The Effects of Trophic Cascading by *Odocoileus virginianus* on Breeding Songbird Populations

Amber VanderGeld, Jason Oosterhouse and Robert Keys, Ph.D.

Cornerstone University

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ABSTRACT

A dynamic ecosystem is maintained by healthy interactions between trophic levels. In recent years, *Odocoileus virginianus* (white tailed deer) populations have increased resulting in trophic cascades. The effects of this cascade on breeding bird populations are not yet fully understood. Research was conducted on five 12 ha sites with varying degrees of deer trail fragmentation (10.74 - 20.83 trails/ha) in a mixed woodland near Hastings, Michigan. Data on breeding bird diversity, predator abundance, vegetative height, percent cover, and diversity at three vegetative layers (herbaceous, mid, and canopy) were collected on each of the sites. We hypothesized that as the density of deer trails increases, the biodiversity of breeding songbirds will decrease due to losses in vegetative cover and increased predation. No significant correlation was found in the diversity of songbirds in relation to the density of deer trails between the sites (Spearman rank coefficient correlation). However, songbird diversity was linked to other factors related to deer density within the woodland. The height of the ground cover was a significant factor in the diversity of woodland songbirds (r_s=0.872, P=0.05) and highly correlated with all songbirds (r_s=0.821) using the woodlands and their edges. The diversity of the ground cover was also strongly correlated with the number and diversity of ground nesting songbirds (r_s=0.700) within the woodland habitat. This leads us to conclude that deer trail density alone is not directly correlated with breeding bird diversity and that deer trail density may not be a good indicator of deer density.

INTRODUCTION

Ecosystem balance is maintained through healthy interactions between various levels of the trophic structure (Costanza 1999). When the trophic structure of the system is changed and becomes imbalanced a number of issues can arise, especially when one species has undue affects on multiple trophic levels. Numerous researchers have shown how trophic cascading affects the natural order of systems, both for the good and the bad (Fortin et al. 2005, Wardle et al. 2005, Migge-Kleian et al. 2006). Fortin et al. found that an increase in *Canis lupus* (wolf) encounters caused *Cervus canadensis* (elk) to change their habitat preference from *Populus tremuloides* (aspen) stands to conifer forests due to a number of behavioral mechanisms. Wardle et al. researched the role of trophic cascading in the relationship between above ground food webs and soil food webs. Wardle et al. found that consumers in above ground food webs can be the driving force for soil food webs. Migge-Kleian et al. report that invasive earthworms can have negative cascading effects on the abundance of micro- and mesofauna through direct and indirect means. In northern hardwoods forests, one of the major influences on the trophic structure is *Odocoileus virginianus*, the white-tailed deer. When populations of white-tailed deer become superabundant, the structure of the trophic pyramid in a system can become skewed resulting in a trophic cascade with negative effects on vegetative density and composition.

According to Martin et al. (2010), top-down and bottom-up consequences on vegetative communities were directly related to deer density in their research done on temperate forest islands that had varying populations of deer. Their results showed that without deer, the vegetation in the understory and shrub layer was very dense with varying structure and composition. Where deer had been present for the longest period of time vegetation below the browse line was extremely simple.

Horsley, Stout, and deCalesta (2003) also attributed the damage of forest vegetation, crops, and wildlife habitat to deer. In their study they showed that as deer density increased, negative linear trends in the height of *Betula lenta* (birch), *Acer rubrum* (red maple), and *Fagus grandifolia* (American beech) trees occurred. The areas avoided by or resilient to deer browsing increased in deer dense areas. This resulted in an altered trophic structure and a forest rich with certain browse resistant or unbrowsed species and a lacking of those species favored by deer.

Trophic cascades in the vegetative community can also be triggered by deer populations through direct and indirect mechanisms (Rooney & Waller 2003). Continual browsing on the same plant species can limit their regeneration and eliminate certain populations, particularly of herbaceous plants. These changes are what trigger trophic cascades and physically modify the habitat. Rooney and Waller also noted that other species, such as small mammals, birds and invertebrates can possibly be influenced by the restructuring in the vegetative community.

Deer can also physically alter the vegetative community through the creation of deer trails. Deer trails are paths through vegetation and forest litter created by deer travel. Vegetation is physically removed in trail locations, and the forest habitat is divided (McCaffery 1976). Heys and Keys (2007) discovered that at the Pierce Cedar Creek Institute ground nesting birds were negatively affected in relationship to their proximity to deer trails. This was due to predator use of deer trails to penetrate the hardwood forest.

In addition to their negative impact on plant species, large densities of white-tailed deer have been shown to profoundly impact the abundance of bird populations and their composition. Studies have generally agreed that large populations of deer decrease the abundance of bird populations (Allombert et al., 2005; deCalista, 1994; McShea & Rappole 2000). The deer cause this decrease of abundance through destruction of understory vegetation and habitat (Allombert et al. 2005).

For example, after performing a study on songbirds in managed forests located in Pennsylvania, deCalista (1994) concluded that species richness and abundance only decreased in intermediate-canopy nesting songbirds. McShea and Rappole (2000) found that the diversity of birds as a whole did not increase when deer were fenced off from an area due to replacement of bird species as the undergrowth went through phases of succession. Although studies have demonstrated that there is a negative effect on the *abundance* of bird populations due to a highly concentrated white-tailed deer population, they are lacking in regards to the *diversity* of birds.

We studied the effects of trophic cascading by white-tailed deer on breeding bird biodiversity and populations within the forested woodlands of the Pierce Cedar Creek Institute properties. For this study, we hypothesized that as the density of deer trails increases, the biodiversity of breeding songbirds will decrease due to losses in vegetative cover and increased predation. Breeding bird populations fluctuate from year to year; thus this study ideally represents the beginning of a multi-year study of these forests, deer influences, and breeding bird diversity.

METHODS

Study Area

The research was conducted on the property of the Pierce Cedar Creek Institute (PCCI) in Barry County, MI (42°36’06”N, 85°18’04”W). The research focused on the mixed woodlands throughout the 267 ha property.

Deer Trail Counts

Our study was performed during the summer causing certain methods for measuring deer abundance, such as a trail camera survey, to be inappropriate. McCaffery performed a study in Northern Wisconsin (United States) to determine if deer trail counts could be used as an index for deer populations (1976). He found that deer trail density indices were positively correlated with sex-age-kill analysis and pellet group surveys. This demonstrated that deer trail counts are an effective index of deer abundance. We used this method to measure summer deer abundance. We mapped the deer trails in the woodlands using a Thales MobileMapper GPS unit (Magellan). Surveying began in early March while the snow was still present and was finalized in early May. During deer trail surveying, only trails showing medium to heavy deer use were mapped. After mapping, deer trails were uploaded into ArcGIS (ESRI) and were analyzed to parse the PCCI woodlands into five 10-12 ha zones based on the density (trails/ha) of deer trails and similarity of woodland types (Walker & Keys 2005)(Fig.1).

Bird Point Counts

We designated six point count sites in each of the five zones. The point count sites were placed an equal distance from each other in each of the five zones with a minimum of 150 m between each of the point count sites (Ralph et al. 1993). Previous research had shown that there are few areas within the PCCI property in which deer trails are more than 40 m apart (Heys & Keys 2007). To document current abundance, distribution, and nesting patterns of breeding birds on Pierce Cedar Creek property we used the point count methods described in the Handbook of Field Methods for Monitoring Landbirds (Ralph et al. 1993). We stood at a designated point count site for a five minute period of time and recorded all seen and heard birds within 75 m. When possible the sex and nest location were recorded. Other conditions such as time of day and weather were also documented. Data collection in the field took place weekly from mid-May to July. We observed all point count sites (30 sites) every week for six weeks, giving a total of 15 hours of bird survey time.

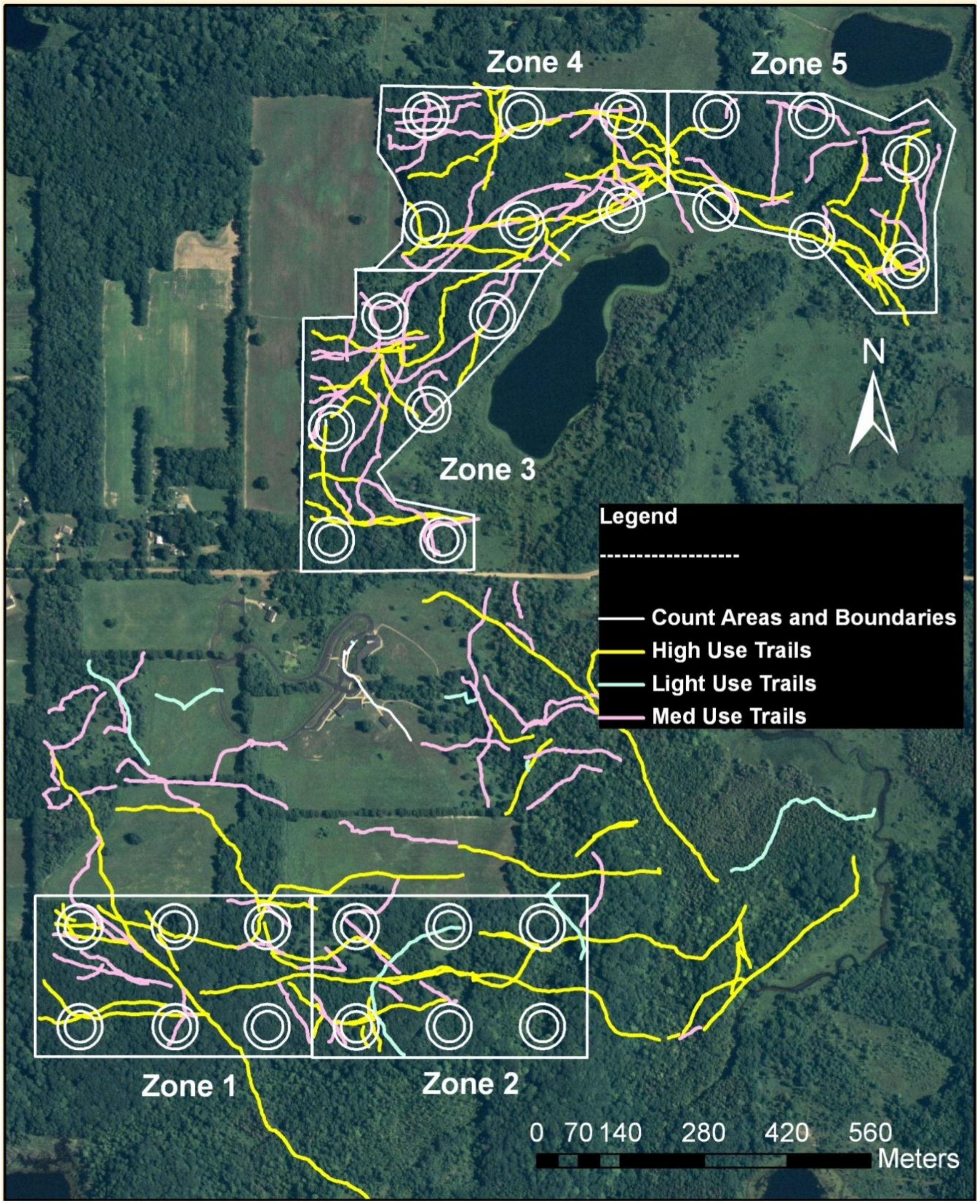

Figure 1. Five study zones displaying mapped deer trails on the 267-ha Pierce Cedar Creek property

Vegetative Analysis

We conducted a vegetative analysis using a 25 m line-intercept transect sampling method to estimate plant community diversity and vegetative cover within each zone (Brower, Zar, & Von Ende 1998). Transects were placed 10 m east of each point count site. The transect line was divided into five meter intervals for more accurate data collection. Only plants physically intercepting the transect line were counted. Data was collected for the height and percent cover for three vegetative layers: herbaceous, mid-canopy, and canopy. The data found at the 30 different sampling sites were then used to calculate the biodiversity of the vegetative community in each zone relative to the deer density of the zone.

Predation

Throughout the research season we used automated cameras to survey potential predatory animals that may impact the nesting success of residential breeding birds. A Scoutguard 550/560 (HCO) infrared trail camera was mounted to a tree at an approximate 40 degree angle to a heavy use deer trail near each point count site. The cameras were attached for a period of 14 days, giving a total of 84 days of predator survey time per zone. Cameras were checked once a week for functionality and pictures were collected. At the conclusion of the fourteen days, camera cards were collected and the pictures were used to determine the relative abundance of bird predators. In order to determine relative abundance, each picture was counted as a predator contact, excluding repeat triggering of the camera by the same predator (i.e repeated pictures within the 1 minute reset of the camera). The mean number of predator contacts per day per zone was then calculated.

Analysis

We used Simpson's inverse diversity index to compare species numbers within zones because it is an index based on the number of species in a sample area. We combined bird point count data from each zone (n=6) to estimate Simpson's inverse diversity index ($1/D$) to establish weekly diversity levels for each zone. Maximum seasonal diversity was also subject to Simpson's inverse diversity index and was contrasted and compared between zones to determine the greatest diversity for each zone.

We correlated bird diversities with trail density, vegetation, and predator activity using Spearman rank coefficient correlation (r_s) tests. Correlations were subjected to a permutation test to determine if significance existed between the various correlates. Correlations were designated as significant if $P < 0.05$. Correlations with r_s values greater than or equal to 0.700 but less than 0.900 were deemed to have high correlative value, but were not significant.

RESULTS

Deer Trail Density

Our analysis of deer trail density (TrailDen) based on digital orthographic maps of PCCI and trail mapping revealed a continuum of trails density across the five study zones. Trail densities ranged from 10.74 to 20.73 trails/ha (Table 1).

Bird Diversity

Total bird diversity (*D*total) ranged from 21.62 to 28.07 using Simpson's Inverse Diversity Index (1/*D*) with the greatest diversity in Zone 3 and the lowest diversity in Zone 1 (Table 1). Ground nesting bird diversity (*D*1) ranged from 5.63 to 7.07 with the greatest diversity found in Zone 4 and the least diversity in Zone 1. For mid-canopy birds (*D2*) diversity ranged from 6.67 in Zone 1 to 13.03 in Zone 2. The diversity of canopy nesting birds (*D*3) ranged from 7.28 in Zone 5 to 11.31 in Zone 3. When looking specifically at woodland nesting birds (*D*wood), diversity ranged from 9.36 in Zone 5 to 12.6 in Zone 2. Finally, edge nesting bird diversity (*D*edge) ranged from 4.06 in Zone 3 to 10.56 in Zone 1 (Table 1).

Table 1. Distribution of trail densities across PCCI mixed woodlands and Simpson's inverse diversity indices (1/*D*) for birds in each study zone.

				Nesting Location			Breeding Habitat	
Zone	Trail Density per ha	Number[a]	Dtotal[b]	D1[c]	D2[d]	D3[e]	Dwood[f]	Dedge[g]
1	13.99	94	21.62	5.63	6.76	9.91	9.38	10.56
2	10.74	120	26.18	5.83	13.03	8.82	12.6	5.67
3	19.07	111	28.07	6.57	10.46	11.31	11.89	4.06
4	20.83	103	25.81	7.07	9.67	8.22	9.83	7.97
5	15.06	111	22.44	5.56	9.5	7.28	9.36	7.58

[a] Total number of birds. [b] Simpsons diversity index of total birds. [c] Simpsons diversity index of ground layer nesting birds. [d] Simpsons diversity index of mid layer nesting birds. [e] Simpsons diversity index of canopy layer nesting birds. [f] Simpsons diversity index of woodland nesting birds. [g] Simpsons diversity index of edge nesting birds.

Vegetation

Percent cover in the vegetative layers ranged from a mean of 15.69 to 66.62 percent in the ground layer (C1), from 18.11 to 28.44 percent in the mid layer (C2), and from 81.53 to 133.19 (multiple overlapping layers) percent in the canopy layer (C3) (Table 2). When examining vegetative height in the ground layer (H1) the greatest mean vegetative height was in Zone 3 (H1=0.41 m) and the shortest mean vegetative height in Zone 5 (H1=0.28 m). Finally, the largest mean diversity in the ground layer (CD1) was in Zone 4 (1/*D*=8.11) and the least diversity in Zone 1 (1/*D*=1.92) (Table 2).

Table 2. Analysis of mean percentage of vegetative cover, mean ground plant height and mean vegetative diversity of ground plants by study zone.

	Vegetative Cover Levels				
Zone	C1[a]	C2[b]	C3[c]	HL1[d]	CD1[e]
1	66.62	28.44	113.22	0.32	1.92
2	60.36	27.33	94.69	0.39	4.97
3	62.78	19.44	81.53	0.41	7.09
4	37.94	26.89	109.81	0.32	8.11
5	15.69	18.11	133.19	0.28	5.7

[a] Percent cover of ground layer. [b] Percent of cover mid layer. [c] Percent of cover canopy layer. [d] Height of ground layer in meters. [e] Diversity of Ground Cover using Simpson's Diversity Index(1/*D*).

Predators

The predator contacts made per zone during the two week sample time varied in species and number of contacts made (Table 3). The mean number of predator contacts per day ranged from 2.29 to 4.36 contacts/day. The least number of predator contacts/day occurred in Zone 5 and the largest number of predator contacts/day occurred in zone 4.

Table 3. Number of predator contacts made per zone during the two week sample time.

Species	Zone 1	Zone 2	Zone 3	Zone 4	Zone 5
Chipmunk	4	0	0	9	1
Coyote	1	1	1	0	0
Fox Squirrel	14	3	6	12	8
Gray Squirrel	0	0	0	4	2
Mouse	0	1	0	1	0
Opossum	3	0	2	0	0
Raccoon	30	44	31	35	21

Correlations

Trail Density. No correlation was found between trail density and total bird diversity (Spearman rank coefficient correlation test; P=0.7471; r_s=0.200). There was a significant positive correlation between trail density and ground level plant diversity (P=0.0374; r_s=0.900).

Bird Diversity and Vegetation. Canopy nesting birds were significantly and negatively correlated to the percentage of ground cover (P=0.037; r_s=-0.900). In the mid-canopy, there were no significant correlations to bird diversity. Total bird diversity was significantly and negatively correlated between the percentage of canopy cover (P=0.037; r_s=-0.900) and woodland bird diversity (P=0.037; r_s=-0.900). Percentage of canopy cover was also positively and negatively correlated with all other bird indices (Table 4).

The diversity of ground nesting birds was correlated strongly with the diversity of the ground cover and percentage of canopy cover. Mid-canopy nesting bird diversity was strongly correlated with the height of the ground cover and the percentage of canopy cover. Canopy nesting bird diversity was significantly correlated with the percentage of ground cover (*P*=0.037; r_s=-0.900) and strongly correlated with the ground cover height. Canopy nesters also showed a strong negative correlation related to the percentage of canopy cover (Table 4).

Table 4. Correlations between bird diversity and vegetation. Significant correlations are in bold.

	CD1[a]		C1[b]		C3[c]		H1[d]	
D[e]	r_s[f]	*P*	r_s	*P*	r_s	*P*	r_s	*P*
*D*total[g]	0.500	0.3910	0.000	1.000	**-0.900**	**0.037**	0.821	0.088
*D*1[h]	0.700	0.189	0.100	0.8730	0.700	0.189	0.564	0.3218
*D*2[i]	0.300	0.6238	-0.100	0.8729	-0.800	0.104	0.718	0.172
*D*3[j]	-0.200	0.7471	**0.900**	**0.037**	-0.700	0.189	0.821	0.089
*D*wood[k]	0.100	0.8729	0.300	0.6238	**-0.900**	**0.037**	0.872	0.053
*D*edge[l]	-0.300	0.6238	0.100	0.8729	0.700	0.189	-0.667	0.2189

[a]1/*D* for ground cover. [b]Percent cover ground layer. [c] percent cover canopy layer. [d]mean height ground layer (m). [e]Simpson's inverse diversity indices (1/*D*). [f] Spearman rank coefficient correlation. [g]total birds.[h] ground nesting birds. [i] mid-canopy nesting birds [j]canopy layer birds. [k]woodland nesting birds. [l]edge nesting birds.

Woodland bird diversity had a significant negative correlation with canopy cover (*P*=0.037; r_s=-0.900) and strong positive correlation with the mean height of the herbaceous layer. Edge species using the mixed woodland also showed a strong positive correlation with the percentage of canopy cover (Table 4).

Predation. An ANOVA comparing the predator contacts in each zone showed that there was no significant difference between the five zones related to predatory contacts (df=4, F=0.121, P=0.974). There were no significant correlations between predators and bird diversity (*P*=0.7471; r_s=-0.200), trail density (*P*=0.7471; r_s=0.200), and vegetative cover (ground: *P*=0.6238; r_s=0.300; mid-canopy *P*=0.1881; r_s=0.700; and canopy *P*=0.8729; r_s=-0.100).

DISCUSSION

Our analysis showed that trail density did not correlate with any aspect of bird diversity in the PCCI mixed woodlands. This nullifies our hypothesis that deer trail density would be negatively correlated with bird diversity. This would lead us to believe that any trophic cascades caused by deer do not affect the diversity of birds at PCCI. While there was a large difference between deer trail densities in the five zones, this did not have an impact on the biodiversity of birds within those zones. Although McCaffery

(1976) noted that deer trail density was directly linked to deer density, it is not known what the persistence of deer trails is after deer have been removed from the system or their abundance has decreased. With an aggressive hunting/culling campaign in place at PCCI it is possible that deer density no longer correlates with deer trail density (Rob Aicken personal communication).

We also expected to see a negative correlation between deer trail density and vegetative cover through the five zones. This also was not supported by our analysis. However, while cover differences were not supported, there was a significant positive correlation between deer trail density and the diversity of herbaceous ground cover. This is inconsistent with the research of Martin et al. (2010) who show that as deer density increased the structure of the vegetative community was simplified. This could be due to the fact that deer choose trail locations based on areas of high plant diversity. An alternative explanation could be that mild disturbances allow for species that prefer disturbance to populate the region surrounding an area of high deer trail density. Future study could address the differences between vegetative communities with the same amount of deer browse, parallel to and at distance from deer trails.

Predator contacts also were not correlated with deer trail density. We proposed that there would be a positive correlation between deer trail density and predator contacts. This was not supported in our analysis. As noted by Heys and Keys (2007) predation on bird nests increases in proximity to deer trails on the PCCI property. However, they also noted that with little exception, the mixed woodlands of the PCCI property are edge forests, with forest depths rarely greater than 250 m. This would allow predators to freely move through the forest system as a whole, and thereby making the usefulness of deer trails less significant than in a non-fragmented forest.

Our study supports that increased deer density is not related to bird diversity. This is consistent with the results of McShea and Rappole (2000). Our results would suggest that forest ecosystems do not need to be managed for deer to preserve breeding bird diversity. However, we do not advise that other factors such as bird composition and abundance be disregarded when managing deer populations.

While our initial hypotheses were not supported, there were multiple significant and strong correlations associated with the canopy cover in the mixed woodlands at PCCI. Canopy cover and overall breeding bird diversity was found to have a significant negative correlation. When breeding birds were divided by nesting habitat, we found a significant negative correlation between woodland nesting birds and canopy cover. This would seem to indicate that the percentage of canopy cover can be important in the diversity of woodland nesting birds. As canopy cover increases in density the diversity of nesting birds decreases. This is supported by Dillinger et al. (2007) on sympatric studies of Turideae (thrushes). Other species such as the *Catharus fuscescens* (veery) prefer less dense canopy cover and heavier herbaceous layers. However, while dense canopy is negatively correlated to woodland nesting bird diversity, the height of the herbaceous layer is positively correlated with the diversity of woodland nesters as well as canopy nesting species. As the plant height increased, so did the diversity of woodland nesting birds. Because plant height is often related to deer browse, it would seem that areas with less deer density would be less susceptible to heavy browse and the subsequent lowering of the herbaceous layer. It also stands to reason that as canopy density decreases the herbaceous layer would receive more sunlight and therefore have opportunities for greater height. Thus, the link between canopy nesting bird diversity, canopy cover and the herbaceous layer is established.

Edge nesting birds were found to be positively correlated to canopy cover. Previous correlations, as discussed above, with canopy cover have been negative, but it appears that breeding birds nesting on the edges of the woodlands prefer a thick canopy. Possible explanations for this difference include: feeding preference, predator avoidance techniques, or nesting site quality. Further study is needed in this area to determine the reason for differing canopy cover preferences.

In conclusion, we believe that deer trail density may not be an adequate measurement of deer abundance, especially in areas where extensive hunting changes the dynamics of the population. A formerly large deer population may leave old trails behind, but not be indicative of actual deer density. Further study needs to be conducted to determine the rate at which deer trails revegetate. Second, other variables may affect vegetative cover in addition to deer browse. For example, factors such as soil type and nutrient concentration should influence both vegetative cover density and diversity and potentially bird diversity. Third, it is possible that deer density is high enough in every zone that there is little variation in vegetative cover. This is very true in the mid-canopy layer which had a mean coverage below 30 percent. Finally, zone-specific differences, such as the presence of a lake edge on three of the five zones may have impacted deer trail densities in those zones and also influenced bird diversity. Future studies could examine the relationship between the lake, adjacent forests, and diversity.

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