WPRA; the remaining 26% consists of open areas, such as cultivated fields, lakes, grassland and roads. The primary forest type in the WPRA is deciduous forest dominated by oak, maple, beech and hickory, which constitutes 72% of its forested land. Coniferous forest and mixed forest, as well as shrubs cover the remaining 28% of the WPRA forest. All forests in the WPRA are secondary growth forests, having been largely logged in the 19<sup>th</sup> century.

The 12 fragmented forest sites are composed of temperate forest communities similar, but on average younger, than the communities on the unfragmented sites. These fragmented forest patches are surrounded by a diverse matrix that includes urban housing and agricultural areas. They are also all situated in Washtenaw County ([Figure 1.](#)). Most of these fragmented forest sites were cleared in the past for agriculture, but some secondary growth forest has sprung back in the second half of the 20<sup>th</sup> century, following shifts in agriculture. All fragmented study sites are smaller than 0.5km<sup>2</sup> (Table 3.).

## ***Birds***

### **1. Bird Surveys**

All bird surveys were conducted in the months of May through July during the summers of 2005 and 2006. I first quantified the passerine bird communities in all forest patches using standardized point counts (Ralph and Scott 1981, Verner 1985, Hamel et al. 1996) (Table 4.).

Before attempting to capture Wood Thrushes (WOTH), I conducted additional surveys using an audio lure to locate male WOTH territories. By conducting standardized playbacks of WOTH song I was able to elicit responses from resident males in areas where I suspected WOTH to be present. To reduce idiosyncratic effects stemming from the identity of playback songs, I used taped songs from two different birds. Once a male WOTH responded to the recording, I stopped the tape and observed the bird's behavior, taking note of its activity range and flight patterns. All surveys were completed during early morning hours (5:30am to 10am) under good weather conditions (no rain). I conducted the playbacks using a Sony m-427 Microcassette-Corder playing WOTH songs from Lang et al. (1997).

### **2. Mist netting of Wood Thrushes**

Once I located an occupied Wood Thrush territory, I waited 2-5 days before conducting targeted mist-netting of the territory holders. To increase capture success, mist nets were placed at locations intersecting WOTH flight corridors identified during the previous survey. The number of nets used was dependent on patch size and vegetation, but typically three 5m×3m nets were arranged in a U-shape. Net lanes were chosen and cleared during a previous visit so as to decrease the amount of disturbance on the day of attempted captures. Mist nets were set up and opened by 6:30 am and closed at noon or after the resident birds were caught.

Because WOTH typically remain in the forest canopy, and descend to the ground only to forage, a field assistant and I used playbacks to attract them into the nets. I found that an effective technique was to use two mobile hand held players, one on each side of a net. Playing the recording would sometimes lure the bird immediately into the nets. Usually, however, the approaching bird would remain in the canopy above the nets. When this occurred, the two handheld players were activated alternately, depending on the location of the bird in relation to the nets. Thus, the tape player on the opposite net side of the bird's location was used to lure the bird and this was alternated, until eventually the bird would fly into the nets.

Because male WOTH responded much more aggressively than females to pre-recorded WOTH songs, I caught more males than females. Female WOTH usually didn't respond to playbacks, although occasionally they would be caught while searching for the previously-captured territorial male.

To obtain a quantitative index of an individual's behavior, I observed male WOTH during playbacks and ranked their aggressiveness. I arranged behaviors to five aggressiveness categories that were defined as:

0 = Bird flew away when approached or when tape was played;

1 = Bird was inquisitive, but remained silent and did not approach;

2 = Bird sang in the vicinity but did not approach;

3 = Bird sang loudly close by;

4 = Bird swooped aggressively at the recorder while singing loudly

### **3. Blood sample collection**

An initial blood sample was collected within 3 minutes of disentangling the bird from the mist net. The bird was held with the abdomen facing upwards in one hand, while one wing was extended between the index and middle fingers. With a small piece of cotton wadding soaked in ethanol, the underwing covers were wiped clear to expose the brachial vein and to sterilize the area. Using a small, unused syringe needle (27G ½ PrecisionGlide® needle, Becton Dickinson, Product No. 305109, Franklin Lakes, NJ), a small puncture was made into the brachial vein, and two full heparinized microcapillary tubes of blood were collected (Fisherbrand, Pittsburgh, PA). The collected blood was immediately placed in an iced container until later use. Further bleeding was stopped by applying pressure to the puncture with a dry cotton wadding for 3-5 minutes.

### **4. Banding and Morphological Data Collection**

After collecting blood samples, each bird was banded with a uniquely numbered Fish and Wildlife Service aluminum leg band (Band size 1A). I collected standard morphological data including sex, age, weight (to the nearest 0.1g), visible subcutaneous fat, wing length (mm), tail length (mm), tarsus length (mm), cloacal protuberance (mm), and brood patch score. Birds were aged and sexed based on plumage characteristics and cloacal morphology. Subcutaneous fat deposits were quantified according to scales developed by Helms and Drury (1960). Ectoparasite load was quantified on the primaries of the right wing by holding the stretched-out wing against the light and counting visible parasites. Ectoparasite numbers were categorized into the following classes: 0, 1-10, 11-50, 51-100, 101-500, and 501-1000; these were used to create an ordinal index of parasitism ranging from 0 to 5. Because of the very small size of the

ectoparasites (<1mm) I did not pursue any species identifications. I obtained a metric of bird condition by calculating the residuals of the regression of body mass on wing chord. Separate regressions were done for males and females. Time of capture was coded as Julian date with May 1<sup>st</sup> arbitrarily set as Day 1.

## 5. Hematology

To identify hemoparasites and quantify hematological variables, three blood smears were prepared from each blood sample. A small drop of blood was placed on a glass slide and then smeared across the surface using the clean edge of another slide. After air-drying the three smears, two slides were stored at -20°C for later immunology assays. The third smear was fixed and stained with a Protocol Hema 3<sup>®</sup> stain set (CAT#: 122-911, Fisher Scientific Company, Middletown, VA), which possesses staining characteristics similar to Wright and Wright-Giemsa stains. Each blood smear was examined under 1000× magnification for an average time of 20 minutes.

I identified three genera of parasites in the examined WOTH blood smears: *Leucocytozoon*, *Haemoproteus* and *Plasmodium*. Because only gametocytes can be identified to genus, I grouped immature stages (e.g., trophozoid) into a generic “immature” category. Total parasitemia in each bird was expressed as the cumulative number of parasitized red blood cells (RBCs) in all three genera per 10,000 RBCs. The total number of white blood cells (WBC) per 10,000 RBC’s was determined by adding the numbers of lymphocytes, monocytes, heterophils, eosinophils, and basophils observed, in 10,000 RBCs. Total WBCs can provide information on the health and immunocopetence of an individual. Changes in numbers of WBCs, whether elevated or depressed, can also reflect health status in terms of parasitic, bacterial or viral

infections (Owen and Moore, 2006). Reduced WBCs may also indicate systemic stress caused by a non-etiological process such as malnutrition, strenuous exercise, or significant weight loss (Gershwin et al. 1985, Hoffman-Goetz and Pedersen 1994, Stinnett 1983). Because lymphocytes operate entirely within the framework of acquired immune responses, they provide an indirect measure of acquired immune function, i.e., cell-mediated and humoral immunity. During periods of stress, birds may experience heterophilia and concomitant lymphopenia, resulting in high heterophil to lymphocyte (H:L) ratios (Gross and Siegel 1986, Ots and Horak 1996, Dabbert et al. 1997, Work et al. 1999). The (H:L) ratio was determined by examining the stained blood smear under an oil immersion microscope and by counting the number of each white blood cell type per 100 WBC's.

Blood that was not used for smear preparation was centrifuged for 5 min at 14,000 RPM to precipitate the cellular components. Hematocrit values were estimated using a Critocaps<sup>TM</sup> Micro-Hematocrit Capillary Tube Reader (Oxford Labware, Lot# 709429) and the readings from 2 capillary tubes were averaged to obtain a final value for each bird. Hematocrit is a measure of nutritional state, with low values indicative of malnutrition and anemia (Campbell and Dein 1984). Elevated hematocrit may result from dehydration or elevated oxygen consumption (Carpenter 1975).

Following centrifugation, the separated plasma was drawn out of the capillary tube using a Hamilton syringe and transferred to a microcentrifuge tube. Red blood cells were dabbed onto filter paper circles to prepare 3 blood dots, which were allowed to dry in a shady place. Tubes of plasma and the dried blood dots were then stored at -20°C for use in later analyses.

### *Statistical Analysis*

Most analyses (T-tests, ANOVAs) were conducted using parametric tests, unless normality assumptions were not met. Data are presented as means  $\pm$  SE. For non-normal variables, (such as sex, age, behavior, and parasites load), I used Chi-square or Mann-Whitney U test statistics. Outliers (standard residual  $>2$ ) were excluded from the analyses. All tests were two-tailed unless otherwise stated, and a priori significance levels were set at  $p < 0.05$ . I performed all analyses using SPSS 12.0 (SPSS 2004).

## Results

### *Sex and Age*

I captured 57 different Wood Thrushes during the 2005 and 2006 breeding seasons (25 in 2005 and 32 in 2006). Birds were captured between May 23<sup>rd</sup> and July 30<sup>th</sup>. Forty-seven out of 57 birds (82.5%) were males, although given the known sex bias of the capturing method, this may not reflect the true sex ratios in the study populations. No significant differences in the fraction of males were found between fragmented (83.3%) and unfragmented (81.4%) sites ( $\chi^2=0.034$ ,  $df=1$ ,  $p=0.854$ ). Birds were assigned to 3 different age categories: After Hatching Year (AHY), Second Year (SY), and After Second Year (ASY) (Figure 2.). I did not identify any significant differences in the age distributions of birds between fragmented and unfragmented sites ( $\chi^2=2.81$ ,  $df=2$ ,  $p=0.245$ ).

### *Morphology*

Male and female Wood Thrushes differed in tail and wing lengths: males had longer tails ( $73.55 \pm 0.563$ mm; mean $\pm$ SE,  $n=46$ ) than females ( $68.70 \pm 0.559$ mm,  $n=10$ ,  $t=3.906$ ,  $p<0.001$ , Independent-Samples T-test). Tail length was negatively correlated with Julian date (Pearson  $r=-0.423$ ,  $p=0.001$ ,  $n=56$ ). I did not detect any effects of fragmentation status on tail length ( $p=0.292$ , 1-way ANCOVA).

Male WOTH also had longer wings ( $106.65 \pm 0.406$ mm; mean $\pm$ SE,  $n=46$ ) than females ( $103.40 \pm 1.056$ mm,  $n=10$ ) ( $t=3.262$ ,  $p=0.002$ , Independent-Samples T-test). Average wing length decreased with Julian date (Pearson  $r=-0.358$ ,  $p=0.007$ ,  $n=56$ ). Again no effects of fragmentation status on wing length were detected ( $p=0.311$ , 1-way ANCOVA).



### ***Total Fat Score and Condition***

I did not detect any difference in total fat score between male and female Wood Thrushes ( $p=0.627$ , Independent-Samples T-test,  $n=56$ ). Total fat, however, was positively correlated with Julian date ( $r=0.499$ ,  $p<0.001$ ,  $n=56$ ), suggesting that birds accumulated fat deposits as the summer progressed. I did not detect any effects of fragmentation status on total fat score ( $p=0.101$ ).

I also did not detect any correlations between Julian date and condition ( $p=0.131$ ). No relationship was found between fragmentation status and bird condition ( $p=0.317$ , Independent-Samples T-test).

### ***Behavior***

Aggressive behavior ranged widely in the birds examined: while some birds simply flew away when playbacks were initiated, others were assertive in defending their territories and some even swooped down to attack the speaker. Birds in fragmented sites were on average less assertive in defending their territories than birds in unfragmented sites ( $U=170.0$ ,  $p=0.004$ ,  $n=51$ ) (Figure 3.). These differences could not be attributed to underlying age or sex differences between birds at different sites.

### ***Hematocrit***

Hematocrit values reported here represent the average of two separate tubes collected during the same trapping session. Hematocrit values ranged widely among the birds examined ( $45.8\pm 0.008$ ; mean $\pm$ SE); Range: 34.5-67) and were significantly correlated to Julian date ( $r=-0.527$ ,  $p<0.001$ ,  $n=54$ ). An ANCOVA with Julian date as the covariate revealed that

fragmentation was significantly correlated to hematocrit ( $R^2=0.316$ ,  $p=0.016$ ). One data point was an outlier (standard residual  $>3$ ) and was excluded from the analysis. The low hematocrit in birds at fragmented sites was more pronounced in the late season, suggesting that the impact of residing in fragmented habitats became increasingly severe as the summer progressed (Figure 4.).

### ***White Blood Cell Counts***

Lymphocyte numbers were positively correlated to Julian date ( $r=0.404$ ,  $p=0.002$ ,  $n=57$ ). I could not identify any relationship between fragmentation and lymphocytes based on an ANCOVA with Julian date as the covariate ( $p=0.746$ ,  $R^2=0.134$ ).

Total white blood cells were also positively correlated to Julian date ( $r=0.357$ ,  $p=0.006$ ,  $n=57$ ). Again, I did not detect any effect of fragmentation on total white blood cells based on an ANCOVA with Julian date as the covariate ( $p=0.246$ ,  $R^2=0.118$ ).

Similarly, my analyses did not reveal any relationship between heterophil numbers and Julian date ( $p=0.606$ ,  $R^2=0.005$ , Liner Regression), nor between H/L ratios and Julian date ( $p=0.151$ ,  $R^2=0.037$ , Liner Regression). Lastly, H/L ratios were not related to fragmentation status ( $p=0.696$ , Independent-Samples T-test).

### ***Infection Status***

I did not detect any differences in the prevalence of *Leucocytozoon* ( $\chi^2=2.341$ ,  $df=1$ ,  $p=0.126$ ), *Haemoproteus* ( $\chi^2=0.291$ ,  $df=1$ ,  $p=0.590$ ), and *Plasmodium* ( $\chi^2=0.133$ ,  $df=1$ ,  $p=0.716$ ) infections between fragmented and unfragmented sites. I also did not find any differences in total parasitemias (total number of cells parasitized) between fragmented and unfragmented sites

( $p=0.811$ ). However I did detect a positive correlation between total parasitemia and the H/L ratios ( $p=0.02$ ,  $R^2=0.094$ , Linear Regression) (Figure 5). This suggests that hemoparasite infections provoke a strong immune system response that distorts the normal hematological profile.

### ***Ectoparasite burden***

Ectoparasite burden, quantified on a bird's primaries, varied substantially among Wood Thrushes; it ranged from 0 to >500 (Ectoparasite score range: 0-5). Ectoparasites score declined with the advance of summer, and was significantly correlated to Julian date (Spearman's  $\rho=-0.503$ ,  $p<0.001$ ,  $n=56$ ). Ectoparasite score was also negatively correlated with total fat score (Spearman's  $\rho=-0.286$ ,  $p=0.032$ ,  $n=56$ ). I did not detect any effects of fragmentation status on bird ectoparasite scores based on a Mann-Whitney  $U$ -test ( $U=322$ ,  $p=0.245$ ,  $n=56$ ).

## Discussion

Wood Thrushes are very susceptible to forest fragmentation; they are among the first species to disappear when a fragment becomes degraded. Nevertheless, I found Wood Thrushes in Midwestern forest patches as small as 0.016km<sup>2</sup>. Although superficially similar, Wood Thrushes found in small fragments differed in several key aspects from those occurring in unfragmented areas.

My results indicate that forest fragmentation does not appear to affect the age distribution of Wood Thrushes, which means that birds in specific age classes did not prefer particular types of forest patches. This result should, however, be interpreted with some caution given that I were not able to distinguish, on the basis of plumage characters, After Second Year birds that were of different ages. Also, I did not detect any differences in sex ratios between fragmented and unfragmented sites. Taken together, these results suggest that birds do not segregate themselves according to age and sex into patches of differing habitat quality.

There appears to be no impact of forest fragmentation on WOTH body size as measured through wing, tail or tarsus length. Male Wood Thrushes had longer tails than females. This is a pattern observed among many passerine taxa, and there is evidence that tail length is an honest indicator of male quality. Birds caught late in the season tended to have shorter tails and wings compared to the birds caught in early summer. The most likely explanation for this pattern is that feathers wore away with the advent of the summer; this is particularly plausible for a ground-foraging species.

Wood Thrushes tend to be fatter in late season than in early season. This might be because in early season, Wood Thrushes have just arrived in the breeding habitat after a long distance migration which is energetically expensive; once settled down, birds start to restore

their fat deposits and gain more weight in breeding season (Oven and Moore, 2006). Alternatively, it is possible that late summer ectoparasite decreases allow birds to build up fat deposits. Fragment quality does not appear to influence either bird fat reserves or condition. Given that all birds arrive on the breeding grounds in the same state of depleted fat reserves, it is perhaps not surprising that habitat quality does not appear to have a clear effect on body condition.

Wood Thrushes in unfragmented areas tended to sing louder and be more aggressive than those in fragmented sites. This probably indicates that they were actually breeding as opposed to being transient summer occupants of fragmented areas and thus less committed to defending their territories. My observations underscore the argument that although some Wood Thrushes may be present in small fragments, they do not necessarily breed there successfully.

Wood Thrushes had higher hematocrit values in early season and the values decreased as the summer progressed. High hematocrit values are generally observed in migrating birds because of increased oxygen demands tied to the aerobic requirements of migration (Carpenter 1975), possible dehydration experienced during migration (Biebach 1990, Carmi et al. 1992), or both. Wood Thrushes in unfragmented sites had higher hematocrit values than those in fragmented sites. A couple of possible explanations may account for these results. First, it is conceivable that because birds in unfragmented sites are more aggressive, and more active (possibly because they are breeding), they face higher oxygen demands. Alternatively, because low hematocrit is indicative of malnutrition (Campbell and Dein 1984), it is possible that lower hematocrit values in fragmented area birds simply reflect the low quality of these sites. Indeed, previous research suggests that temperate forest fragments offer only reduced food resources (Zanette, et al. 2000).

I found that Wood Thrushes caught in early season tended to have lower leukocyte counts than those caught in late season. This may reflect that birds arrive in poor condition after migration and start to recover during their breeding season. It is also possible that during migration, a host faces reduced exposure to pathogens and consequently down regulates its immune system.

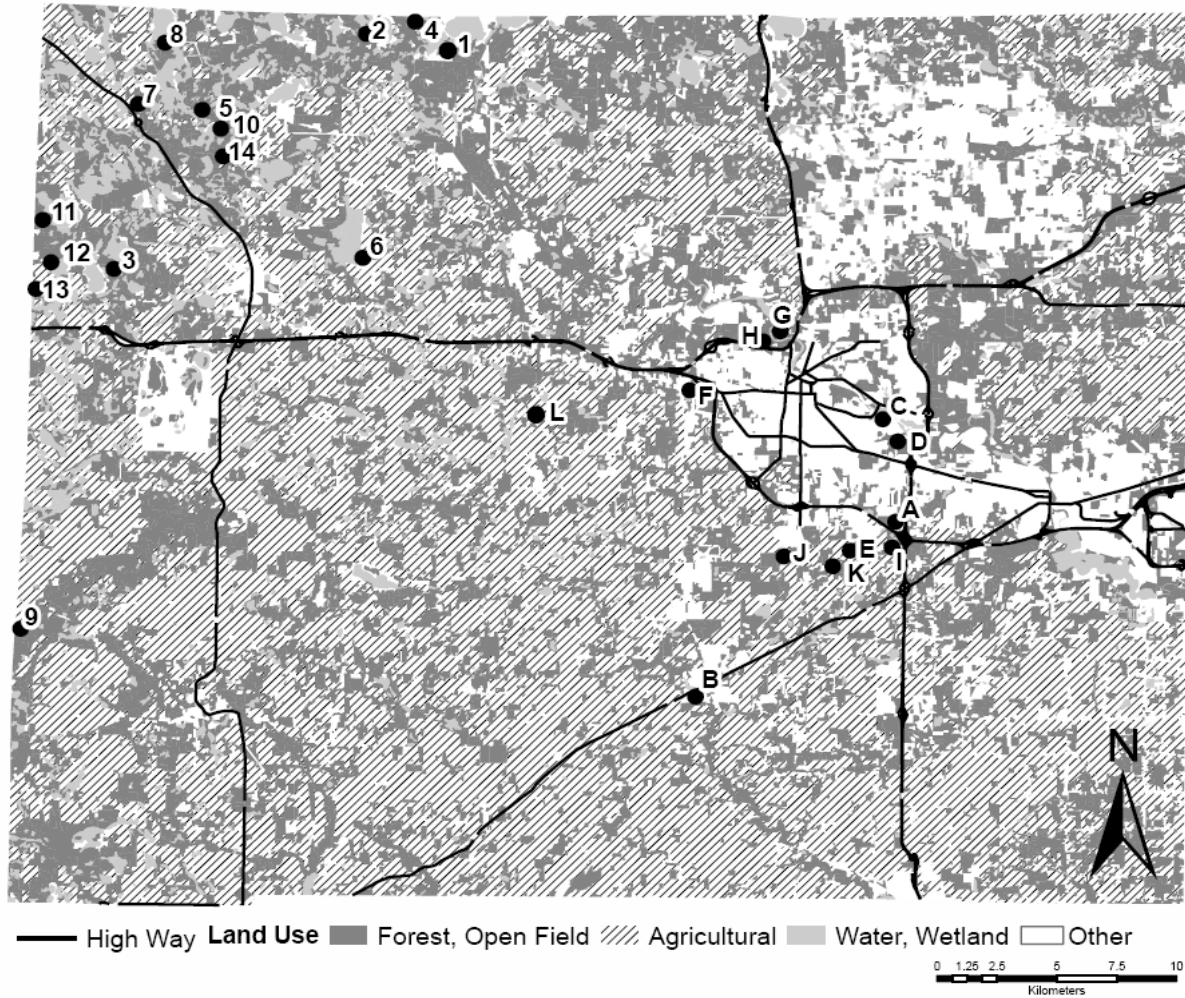
Contrary to my expectations, H/L ratios of Wood Thrushes in fragmented sites were no higher than those in unfragmented sites. Previous investigations in Wood Creepers showed that nestlings growing in the small forest patches experienced higher H/L ratios compared with the nestlings growing in the large forest patches because of food limitations (Suorsa et al. 2004). My results did not reveal any differences between WOTH H/L ratios in fragmented and unfragmented areas. This may be because the birds I studied were adults, rather than nestlings, with H/L ratios affected factors other than food resource. I found that total parasitemia can affect Wood Thrushes' H/L ratios: Wood Thrushes who have higher parasitemia also have higher H/L ratios. Lymphocytes are responsible for immunity, and since heterophil numbers differed little among seasons, higher H/L ratio probably reflected a reduced number of lymphocytes. This could indicate that birds with lower immunity were more likely to develop a patent infection.

Ectoparasite score was negatively correlated with the total fat score, reflecting the fact that birds with higher ectoparasite burdens were thinner than those with lower ectoparasite burdens. This might be because more ectoparasites consume energetic resources that are then not available to the bird. This relationship suggests that ectoparasites have a deleterious effect on their Wood Thrush host, although experimental manipulations would be necessary to confirm this. My results also show that birds caught during early season, and which were in poorer body

condition had more ectoparasites than those caught in late season, when they had started to recover and restore their fat.

In conclusion, Wood Thrushes in unfragmented sites were in better condition and were behaviorally more aggressive than those in fragmented sites. Ectoparasite burden decreased during the summer and was negatively correlated to fat deposits, suggesting that ectoparasites had a negative impact on the energetic balance of the bird. Fragmentation did not appear to have an impact on the hemoparasite infection and ectoparasite burden, most likely because birds acquired parasites during the previous season or in their wintering grounds. My results suggest that fragmentation has some impacts on the physiology and health status of Wood Thrush, but some other effects might not be detected immediately. In addition, the timing of measurements appears to be an important issue that should always be considered as a covariate to the physiological condition and infection status of Wood Thrushes.

## Figures

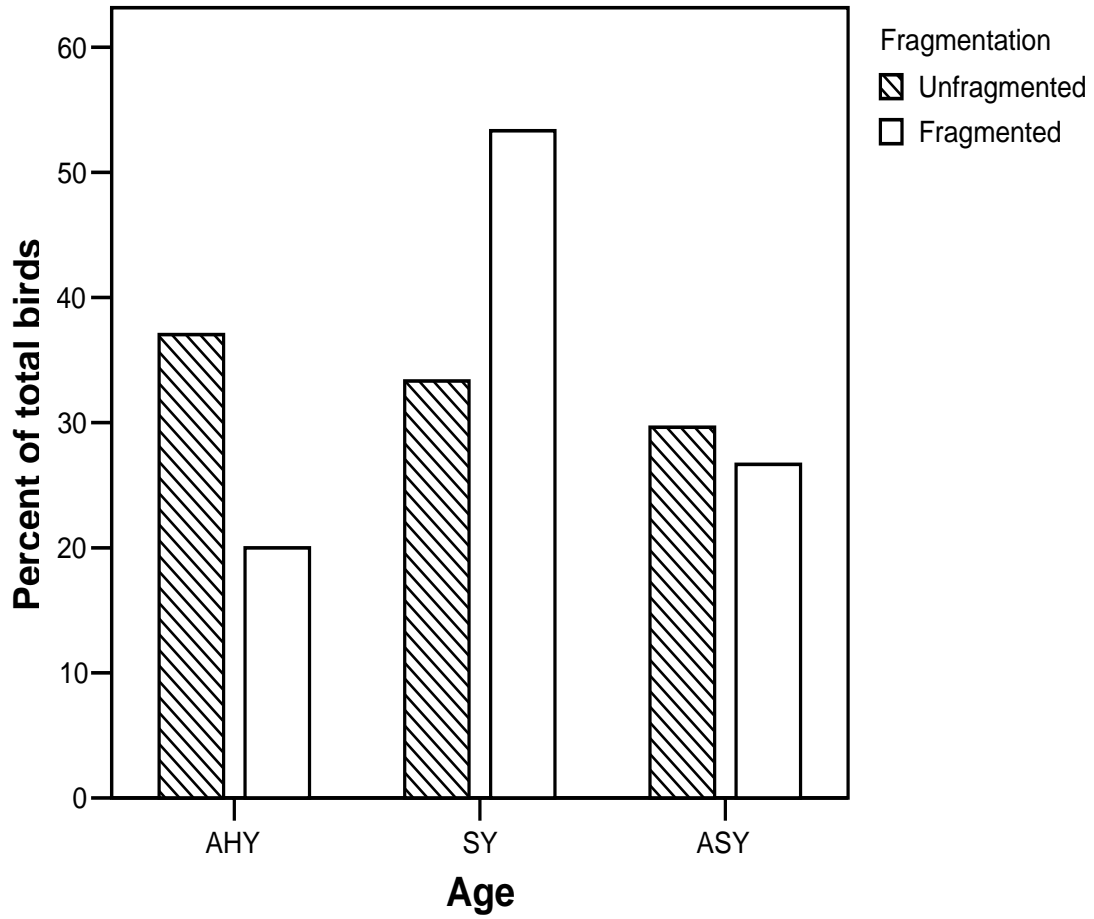


**Figure 1.** GIS map of Washtenaw County, Michigan, with locations of fragmented and unfragmented study sites.

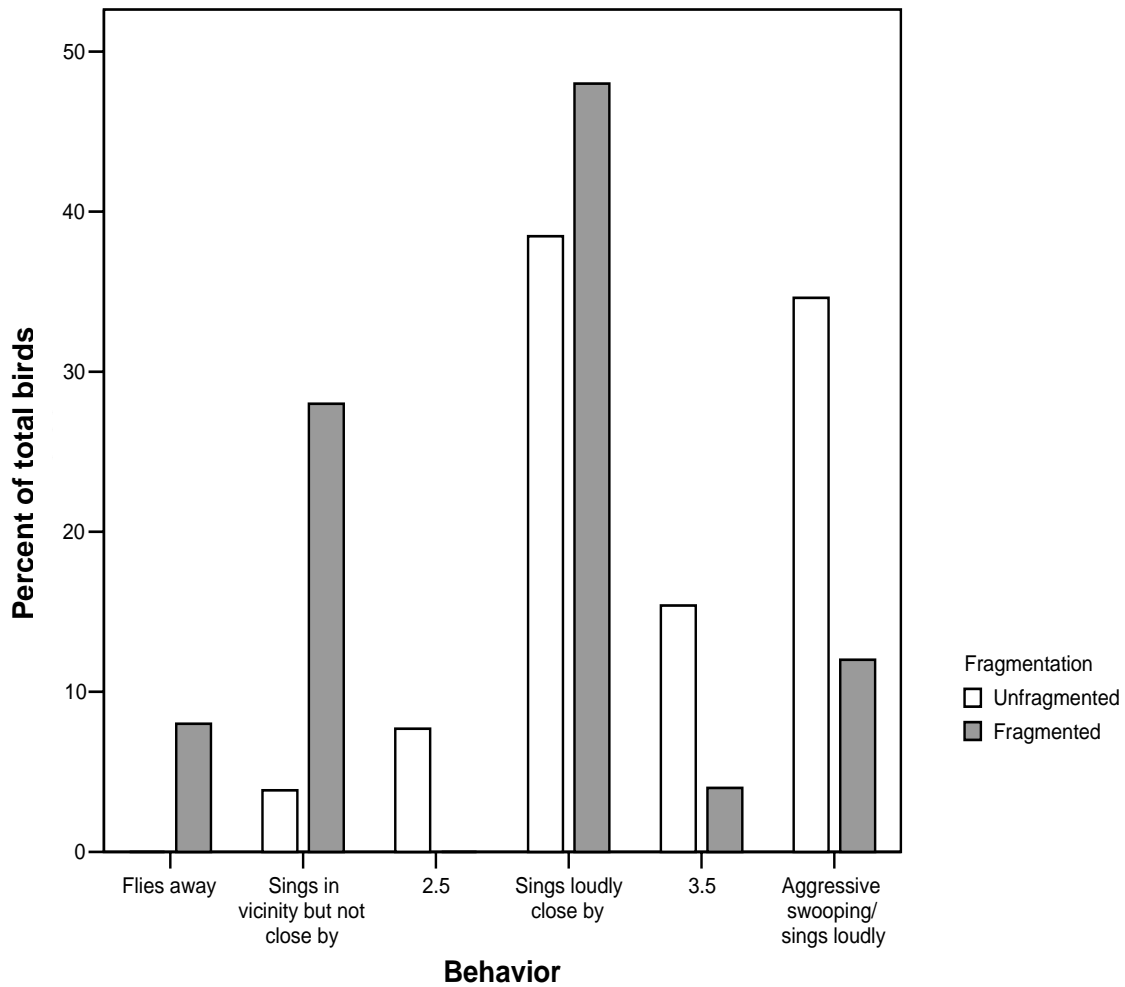
**Unfragmented sites:** 1. Potawatomi Trail; 2. Pickerel Lake; 3. Discovery Center; 4. Silver Lake; 5. Pinckney; 6. Four Mile Lake; 7. Roepke Rd.; 8. Joslin Lake; 9. Sharon Hollow Area; 10. Embury/N.Territorial; 11. Waterloo-Glenn Rd.; 12. Waterloo-Katz/Glenn Rd.; 13. Waterloo-List Rd.; 14. Gorman Lake

**Fragmented sites:** A. Scarlett Mitchell; B. Curtiss Park; C. Huron Hill; D. Huron Pkw nature area; E. Landfill area; F. Dolph Park; G. Barton Park; H. Bird Hills; I. Lillie Park; J. AA Municipal Airport; K. Stone School Rd; L.1457 Lima Center Rd.

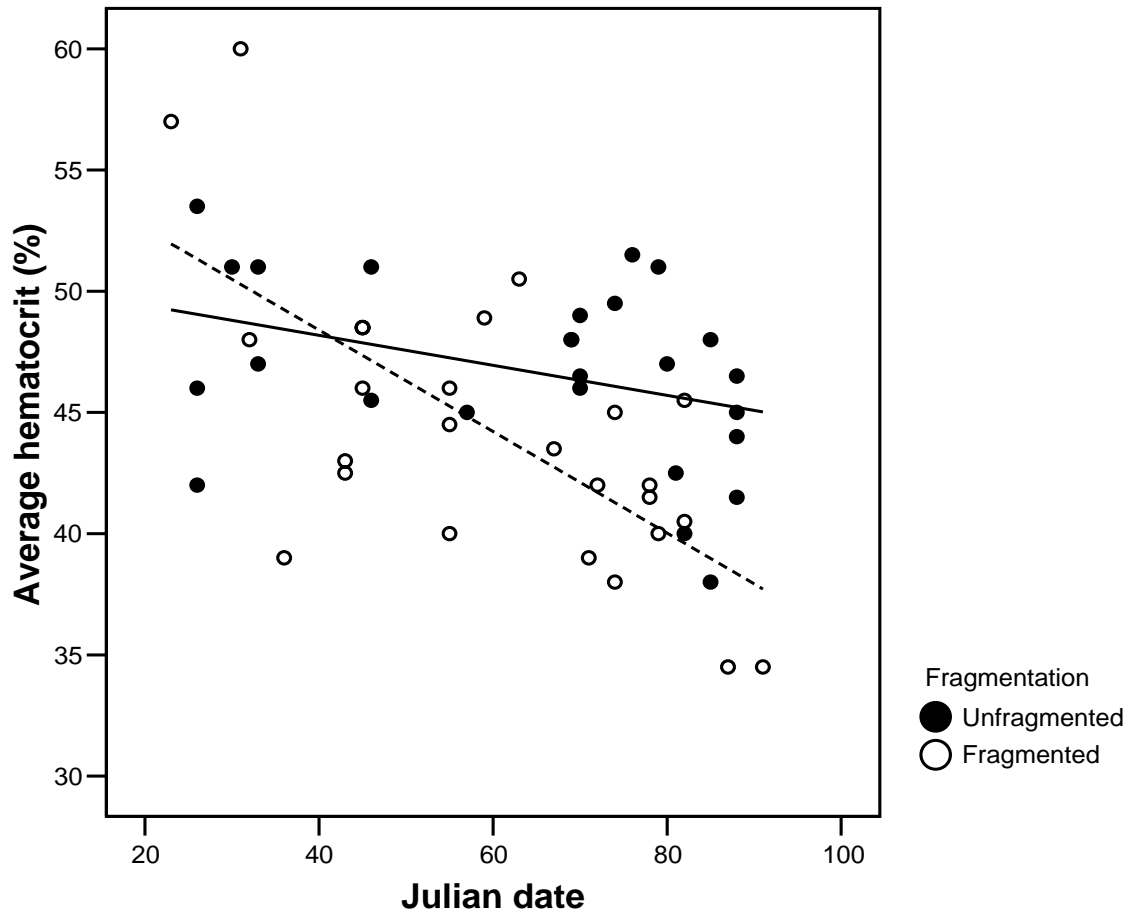




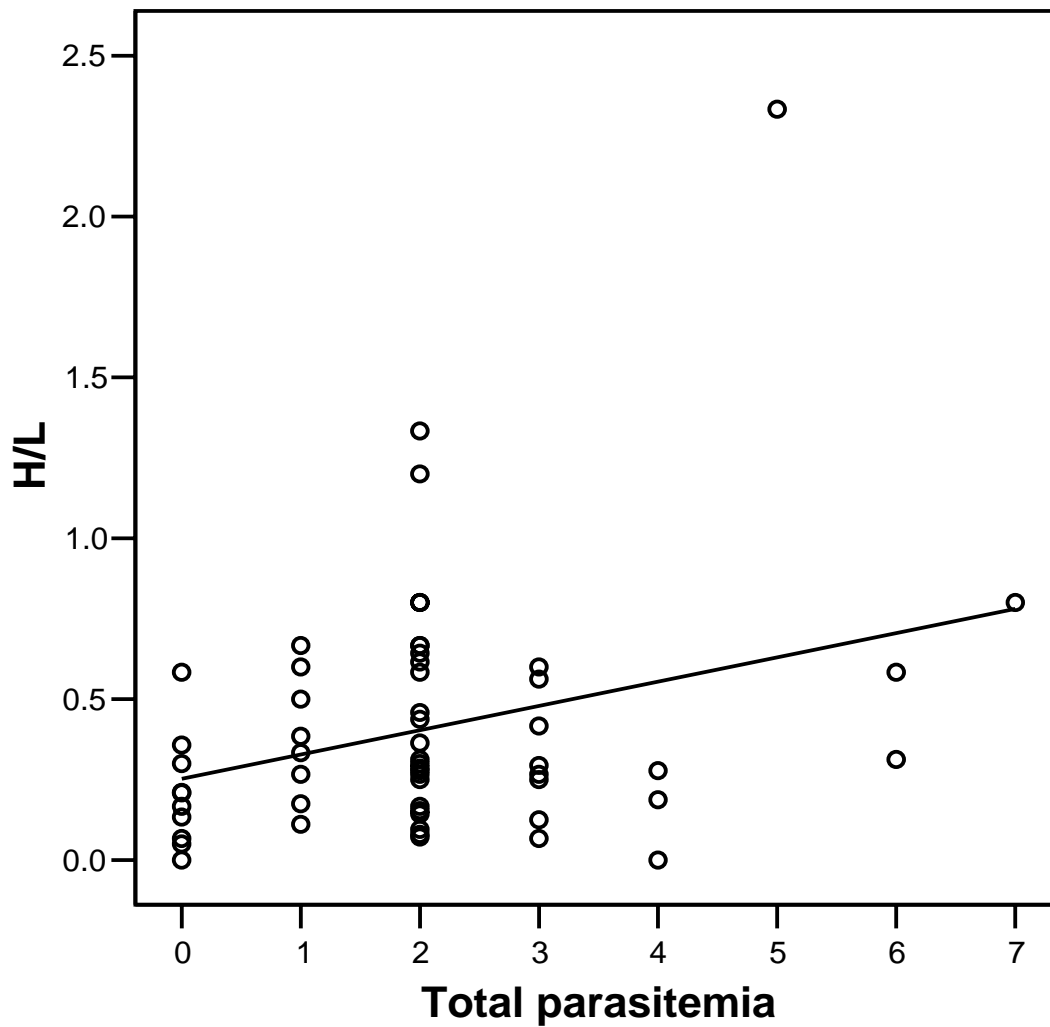
**Figure 2.** Age distributions of WOTH in fragmented and unfragmented areas. AHY= After Hatching Year; SY=Second Year; ASY=After Second Year.



**Figure 3.** Resident Wood Thrush behavior (as % of total birds) in fragmented and unfragmented areas. Fragmented sites (gray bar), and unfragmented sites (open bar).



**Figure 4.** Birds from fragmented sites had lower hematocrit especially towards the end of the summer. Unfragmented sites (black circles, solid line), and fragmented sites (open circles, dashed line).



**Figure 5.** Heterophil to lymphocyte (H/L) ratios in Wood Thrushes in relation to total parasitemia (total infected cells per 10,000 RBCs) ( $r=0.3$ ,  $p=0.02$ ).

## Tables

**Table 1.** Wood Thrush conservation references.

Reference	Area	Effect
Longcore, J.R. and Jones, R.E. 1969	Delaware	The greatest nest success was associated with late season nests (June and July), with spicebush and black gum vegetation and with the lower heights of nest above ground level (below 8.5 feet). Low nest success was associated with May nesting, red maple and heights above nine feet.
Bertin, R.I. 1977	Western Connecticut	WOTH tended to select sites with the wettest ground. Proximity to water and density of understory cover may have been important to a lesser degree. Required trees greater than about 12m in height, perhaps for use as song perches.
Trine, C.L. 1998	Southern Illinois	Maintaining WOTH populations in the Midwest might require much larger (>2500 ha) reserves than populations in the east, where even a small woodlot (<20 ha) has been shown to be a consistent population source. Impacts of habitat fragmentation may have greater regional variation that has previously been acknowledged.
Powell, L.A. et al. 2000	Georgia	Thinning and prescribed burning didn't reduce adult or juvenile survival during the breeding season or apparent annual adult survival.
Fauth, P.T. 2000	Northern Indiana	Density of WOTH was negatively related to area of forest fragments. Be part of a regional sink for WOTH.
Weinberg, H.J. and Roth, R.R. 1998	Delaware	Small fragments were populations sinks
Underwood, T.J. and Roth, R.R. 2002	Delaware	Productivity indices based on non-reproductive variables didn't reflect productivity trends or changes. Only an intensive measure of actual productivity or a partial measure of it be used to make inferences about annual productivity of a population
Brown, W.P. and Roth, R.R. 2002	Delaware	Clutch size, number of eggs incubated and number of eggs hatched were greater in early nests than in late nests. Fledglings from early nests were more likely to be recruited as breeders in the local population. ASY birds returned to breed at higher rates than did SY birds. SY males returned at a higher rate than did SY females.
Artman, V.L. and Downhower, J.F. 2003	Ohio	Prescribed burning had minimal effects on nesting ecology of WOTHs.
Phillips, J. et al. 2005	Ontario	WOTH breeding in woodlots with embedded house had higher rates of parasitism by cowbirds than WOTH in woodlots with adjacent house or undeveloped woodlots. This increased nest predation resulted in significant reductions in seasonal productivity in developed woodlots.
Aquilani, S.M. and Brewer, J.S. 2004Oct 2004	Northern Mississippi	Nests < 150 m from clearcut edges had lower nesting success compared to forest interior habitats and other edge types. Abundance of forest obligates and success of WOTH nests was greater in fragments>55 ha than in smaller fragments.
Hames, R.S. et al 2002	Eastern US	Acid rain has negative effect on the predicted probability of breeding.

**Table 2.** References on birds in fragmented habitats in the upper midland of Michigan.

<b>Reference</b>	<b>Species</b>	<b>Area</b>	<b>Effect</b>
Roth, R.R. and Johnson, R.K. 1993	WOTH	Delaware	The dynamics of a population of WOTH in a Delaware woodlot didn't meet all predictions of the forest fragmentation hypothesis. A period of elevated predation caused failure prompted greater emigration by an ever younger, less site faithful population. High emigration coupled with stable immigration, stable recruitment of local young and even normal mortality of residents would yield a declining population.
Hoover, J.P. and Brittingham, M.C. 1995	WOTH	Pennsylvania	Nesting success differs significantly among forest size categories. Rates of predation differ significantly. Relative abundance of avian nest predators higher in small forest fragments than in the large forest size.
Burke, D.M. and Nol, E. 2000	Ovenbird, Red-eyed vireo, Rose-breasted Grosbeak, Veery, WOTH	South-central Ontario	Only the largest fragments acted as sources for ovenbird and WOTH. Ovenbird and WOTH were the most area-sensitive, and rose-breasted Grosbeak and veery the least. All four species had significantly lower reproductive success in small as compared to large forest fragments.
Driscoll, M.J.L. and Donovan, T.M. 2004	WOTH	New York	In contiguous landscapes, daily survival rate didn't differ between edge nests and interior nest. In fragmented area, daily survival was higher in interior than edge.
Hoover, J.P. et al. 2006.	Acadian flycatchers	Illinois	Nest predation and brood parasitism were highest near the edge and decreased with increasing distance from the edge.
Mazerolle, D.F. and Hobson, K.A. 2003	Ovenbird	Central Saskatchewan	Boreal forest edges abutting agricultural fields do not appear to reduce habitat use or quality for breeding male ovenbirds.
Imbeau, L. and Desrochers, A. 2002	Three-toed woodpecker	Quebec	Individual woodpeckers in shredded forests did not select foraging trees further away from clear-cut edges than available ones. Continuous forests might provide better nesting habitat than residual, shredded forests.
King, D.I. et al. 1996	Ovenbird	New Hampshire	Nest survival was higher in the forest interior. Clearcutting in extensively forested landscapes can affect ovenbird reproductive success.
Knutson, M.G. et al. 2004	Cavity nestling species, cup nesting species	Southeastern Minnesota, Southwestern Wisconsin, Northeastern Iowa	Nest success was lowest for open-cup nesters, species that reject brown headed cowbird eggs, species that nest near forest edges and neotropical migrants. Forest area may not be a strong indicator of nest success in landscapes where all the available forests are fragmented.

**Table 3.** Sizes and geographic coordinates of fragmented and unfragmented study sites investigated in this project. Area for unfragmented sites represents area of the total WPRA forest complex.

<b>Unfragmented sites in WPRA</b>	<b>Area</b>	<b>Coordinates</b>
1. Potawatomi Trail	83 km <sup>2</sup>	42°24'25.47"N. 83°57'39.58"W
2. Pickerel Lake	"	42°24'42.86"N. 83°59'11.93"W
3. Discovery Center	"	42°19'19.63"N. 83°05'01.51"W
4. Silver Lake	"	42°25'02.22"N. 83°58'03.32"W
5. Pinckney	"	42°23'01.16"N. 84°03'35.10"W
6. Mile Lake	"	42°19'42.69"N. 83°57'59.12"W
7..Roepke Rd	"	42°23'13.64"N. 84°04'50.49"W
8. Joslin Lake	"	42°24'40.87"N. 84°04'14.53"W
9. Sharon Hollow area	"	42°10'45.78"N. 84°07'59.44"W
10. Embury/N.Territorial	"	42°22'42.38"N. 84°03'16.17"W
11. Waterloo-Glenn Rd	"	42°18'49.93"N. 84°13'07.23"W
12. Waterloo-Katz/Glenn Rd	"	42°18'38.05"N. 84°11'59.09"W
13. Waterloo-List Rd	"	42°19'05.97"N. 84°14'20.17"W
14. Gorman Lake	"	42°22'05.72"N. 84°02'16.19"W

<b>Fragment sites</b>	<b>Area</b>	<b>Coordinates</b>
1. Scarlett Mitchell	0.15km <sup>2</sup>	42°13'57.52"N. 83°41'33.45"W
2. Curtiss Park	0.09km <sup>2</sup>	42°09'37.05"N. 83°47'22.22"W.
3. Huron Hill	0.04km <sup>2</sup>	42°16'11.61"N. 83°41'48.90"W
4. Landfill area	0.05km <sup>2</sup>	42°13'16.91"N. 83°42'46.04"W
5. Dolph Park	0.23km <sup>2</sup>	42°16'50.80"N. 83°47'47.13"W.
6. Barton Park	0.16km <sup>2</sup>	42°18'14.41"N. 83°45'07.50"W
7. Bird Hills	0.25km <sup>2</sup>	42°18'07.52"N. 83°45'35.68"W
8. Lillie Park	0.19km <sup>2</sup>	42°13'22.44"N. 83°41'27.94"W.
9. AA Municipal Airport	0.24km <sup>2</sup>	42°12'57.44"N. 83°44'43.66"W.
10. Stone School Rd	0.016km <sup>2</sup>	42°12'57.27"N. 83°43'07.46"W
11. 1457 Lima Center Rd	0.13km <sup>2</sup>	42°16'06.24"N. 83°57'16.58"W
12. Huron Pkw nature area	0.08km <sup>2</sup>	42°15'43.50"N. 83°41'30.92"W

**Table 4.** Results of bird censuses for the different areas surveyed.

Bird species	A	B	C	D	E	F	G	H	I	J	K	L	M	#
ACFL (Acadian Flycatcher)								x	x				x	3
AMCR (American Crow)								x				x		2
AMGO (American Goldfinch)	x		x			x	x		x	x	x	x	x	9
AMRE (American Redstart)						x						x	x	3
AMRO (American Robin)	x	x	x	x	x	x	x	x		x	x		x	11
BAOR (Baltimore Oriole)			x			x			x					3
BCCH (Black-capped Chickadee)		x	x			x	x	x	x	x	x		x	9
BGGN (Blue-gray Gnatcatcher)									x					1
BHCO (Brown-headed Cowbird)						x		x	x				x	4
BLJA (Blue Jay)		x	x				x		x		x		x	6
BWWA (Blue-winged Warbler)												x	x	2
CAWR (Canada Warbler)		x												1
CEWA (Cedar Waxwing)		x					x			x			x	4
COGR (Common Grackle)		x		x	x			x	x	x				6
COYE (Common Yellowthroat)									x			x	x	3
CSWA (Chestnut-sided Warbler)												x		1
DOWO (Downy Woodpecker)		x	x				x				x			4
EATO (Eastern Towhee)									x			x		2
EWPE (Eastern Wood Pewee)		x	x	x	x		x	x	x	x	x	x	x	11
GCFL (Great-crested Flycatcher)		x	x										x	3
GRCA (Gray Catbird)		x				x		x				x		4
HAWO (Hairy Woodpecker)									x					1
HOWA (Hooded Warbler)												x		1
HOWR (House Wren)			x				x							2
INBU (Indigo Bunting)		x				x								2
KILL (Killdeer)										x				1
MODO (Mourning Dove)		x												1
NOCA (Northern Cardinal)	x	x	x	x		x	x	x	x	x	x	x	x	12
NOFL (Northern Flicker)		x			x									2
OVEN (Ovenbird)								x						1
PIWA (Pine Warbler)													x	1
RBGR (Rose-breasted Grosbeak)			x			x		x		x				4
RBWO (Red-bellied Woodpecker)								x		x	x		x	4
REVI (Red-eyed Vireo)				x			x	x	x	x		x	x	7
RTHU (Ruby-throated Hummingbird)							x							1
RWBL (Red-winged Blackbird)		x									x		x	3
SCTA (Scarlet Tanager)		x						x		x			x	4
SOSP (Song Sparrow)		x				x		x			x		x	5
SSHA (Sharp-shinned Hawk)		x												1
TUTI (Tufted Titmouse)		x	x				x	x	x			x	x	7
VEER (Veery)								x				x	x	3
WBNU (White-breasted Nuthatch)						x		x	x	x	x	x	x	7
WOTH (Wood Thrush)	x	x	x	x	x	x	x	x	x	x	x	x	x	13
YEWA (Yellow Warbler)		x				x		x				x		4
YTVI (Yellow-throated Vireo)		x			x	x		x	x		x	x	x	8
<b>Number of bird species</b>	<b>4</b>	<b>22</b>	<b>13</b>	<b>6</b>	<b>6</b>	<b>15</b>	<b>13</b>	<b>21</b>	<b>18</b>	<b>14</b>	<b>13</b>	<b>18</b>	<b>24</b>	

**Location Code:**

**A:** Scarlett Mitchell; **B:** 4 Mile Lake; **C:** Ann Arbor Airport; **D:** Lillie Park; **E:** Landfill; **F:** Barton Park; **G:** Bird Hills; **H:** Lakeview Trail; **I:** Silver Lake; **J:** Curtiss Park; **K:** Huron Pkwy Nature area; **L:** Potawatomi Trail; **M:** Pickerel Lake; **#:** Number of Parks



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