To the Graduate Council:

I am submitting herewith a thesis written by Chris D. Newbold entitled "The Effects of Tornado and Clearcut Disturbances on Breeding Birds in a Tennessee Oak-Hickory (*Quercus-Carya* Spp.) Forest." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Wildlife and Fisheries Science.

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and recommend its acceptance:

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THE EFFECTS OF TORNADO AND CLEARCUT DISTURBANCES ON BREEDING BIRDS IN A TENNESSEE OAK-HICKORY (*QUERCUS-CARYA* SPP.) FOREST

A Thesis
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ABSTRACT

Avian species evolved with and adapted to specific disturbance patterns and regimes. To compare the effects of natural and anthropogenic disturbances on bird communities, I sampled birds and habitat conditions in undisturbed, tornado-disturbed and clearcut forests. I measured vegetation in the two disturbance treatments and undisturbed forest to characterize habitat conditions in the University of Tennessee's Forestry Experiment Station in Oak Ridge, Tennessee. I censused birds in the breeding seasons (May 15- July 15) of 1994 and 1995 using 50 m radius point counts and spot maps.

Overstory vegetation, herbaceous cover and coarse woody debris differed among treatments. Overstory vegetation was greatest in undisturbed forest, intermediate in tornado-disturbed areas and least in clearcuts ($P \leq 0.017$). Density of herbaceous cover was greatest in clearcuts, intermediate in tornado sites and least in undisturbed forest ($P \leq 0.017$). Coarse woody debris did not differ between clearcuts and tornado sites ($P = 0.417$, Bonferonni-adjusted $\alpha = 0.017$), but was less abundant in undisturbed forest than in both disturbance treatments ($P \leq 0.017$). Shrub and grass cover were greatest in clearcut areas, intermediate in undisturbed forest and least in tornado sites ($P \leq 0.017$). Snag basal area was greatest in undisturbed forest, intermediate in tornado sites and least in clearcuts ($P \leq 0.017$). Conifer basal area and litter depth did not differ between clearcuts and tornado sites ($P > 0.017$), but were significantly greater in undisturbed forest than the two disturbance treatments ($P \leq 0.017$). Sapling density did not differ between

tornado sites and undisturbed forest ($P = 0.070$), but was significantly greater in clearcuts than in undisturbed forests and tornado sites ($P \leq 0.017$). Seedling density did not differ among the three treatments ($P = 0.5867$).

I observed 42 and 48 bird species on 50 m point counts in 1994 and 1995, respectively. I also recorded 37 and 38 species that had established breeding territories in 1994 and 1995, respectively.

Avian communities were more similar to one another on clearcuts and tornado sites than to those on undisturbed forests, based on Horn's Index of Community Similarity. Avian abundance, species richness and diversity did not differ between clearcut and tornado-disturbed areas ($P > 0.017$), but were significantly lower in undisturbed forests ($P < 0.017$). Equitability estimates did not differ among treatments ($P = 0.1213$).

Cavity nesting birds were most abundant in tornado sites, intermediate in undisturbed forest and least abundant in clearcuts ($P \leq 0.017$). Apparently, damaged and dying trees in the tornado sites provided suitable nesting and foraging sites for cavity nesters. Canopy nesters and foragers were most abundant in undisturbed forests, intermediate in tornado sites and least abundant in clearcuts ($P \leq 0.017$). Residual overstory vegetation in the tornado sites may have provided habitat for these canopy nesting and foraging birds. Shrub nesters and foragers were most abundant in clearcuts, intermediate in tornado sites and least abundant in undisturbed forest ($P \leq 0.017$). Dense understory vegetation may have provided nesting and foraging sites for these birds in the clearcuts and tornado sites. Ground nesting and foraging birds were most abundant in tornado sites, intermediate in clearcuts and least abundant in undisturbed forest ($P \leq$

0.017). Coarse woody debris and dense understory vegetation in the clearcuts and tornado sites may have provided habitat for ground nesters.

Species compositions differed among the three treatments. Clearcuts primarily had early successional birds, undisturbed forest had late successional species and tornado sites had both types of species. The residual overstory vegetation and dense understory vegetation found in tornado sites may have allowed both early and late successional species to coexist. Species-habitat association models and species distributions suggest that birds were selecting specific habitat characteristics, such as overstory vegetation, rather than simply late or early successional habitats. Late successional species may have also occurred in tornado-disturbed sites because of other factors, such as site fidelity.

Forest managers may be able to mimic natural disturbance more closely by managing overstory vegetation and coarse woody debris during timber harvests. By managing the overstory vegetation, forest managers can control most other vegetation characteristics and the associated bird community. Future research is needed to determine if the different bird communities in the two disturbed sites will become similar as forest conditions redevelop post-disturbance.

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CHAPTER 1

INTRODUCTION

Historically natural disturbances have played an important role in shaping forests and recently ecologists and natural resource managers have become more aware of the frequency, universality, and importance of these disturbances in forest ecosystems (Bormann and Likens 1979, Pickett and White 1985, Suffling et al. 1988, Abrams and Scott 1989, Oliver and Larson 1990, Thiollay 1990, Sprugel 1991, Attiwill 1994). Many plant and animal species have evolved with and adapted to historic disturbance patterns and regimes (White 1979, Hobbs and Huenneke 1992, Attiwill 1994, Noss and Cooperrider 1995:43-47 and 178-219). In fact, many plant and animal species depend on disturbance to provide important life history requirements. For example, Kirtland's warbler requires early successional stands of pine created by fire for breeding habitat, and fire suppression has led to a loss of critical breeding habitat (Norse et al. 1986:82-83, Noss and Cooperrider 1995:44). Similarly, longleaf pine (*Pinus palustris*) communities also require fire disturbance for regeneration and maintenance of diversity (Noss and Cooperrider 1995). Without fire, less diverse hardwood forests may replace these communities. Intermediate levels of disturbance may also maximize species diversity in forest ecosystems (Connel 1978; Petratis et al. 1989; Hobbs and Huenneke 1992; Noss and Cooperrider 1995:43-47 and 178-219). Without sufficient disturbance, a few superior competitors may dominant the community. Conversely, frequent or intense disturbances may allow only a few resistant species to persist. However, many species may persist in areas comprised of various patches created by intermediate levels of disturbance.

Wind storms may be an important source of large-scale disturbance in many forests. In one New England forest, 13 major wind storms occurred in a 300 year span (Foster 1988) and may have been important in determining stand composition (Henry and Swan 1974). In forests where both fires and hurricanes may be infrequent, thunderstorms and tornadoes may be a previously unappreciated source of large-scale disturbance. In a 6.5 million-ha pre-settlement Wisconsin forest, approximately 50 wind storms disturbed an average of 4,828 ha annually (Canham and Loucks 1984). Similar to pre-settlement forests of western New York (Seischab and Orwig 1991), most patches were in the size range of 1-50 ha, with some reaching > 500 ha. This frequency and spatial regime would have maintained 17-25% of the pre-settlement Wisconsin landscape in early successional forests (Canham and Loucks 1984). In a given stand, the estimated return time for large scale wind disturbance in the north-central hardwoods was more than 1,000 years (Lormier and Frelich 1994, Canham and Loucks 1984, Seischab and Orwig 1991); in other words, it would take more than 1,000 years for an area equal to the entire forest to be disturbed. This return time may be less than in the mesic forests of New England (Bormann and Likens 1979). Because topography, stand composition and stand structure affect forest susceptibility, actual return times for large-scale wind disturbance are probably quite variable. The frequency of wind disturbance may be higher in other regions, such as the southern U. S. where thunderstorms and other storms are more common (Court 1974). Unlike small-scale "gap-dynamic" disturbance, little is known about the frequency of large scale wind disturbances in the Southeast (Lormier 1980, Runkle 1982, 1985).

Timber harvests are the primary disturbance source in present-day forests (Powell et al. 1992, Attiwill 1994). In 1991, a total of 489 million m^3 of timber was removed from 3.7 million ha of forests in the U. S.; 2% greater than in 1986 and 21% higher than in 1970 (Powell et al. 1992). A majority of these timber harvests (2.6 million ha) came from the South, which continued to increase its proportion of timber harvests (up 10% from 1970). In Tennessee alone, timber harvests removed over 10.5 million m^3 from 106,357 ha of forest in 1991, an increase in m^3 of 30% since 1970 (Powell et al. 1992). As the U. S. population and economy continue to grow, additional harvesting pressure will occur on forests, especially in the East as timber harvest on public lands in the West decline (Powell et al. 1992).

Natural disturbances still occur in forests, but are not as prevalent as timber harvest disturbances. For example, in the U. S. fire protection has reduced the amount of naturally-disturbed area by 90% in the past 60 years; from 8 - 20 million ha per year in 1930 to 0.8 - 2 million ha per year in 1990 (Powell et al. 1992). Tornadoes are also not as common as timber harvests. Only 1,167 and 1,076 tornadoes occurred in the U. S. in 1993 and 1994, respectively (Crowther 1994, Crowther 1995). Between 1950 and 1971, an average of only 9 tornadoes ccurred in Tennessee per year (Vaiksnoras 1972); 10 and 28 tornadoes occurred throughout the state in 1993 and 1994, respectively. Since the average area covered by a tornado is 768 ha (Flora 1963), these storms disturb an estimated average of 6,912 ha per year in Tennessee.

Many authors have suggested resource managers may wish to emulate natural disturbances through managed, anthropogenic disturbances for two primary reasons (Bormann and Likens 1979, White 1979, Pickett and White 1985, Norse et al. 1986, Franklin 1989, Hunter 1990, Hansen et al. 1991, Hobbs and Huenneke 1992, Hunter 1992, Attiwill 1994, Grumbine 1994, Noss and Cooperrider 1995). First, species diversity may decrease if managed disturbances do not mimic natural disturbances. The underlying assumption behind this idea is that species have adapted to past disturbance regimes and patterns. If managed disturbances alter historic patterns and regimes, some species may not persist because they have not adapted to the new disturbance conditions (White 1979, Franklin 1989, Hansen et al. 1991 Hunter 1992, Attiwill 1994; Noss and Cooperrider 1995:43-47 and 178-219). For example, in the Pacific Northwest, anthropogenicly-disturbed stands had lower vertebrate species richness, bird abundance and amphibian abundance than naturally-disturbed forests (Hansen et al. 1991). Naturally-disturbed forests provided more within-stand microhabitat features (i. e., canopy gaps, large trees, snags, coarse woody debris) than managed forests. Therefore, in anthropogenicly-disturbed forests, species requiring these features may be lost (Hansen et al. 1991). Secondly, unnatural disturbance regimes and patterns may create opportunities for the invasion of exotic species by creating new microhabitat conditions (Hobbs and Huenneke 1992). Hence, managed disturbances that mimic natural disturbances may maintain populations of native species and preclude non-native species invasions.

In forest ecosystems, timber harvest techniques have the potential to both mimic natural disturbances and maintain resource utilization. By imitating natural disturbances, timber harvests have the potential to maintain "the patterns and processes of ecosystems for the benefit of future generations, while providing goods and services for each generation" (Grumbine 1994). Timber harvests can be managed to emulate natural disturbance in three fundamental ways (Hunter 1990:80-234). First, the harvest frequency can simulate the natural disturbance regime. Second, the size of harvested patches can match the size distribution of natural disturbances on the landscape. Third, within stand vegetation structure could be managed to imitate natural disturbances.

Timber harvest disturbances may more closely mimic natural disturbances if forest managers practice a few specific management techniques. Generally, longer harvest rotation periods mimic natural disturbance regimes better than short rotations (Canham and Loucks 1984, Thompson et al. 1993). Species have co-evolved with natural disturbances, and the proportion of late and early successional habitats they create. Therefore, rotation length should be similar to natural disturbance regimes to provide adequate amounts of both early and late successional habitats to support viable populations of all forest species. Large natural disturbances are less common than smaller ones; hence, maintaining many small and few large timber harvests on the landscape will probably provide suitable habitat for many species with varying spatial requirements (Hunter 1990:86-100). Current clearcutting practices may also create patterns that differ from patterns created by natural, large-scale wind disturbance. A landscape of clearcuts probably has less vegetation structure within patches and more pronounced edge effects than areas with large-scale wind disturbances (Hunter 1990:80-234, Hansen et al. 1991, Noss and Cooperrider 1995:30-66 and 178-119). Finally, snags, coarse woody debris and residual live trees may be maintained after timber harvests to resemble a naturally-disturbed stand. Shelterwood harvests may closely mimic the natural disturbance of a mild to strong wind storm because they leave strong, living trees standing (Runkle 1985).

On February 21, 1993, a series of tornadoes touched down in various locations throughout eastern Tennessee. One or more tornadoes followed a 27-km path from the southern portion of Anderson County, within the city limits of Oak Ridge, to the northern portion of Knox County, near the settlement of Powell. Along this 27-km path, funnel clouds touched down for varying distances in many locations. One of the locations where the tornado touched down was the University of Tennessee's Oak Ridge Forestry Experiment Station (UTFES). This natural disturbance event provided an exceptional opportunity to study the effects of a natural disturbance, namely tornado damage, on avian communities. Two three-year-old clearcuts were present on the Experiment Station when the tornado occurred. The two clearcut areas provided an opportunity to directly compare avian community response to anthropogenic and natural disturbance. In this study, I tested the research hypothesis that avian response to natural disturbance (severe wind) differed from avian response to anthropogenic disturbance (clearcutting). The objectives of this research were:

1) to identify key habitat parameters related to avian communities in a tornado-disturbed, clearcut-disturbed and undisturbed oak-hickory forest in eastern Tennessee;

2) to compare avian communities (abundance, composition and diversity) among tornado-disturbed, clearcut-disturbed and undisturbed oak-hickory (*Quercus* sp.-*Cayra* sp.) forests in eastern Tennessee; and

3) to develop habitat models for common bird species that occur in tornado-disturbed, clearcut-disturbed and undisturbed oak-hickory forests in eastern Tennessee.

CHAPTER 2

LITERATURE REVIEW

Effects Of Managed Disturbance On Forest Vegetation

The effects of even-age forest management on forest vegetation have received recent research attention. The most obvious effect of clearcuts is the total removal of overstory vegetation (USDA Forest Service 1973, Norse et al. 1986:38-44, Hunter 1990:84-85). By removing overstory, clearcuts re-initiate succession and radically change stand species compositions (Norse et al. 1986:38-44, Smith 1986:367-397). Early-successional, shade-intolerant species are usually most common in clearcuts because they out-compete shade-tolerant species in the hot, dry conditions created by overstory removal (Smith 1986:367-397). Poor sites may slow stand development and early-successional conditions may persist for a long period of time (Norse et al. 1986).

Clearcutting releases understory vegetation from overstory shade and root competition, resulting in dense sapling and herbaceous vegetation. Vegetation diversity and density tend to immediately increase following clearcutting, with herbaceous vegetation being more abundant than woody vegetation (Nixon and Brooks 1991). Herbaceous vegetation diversity and abundance tend to peak 3 - 4 years following clearcutting and subsequently decline as the stand begins to regenerate. Abundance and diversity of woody vegetation tend to increase and peak later than herbaceous vegetation, but then decline as the canopy develops and closes (Nixon and Brooks 1991). Even after regeneration, herbaceous vegetation communities in managed forests may differ from herbaceous vegetation communities in unharvested forests (Duffy and Meier 1992).

Effects Of Natural Disturbance On Forest Vegetation

Extensive research has been conducted on the effects of natural disturbance on forest vegetation (see Attiwill 1994 for review). Large scale forest disturbances include fire, insects and disease, ice-storm damage and wind damage (Bormann and Likens 1979, Seischab and Orwig 1991, Attiwill 1994). Sprugel (1991) noted that disturbance is an important component of steady-state, stable ecosystems. Fire disturbance in Ontario forest systems may help develop and maintain landscape diversity (Suffling et al. 1988). The occurrence of fire in eastern North America may have promoted the development and sustainablity of oak forests by controlling competing, fire-intolerant species (Abrams 1992). Furthermore, insect outbreaks in eastern North American balsam fir (*Abies balsamea*) forests regenerate older stands into newer, healthier stands (Ostaff and MacLean 1989).

Ice and wind disturbances have also been shown to be important in forest ecosystems. For example, ice storms have been demonstrated to increase vegetation heterogeneity of forest systems (Whitney and Johnson 1984, Bruederle and Stearns 1985, Boerner et al. 1988, Seischab et al. 1993). Wind damage in forests occurs along a continuum from small scale "gap dynamic" disturbances and large scale "catastrophic" disturbances (Bormann and Likens 1979, Pickett and White 1985). Understanding these extremes in wind disturbance is important because different patch sizes are produced, different successional patterns are created, and forest structure is impacted differently by these two disturbance classes (Picket and White 1985, Abrams and Scott 1989, Foster and Boose 1992, Attiwill 1994). Although "gap dynamic" disturbances have received a moderate amount of attention, large scale "catastrophic" disturbances have only recently received research interest.

A few studies have examined the effects of catastrophic winds on forests. Hurricanes create a heterogeneous landscape because stand susceptibility varies with stand structure (age, height and density), composition (pine vs. hardwood stands) and exposure to wind (windward vs. leeward sites) (Foster and Boose 1992, Foster 1988). A study of a tornado-disturbed hardwood forest in northern Kentucky found that the developing forest was different from the pre-tornado forest. (Held and Bryant 1989). A study on the effects of tornado disturbance on forests in southeast Texas found that although canopy cover, basal area, and density in the disturbed forest were substantially reduced, a large proportion of stems (often near 30%) survived, with vigorous re-sprouting (Glitzenstein and Harcombe 1988). Hence, catastrophic wind damage may not impact forest vegetation as severely as catastrophic fire, because all above ground biomass is not eliminated. Rather than setting succession back to an earlier stage, large-scale wind disturbance can accelerate succession by removing large early successional trees and releasing the growth of the shade-tolerant understory (Glitzenstein and Harcombe 1988). Large-scale wind disturbance, however, may increase the probability of other catastrophic disturbance, such as insect and disease infestations or fire (Bormann and Likens 1979, Glitzenstein and Harcombe 1988, Attiwill 1994).

Effects Of Managed Disturbance On Avian Communities

Many studies have examined the effects of clearcutting on avian communities (see DeGraaf et al. 1993, Dickson et al. 1993 and Thompson et al. 1993 for review) because of the possible role of forest management in the decline of neotropical migrant birds (Terborgh 1989). In pine-oak forests, bird species diversity, density and richness were lower in clearcuts than in mature forests (Conner et al. 1979). However, when hardwood forests were clearcut, avian species diversity, density and richness increased to equal or often greater numbers than bird populations in undisturbed forests (Ambrose 1975:70-122, Conner and Adkisson 1975, Webb et al. 1977, Titterington et al. 1979, Horn 1984, Yahner 1986, Yahner 1987a, Derleth et al. 1989). Bird species abundance tended to peak in 7 year old clearcuts (Ambrose 1975:70-122, Conner and Adkisson 1975, Webb et al. 1977, Horn 1984, Derleth et al. 1989). Breeding bird diversity peaked in clearcuts 3-12 years old. Birds apparently were attracted to the dense growth of sapling, shrub and herbaceous vegetation in the regenerating clearcut (Crawford et al. 1981, Yahner 1986, Yahner 1987a, Probst et al. 1992, Dickson et al. 1993, Thompson et al. 1993).

In many studies, clearcutting resulted in high avian species turnover rates within regenerating stands (Crawford et al. 1981, Yahner 1987b, Kerpez and Stauffer 1989, Probst et al. 1992). Because grasses and forbs are abundant, early successional species, such as American goldfinches (scientific names for all birds are given in Appendix A) and field sparrows, were common (Conner and Adkisson 1975, Crawford et al. 1981, Probst et al. 1992). As shrub and sapling development began, other species invaded, including indigo buntings, yellow-breasted chats, prairie warblers, chestnut-sided warblers, Kentucky warblers, common yellowthroats, white-eyed vireos, rufous-sided towhees, hooded warblers, and gray catbirds (Conner and Adkisson 1975, Dickson et al. 1980, Crawford et al. 1981, Yahner 1986, Thompson and Capen 1988, Thompson and Fritzell 1990, Probst et al. 1992, Thompson et al. 1992, Welsh and Healy 1993). Finally, as regenerating stands matured, many canopy and bark foragers, aerial pursuers, and other late successional species, such as red-eyed vireos, wood thrush, ovenbirds, Louisiana waterthrushes, white-breasted nuthatches, black-and-white warblers, eastern wood pewees, acadian flycatchers, pileated woodpeckers, scarlet tanagers and red-bellied woodpeckers, became common (Conner and Adkisson 1975, Thompson and Fritzell 1990, Probst et al. 1992, Thompson et al. 1992, Welsh and Healy 1993).

Forests managed with even-aged techniques may have greater diversity and abundance of birds than fire-protected forests with no timber harvest (Welsh and Healy 1993). In New Hampshire, no species were unique to unharvested, fire-protected hardwood forests, whereas 18 species occurred only in even-aged managed forests (Welsh and Healy 1993). Missouri oak-hickory forests under even-aged management had higher avian diversities than similar fire-protected, unharvested forests (Thompson et al. 1992). Forests managed with even-aged techniques had greater avian diversity and abundance than unmanaged forests because both early and late successional habitats were available. Unless natural disturbances were present, unharvested, fire-protected forests provided primarily late successional habitats and, thus supported fewer species than managed forests.

In addition to providing early successional habitat, forests under even-aged management have relatively large amounts of edge (Wilcove 1988, Thompson et al. 1993). Forest-edge habitats generally support greater avian density, diversity and abundance than do interior habitats (Strelke and Dickson 1980, Kroodsma 1984). Edges, however, may also have adverse effects on some bird species. Edges may lead to lower songbird nesting success because nest and brood predation may increase near edges (Gates and Gysel 1978, Wilcove 1985, Yahner and Scott 1988, Robinson 1992, Rudnicky and Hunter 1993, Miles 1995). Nest parasitism by brown-headed cowbirds also increases in edges, thus lowering host productivity (Gates and Gysel 1978, Brittingham and Temple 1983, Robinson 1992, Miles 1995).

Edge effects may not be as significant between even-aged stands in extensively forested areas (Rudnicky and Hunter 1993, Thompson 1993). In two separate studies, no avian species that occurred in unmanaged forests disappeared from forests that were managed with even-aged techniques (Thompson et al. 1992, Welsh and Healy 1993). In these studies, forest interior species occurred in the interiors and tolerated, at a distance, edges created by clearcutting. In fragmented landscapes, however, edges created by timber harvests may be detrimental to forest interior bird populations because of the associated increases in predation and parasitism (Thompson and Fritzell 1990, Freemark et al. 1993, Robinson et al. 1993). Therefore, the extent of edge effects created by even-aged management will depend upon the landscape setting (Freemark et al. 1993, Robinson et al. 1993). Careful evaluation of landscape context can minimize detrimental edge effects and maintain an adequate balance of early and late successional forest habitats to ensure the viability of all forest bird species.

Harvest rotation length also can affect bird communities. When the time between harvests of a stand is short (e. g. 40 years), vegetation structure found in mature forests is prevented from developing (Egerton and Thomas 1978, Thompson et al. 1993). Large trees, downed woody debris, snags, den trees and development of multiple canopies are largely absent from forests managed with short rotations (Thompson et al. 1993). Also, when short rotations are used, a higher proportion of the forest is in early-successional stands (Thompson et al. 1992). Bird communities in the forests may favor early successional species; species that are specialized for late successional habitats may be under represented (Thompson et al. 1993). Forests managed with long rotations (e. g. 120 years), may have a greater proportion of the forest in late successional stages. The avian community in these forests may be better balanced between early and late successional species (Thompson et al. 1993).

Effects Of Natural Disturbance On Avian Communities

Most of the studies of avian response to natural disturbance have focused on the effects of fire (see Bendell 1974 and Attiwill 1994 for review) and hurricanes (Askins and Ewert 1991, Wauer and Wunderle 1992, Wunderle et al. 1992, Wiley and Wunderle 1993, Wunderle 1995). With the exception of these two disturbance sources, few studies have documented avian response to natural forest disturbances. I located only three published accounts of the effects of tornadoes on birds (McClure 1945, Webster 1968, Wiendenfeld and Wiendenfeld 1995). One descriptive account detailed the immediate effect of a tornado on migrating birds in southern Louisiana (Wiendenfeld and Wiendenfeld 1995). In an anecdotal study in Iowa, bird populations were estimated to be only 40% of pre-tornado levels (53 birds/40 ha immediately following the tornado vs. 127 birds/40 ha before the tornado); six of eight common species bred in the tornado-damaged area (McClure 1945). Although this study documented the presence of birds immediately following a tornado, it did not examine the effects of tornado disturbance on avian habitat nor did it compare avian communities in other disturbed or undisturbed areas. An Indiana bird census documented avian use of a tornado-damaged forest during the non-breeding season (Webster 1968). This study, however, did not measure avian use prior to the disturbance to document avian response to the tornado. These three studies did not quantify avian-habitat relations and were not designed to compare naturally disturbed ecosystems with managed, anthropogenicly-disturbed systems. More in-depth studies are needed if natural resource managers are to understand how birds respond to disturbance and whether managed, anthropogenic disturbances can emulate natural disturbances. However, studies that directly compare managed and anthropogenic disturbances are difficult to design and conduct because of the unpredictable occurrence of natural disturbance events.

CHAPTER 3

STUDY AREA

Description Of The University Of Tennessee's Forestry Experiment Station

The UTFES in Oak Ridge is a 904-ha forest situated in southwestern Anderson County, Tennessee (Figure 1). The forest is located in the ridge and valley physiographic province of Tennessee, a broad valley between the Cumberland Mountains and the Blue Ridge Mountains (Forestry Experiment Station, University of Tennessee 1994). Long parallel ridges, comprised of dolomite, shale, sandstone and limestone, are separated by narrow valleys extending in a northeast-southwest direction throughout this region (Moneymaker 1981). The elevation of the experimental forest ranges from 243-m to 365-m above sea level. UTFES soils are in the Fullerton series, characterized by a well-drained cherty, silty loam with red clayey subsoil (Moneymaker 1981).

Temperatures and precipitation in the region are moderate. The average summer and winter temperatures are 24.2° C and 5.3° C, respectively, and the average precipitation is 139.7 cm per year (Forestry Experiment Station, University of Tennessee 1994). Of the total precipitation per year, 27.94 cm is in the form of snow (Moneymaker 1981). Average relative humidity of the area is 55% (Moneymaker 1981). Rainfall was high in 1994 relative to 1995; the mean seasonal temperatures were similar for both years (Table 1).

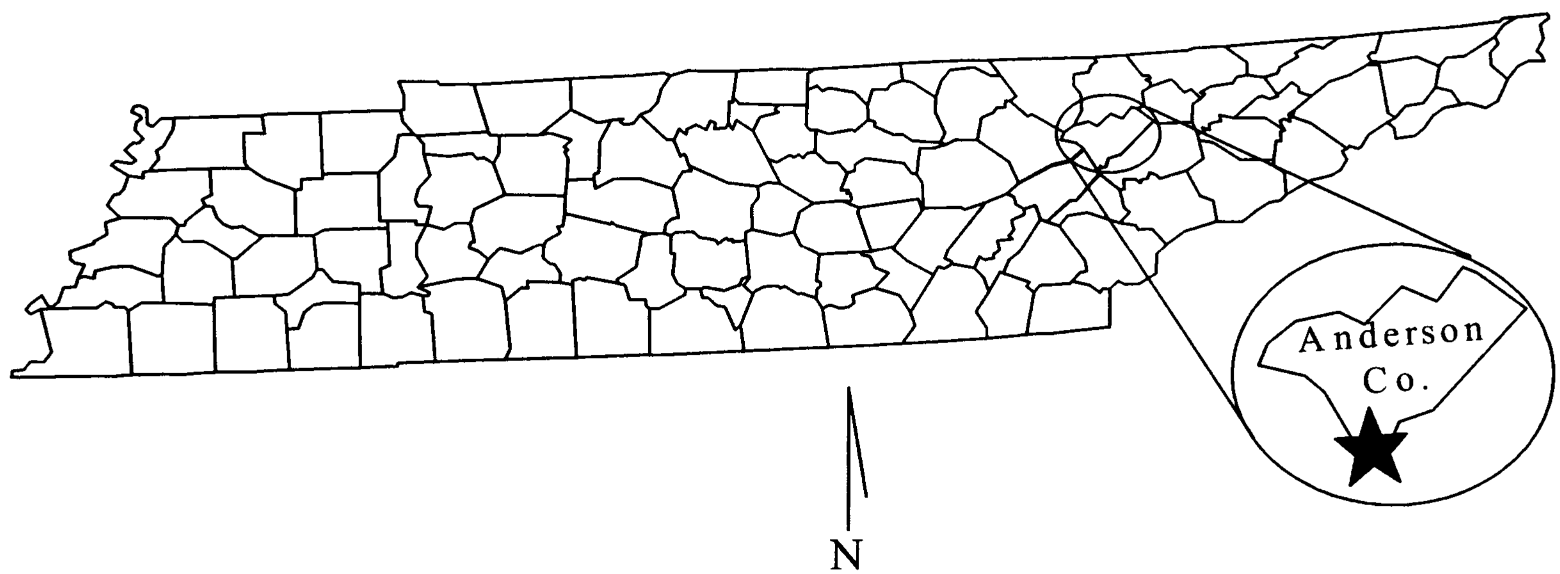


Figure 1. Location of the University of Tennessee's Oak Ridge Forestry Experiment Station, Oak Ridge, Tennessee.

Table 1. Total seasonal precipitation (cm) and mean temperatures (C) in Oak Ridge, Tennessee, spring-summer 1994 and 1995.[1]

	Precipitation	Temperature
March 1994- September 1994	94.33	20.17
March 1995- September 1995	48.31	19.94

[1] Source: National Oceanic and Atmospheric Administration. Oak Ridge, unpublished data.

The forest that was damaged by the tornado was predominately a second growth oak-hickory forest with some scattered pines (scientific names of all plant species observed in the Oak Ridge Experimental Forest are given in Appendix B). The forest was two-aged with a 100-120 year age group and a 50-60 year age group. Within the younger age group was a considerable amount of yellow poplar. The forest has been protected from fire for the past 50 years and timber harvests have been limited in acreage (R. Evans, UTFES, pers. commun.).

The tornado damage was confined to the Chestnut Ridge portion of the UTFES. Wind velocity at the tornado's vortex was estimated to be in excess of 322 KPH (Kevin Birdwell, NOAA, Oak Ridge, Tenn., pers. commun.). The path left by the tornado averaged 0.72 km in width, and was irregularly shaped. The intense wind event severely damaged an estimated 108 ha of forest. Almost every pole and sawtimber sized tree in this area was windthrown or sustained some type of stem damage. About 75% of the damage was a result of windthrow and 25% was a result of stem damage. The tornado moderately or lightly damaged an additional 80 ha. Damage to trees in these areas was primarily from windthrow. A salvage harvest was conducted in 170.8 ha of the damaged forest; two areas (9.6 ha and 7.6 ha, respectively) were not salvaged and served as disturbance study areas.

Study Site Selection

Two study areas in each of two disturbance treatments where chosen (tornado-disturbed and clearcut-disturbed) for comparison with two undisturbed forest study areas (Figure 2). The two tornado-damaged study areas, 9.6 and 7.6 ha in size, were unsalvaged. The clearcut study areas, 4 and 7.2 ha in size, were three years old in 1994. The clearcut study

a.)

b.)

Figure 2. Undisturbed (a), clearcut (b) and tornado-disturbed (c) study areas, Oak Ridge Forestry Experiment Station, Oak Ridge, Tennessee, 1994-1995.

c.)

Figure 2. (Continued).

sites were managed to regenerate into a mixed pine-hardwood stand had received four distinct site preparation treatments in a previous study. The site preparation treatments were: 1) a control treatment that had no site preparation treatment after a commercial clearcut, 2) a slash down of all standing trees, 3) a slash down of all standing trees followed by burning, and 4) a slash down of all standing trees followed by herbicide application and burning. Because tornado-damaged and clearcut study areas were isolated by intact forest, power line rights-of-way, roads, and salvaged tornado-damaged areas, I selected two similarly isolated, small undisturbed forest study areas for comparison (8 ha and 10 ha, respectively).

Patch size can affect breeding bird response to any forest disturbance (Bond 1957, Galli et al. 1976, Anderson and Robbins 1981, Robbins et al. 1989, Askins et al. 1990, Freemark and Collins 1992). Study area size in this case was small because clearcut size was specified prior to the tornado event based on other research objectives. To control patch size effects, I selected comparably sized tornado-disturbed and undisturbed-forest study areas. The study sites were restricted to one forest in Oak Ridge, Tennessee because natural disturbance is often a localized, unpredictable event, making the task of locating naturally-disturbed sites adjacent to clearcut sites difficult. All of my study sites occurred in a similar forest type with similar age class and management history before the tornado struck. Therefore, most of the observed variability that occurred in avian response to study site conditions could be attributed to the different treatments.

The Oak Ridge forest provides an excellent opportunity to examine simultaneously and under the same conditions, the effect of both tornado and clearcut disturbances on an avian community. This study does not, however, allow examination of avian response to tornado disturbance over the full range of forest systems in the Southeast, or even Tennessee. Therefore, this study was an intensive examination of the effects of a tornado disturbance on a bird community, rather than a more generalized study of the effects of natural disturbance on avian communities.

CHAPTER 4

MATERIALS AND METHODS

Overview Of Sampling Design

I laid out 0.4-ha grids (61 m X 61 m) over each study area. I located grid boundaries at least 25 m from study area edges to reduce edge effects. Bird surveys and vegetation sampling were designed to evaluate characteristics within individual 0.4-ha grid cells.

Vegetation Sampling

The grid acted as a reference for locating vegetation measurement points in the tornado-damaged, clearcut and undisturbed forest study areas. I placed 4 sampling points in each 0.4-ha grid-cell. I located each point 15.2 m from the edge of the 0.4-ha grid lines, 30.5 m from adjacent points and 21.5 m from grid cell intersections (Figure 3).

I measured living vegetation characteristics using two different techniques (Table 2). I used point sampling (Grosenbaugh 1952) to measure physical and tree characteristics (Table 2). I used plot sampling (Avery and Burkhart 1983:164-184) to measure the characteristics of saplings, shrubs, seedlings and herbaceous vegetation and woody vines at each sampling point. I used a 0.004-ha (3.58-m radius) plot to measure saplings and shrubs (Table 2). I used a 0.0004-ha (1.12-m radius) plot to measure seedlings, herbaceous vegetation and woody vines (Table 2). I measured woody debris volume using a line intersect method (Van Wagner 1968).

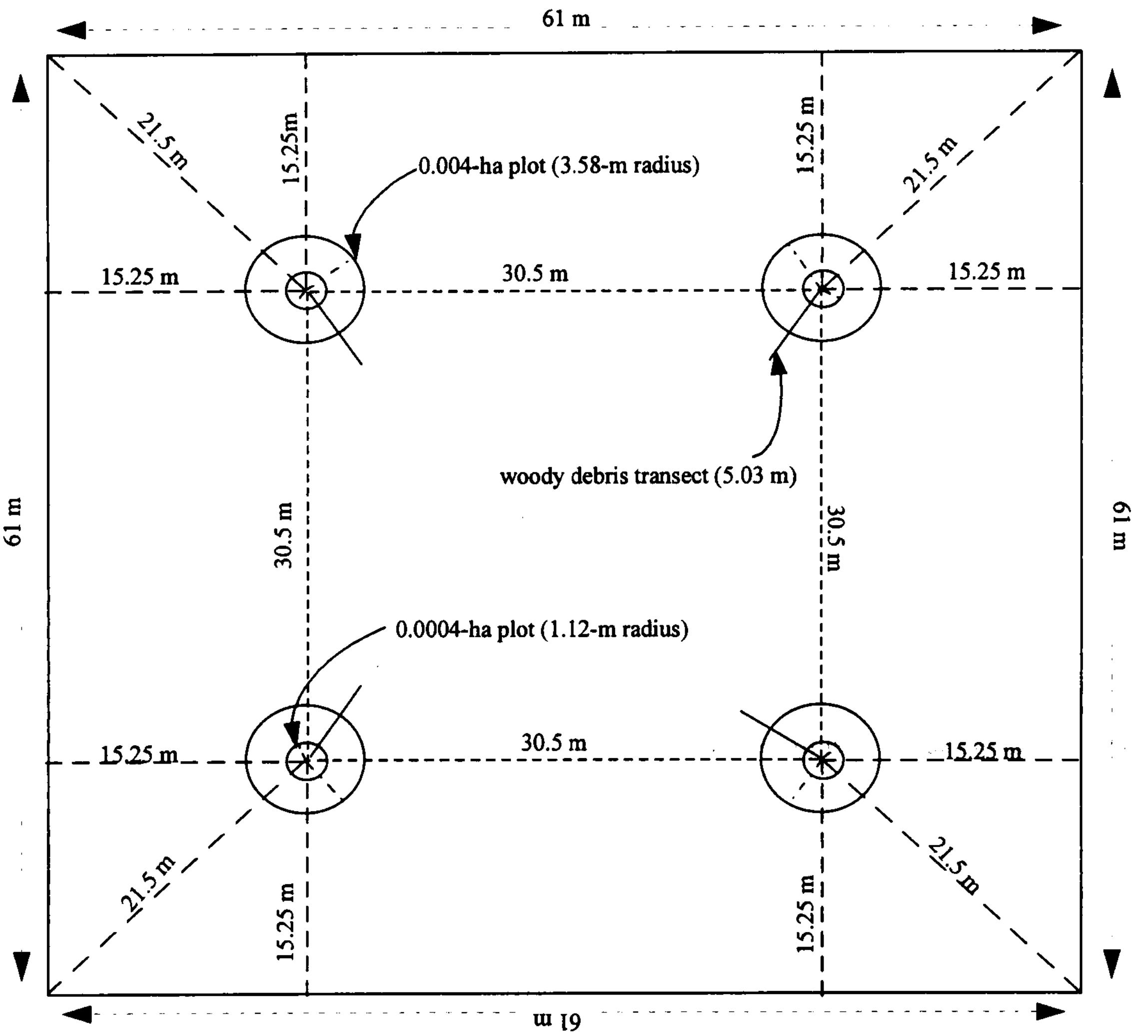


Figure 3. Point and fixed plot sampling configuration on 0.4-ha cells in two disturbance treatments and undisturbed forest, Oak Ridge Forestry Experiment Station, Oak Ridge, Tennessee.

Table 2. A summary of vegetation sampling techniques used to measure habitat characteristics in 1994 and 1995, Oak Ridge Forestry Experiment Station, Oak Ridge, Tennessee.

Sampling Method	Vegetation Type	Variable	How Measured
Point Sampling	Physical Characteristic	Slope	Clinometer; 5° Classes
Point Sampling	Physical Characteristic	Aspect	Compass; 8 Standard Directions (N, NE, E, etc.)
Point Sampling	Physical Characteristic	Position of Slope	Ocularly Estimated; Crest, Upper, Mid, Lower, Bottom; And Convex, Concave
Point Sampling	Ground Level Vegetation	Horizontal Vegetation Density[1]	0.3 X 1.5-m Cover Board; 5% Classes
Point Sampling	Litter Layer	Litter Depth	Ruler; 0.64-cm Classes
Point Sampling	Trees	Residual Standing Canopy Cover	Ocularly Estimated; 5% Classes
Point Sampling	Trees	Percent Canopy Cover	Spherical Densitometer; 5% Classes
Point Sampling	Trees	Frequency	20 BAF Prism
Point Sampling	Trees	Species	Scientific Name
Point Sampling	Trees	DBH	DBH Tape; 2.54-cm Classes
Point Sampling	Trees	Tree Height	Clinometer; 1.525-m Classes
Point Sampling	Trees	Degree of Tree Lean	Ocularly Estimated; 5° Classes
Point Sampling	Trees	Direction of Tree Lean	Compass; 8 Standard Directions (N, NE, E, etc.)
Point Sampling	Trees	Root Sprung	Yes or No
Point Sampling	Trees	Decay Class[2]	Classes 0-5
Point Sampling	Trees	Damage Class[3]	Classes 0-4
0.004-ha Plot	Saplings	Species	Scientific Name

Table 2. (Continued).

Sampling Method	Vegetation Type	Variable	How To Be Measured
0.004-ha Plot	Saplings	DBH	DBH Tape; 2.54-cm Classes
0.004-ha Plot	Saplings	Height	Clinometer; 1.525-m Classes
0.004-ha Plot	Saplings	Degree of Lean	Ocularly Estimated; 5° Classes
0.004-ha Plot	Saplings	Direction of Lean	Compass; 8 Standard Directions (N, NE, E, etc.)
0.004-ha Plot	Saplings	Damage Class[3]	Classes 0-4
0.004-ha Plot	Shrubs	Total Percent Cover	Ocularly Estimated; 5% Classes
0.004-ha Plot	Shrubs	Three Most Dominate Species	Scientific Names; % Cover, 5% Classes
0.0004-ha Plot	Seedlings	Species	Scientific Names
0.0004-ha Plot	Seedlings	Sprout Origin	Root, Stump, or Seed
0.0004-ha Plot	Herbaceous Cover	Total Percent Cover	Ocularly Estimated; 5% Classes
0.0004-ha Plot	Herbaceous Cover	Three Most Dominate Grasses	Scientific Names; % Cover, 5% Classes
0.0004-ha Plot	Herbaceous Cover	Three Most Dominate Forbs	Scientific Names; % Cover, 5% Classes
0.0004-ha Plot	Herbaceous Cover	Three Most Dominate Woody Vines	Scientific Names; % Cover, 5% Classes
Line Intersect	Woody Debris	Species	Scientific Name
Line Intersect	Woody Debris	Diameter	DBH Tape; 2.54-cm Classes
Line Intersect	Woody Debris	Disturbance Source	Pre-,Post- or Tornado
Line Intersect	Woody Debris	Decay Class[2]	Classes 0-5

[1] Source: Nudds 1977
[2] Source: Cline et al. 1980
[3] **Damaged classes are: 0 = no damage, 1 = slight damage (leaning, limbs broken etc.), 2 = main trunk broken but still connected, 3 = main trunk broken completely off and 4 = tree on the ground or greater than 80° lean.**

The line transect started at the first point of each 0.4-ha cell and proceeded 5.03 m in a randomly chosen direction (Figure 3). At each successive vegetation plot center, I rotated the direction of the line transect 90° to reduce any bias that might occur due to debris orientation (Van Wagner 1968). I measured woody debris only above 1.27 cm in diameter. A photograph of each 0.4-ha cell was taken to serve as a visual record of vegetation structure.

Bird Sampling

Breeding birds were censused weekly in each study area during the 9-week breeding season, (May 15 to July 15), 1994 and 1995. I used both spot mapping (Kendeigh 1944) and 50-m radius point count (Hutto et al. 1986) methods to survey bird communities in the study areas. I chose to use spot mapping because it yields more accurate estimates of bird populations than other techniques (Robbins 1978, Franzreb 1981) and because the censused areas were relatively small. Spot mapping procedures followed International Bird Census Committee (1970) standards. Many avian population studies use the point count method to census birds because of its ease of use and efficiency in estimating avian populations. I used the 50-m radius point count method so that the results of this study could be directly compared to other bird studies.

I detected birds by sight and/or sound. I conducted bird censusing within the first 4 hours after sunrise (Robbins 1981a). I recorded environmental conditions (i. e. precipitation, cloud cover, temperature and wind) on each trip. Because bird activity is inversely related with wind speed and amount of rain (Robbins 1981b), I did not conduct bird censuses on excessively windy or rainy days. I conducted point counts and spot mapping simultaneously every time I censused the study areas.

I conducted the spot map census by systematically walking the grids in each study site. I recorded the location of every bird encountered on the plot map (Williams 1936, Kendeigh 1944). I walked the grid lines at an approximate speed of 50 m/3 minutes. To minimize mapping bias related to time of day, I alternated starting and ending points on successive census trips. Whenever possible, I noted bird species, sex of the bird and activity. I compiled the 9 weekly spot maps to develop an estimate of bird abundance for each study area. I also used the spot maps to develop species richness, diversity, and equitability estimates for each study area.

I placed 50-m radius point count stations throughout the study areas at the intersection of grid lines. To ensure independence between successive counts, I placed the point count stations at 122-m intervals; thus, there was a 22-m buffer between each 50-m radius point count. I established point count stations at least 61 m from the edge of the study grids so that fixed radius plots would not overlap study area boundaries (Reynolds et al. 1980). These placement restrictions resulted in 4 and 3 point count stations in the tornado-disturbed areas, 4 and 2 in the clearcut areas and 4 in both undisturbed forest plots. I conducted point counts for 10 minutes to minimize bias in population estimates due to long point count periods (Scott and Ramsey 1981, Hutto et al. 1986). I divided the 10-minute interval into 0-3, 3-5 and 5-10 minute classes. I estimated the distance of each bird from the census point as either in the 0-25, 25-50 or >50-m distance class. Recording the data by these time and distance intervals allowed for comparison of results with point count data from other studies.

CHAPTER 5

DATA ANALYSIS

Vegetation Characteristics

From the vegetation measurements I derived 18 variables to characterize habitat conditions across the treatments (Table 3). I used a factor analysis to reduce the number of habitat parameters and simplify the analysis. I used the maximum likelihood method to extract three factors and the Varimax method to rotate their pattern. I then tested for differences among the variables defined by the factor analysis using a 1-way multivariate analysis of variance (MANOVA). The null hypothesis of the MANOVA was that no differences occurred in the habitat parameters among the clearcut, tornado and undisturbed forest. For variables that demonstrated significant differences ($P \leq 0.05$), I made pairwise comparisons between specific estimates using a Bonferroni adjustment that controlled the family-wise alpha level at 0.05.

Avian Characteristics

Community analysis

Spot maps

Because of the low number of treatment replications (two study areas per treatment per year), I used spot maps only to provide descriptive statistics. I determined the number of

Table 3. Variables selected to characterize habitat conditions for breeding bird species across clearcut-disturbed, tornado-disturbed and undisturbed forest stands in May-August 1994 and 1995, Oak Ridge Forestry Experiment Station, Oak Ridge, Tennessee.

Variable Name	Variable Description
BAACRE	Basal area/0.4 ha of all trees measured in the prism plots (m^2/0.4 ha)
BACONF	Basal area/0.4 ha of coniferous trees measured in the prism plots (m^2/0.4 ha)
BADECD	Basal area/0.4 ha of deciduous trees measured in the prism plots (m^2/0.4 ha)
BASNAG	Basal area/0.4 ha of dead trees measured in the prism plots (m^2/0.4 ha)
CANPYCOV	Average of four measured locations per point using a spherical densiometer (%)
CANPYHT	Average tree height (m), measured with a clinometer, of the trees measured in the prism plot
FORBCOVR	Ocular estimate of the forb cover on a 0.004-ha plot (%)
GRASCOVR	Ocular estimate of the grass cover on a 0.004-ha plot (%)
GRNDCOVR	Ocular estimate of the total amount of horizontal ground cover on a 0.004-ha plot (%)
LITTER	Average litter depth of four measured locations per point (cm)
RESIDUAL	Ocular estimate of the residual overstory vegetation on a 0.04-ha plot (%)
SAPLDENS	Density of saplings estimated from a count of all the saplings on a 0.04-ha plot (#/0.4 ha)
SEEDDENS	Density of seedlings estimated from a count of all the seedlings on a 0.004-ha plot (#/0.4 ha)
SHRBCOVR	Ocular estimate of the shrub cover on a 0.04-ha plot (%)
VEGDENS	Vertical density of understory vegetation measured using a vegetation cover board (%)
VINECOVR	Ocular estimate of the vine cover on a 0.004-ha plot (%)
WDYDEBR	Total volume of woody debris estimated from a 5.03-m transect (m^3/0.4 ha)
WDYFREQ	Number of downed logs greater than 7-cm in diameter (#/5.03 m-transect)

territories for each species that I observed three or more times in a study area. I then calculated the density (number per 40 ha) of each species by counting the number of territories in each study area and extrapolating to number per 40 ha. Finally, I used the number of mapped territories for each species to calculate Horn's Index of Community Similarity (Horn 1966) for all possible treatment pairs during each year and within treatments between the two years.

Point counts

I defined a measure of avian abundance as the number of individual birds observed on each 50-m radius point count. I also calculated species richness, diversity and equitability estimates for each 50-m radius point count. I defined species richness (S) as the total number of species observed on each point count. I used the Shannon-Weaver Information Function to measure species diversity. The Shannon-Weaver diversity index (H') was calculated as: $H' = -[\sum p_i Log(p_i)]$, where p_i = the proportion of individuals of the ith species. This diversity index measured the average degree of uncertainty of predicting the species of a given individual picked at random from a community (Eliott 1990). Species equitability (J') measured how evenly distributed the abundance of birds was among all species. If all species had equal densities, then equitability equaled one. Conversely, equitability approached zero if one species predominated. I calculated equitability as: H'/H maximum, where H maximum = Log (S). I assigned bird species to 4 nesting and 3 foraging guilds based on the Southeastern Working Group Partner's in Flight designations (Hamel 1992). I calculated abundance estimates per point count for each nesting and foraging guild. I defined nesting guilds as ground-, shrub-, cavity- and canopy-nesters and foraging guilds as ground-, shrub- and canopy-foragers.

I used a fixed-effects MANOVA, with repeated measures over the count week and year, to test for differences in estimate means among treatments (Table 4). The MANOVA tested the null hypothesis that estimate means did not differ among treatments. For means that demonstrated significant differences among treatments ($P \leq 0.05$), I made pairwise comparisons between specific estimates using a Bonferroni adjustment that controlled the family-wise alpha level at 0.05.

Species compositions

I used avian species frequency data from the 50-m radius point counts in a logit model (Agresti 1990:91-96) to test for community composition differences among treatments. The null hypothesis of the logit model was that species presence/absence was independent of treatment. To test this hypothesis, I fit a logit model that tested for the species and treatment interaction term for significance. If this interaction term was not significant ($P > 0.05$), then species presence/absence was independent of treatment. If, on the other hand, the term was significant ($P \leq 0.05$), then this interaction term was needed to accurately predict presence/absence of species in the three treatments. I also used a model that omitted the species and treatment interaction term to determine which species and treatment combination would have expected frequencies different from observed. I compared the expected frequencies' standard errors to the deviations (residuals) between the observed and expected frequencies to determine how species differed among

Table 4. Analysis of variance table and expected mean squares for a repeated measures MANOVA used to compare avian community estimates in 1994 and 1995, Oak Ridge Forestry Experiment Station, Oak Ridge, Tennessee.

Source	D.F.	Expected MS
Disturbance treatment	2	var(Error) + var(Point) + var(Treatmnt)
Repetition (disturbance treatment)	3	var(Error) + var(Point) + var(Rep(Treatmnt))
Point (repetition disturbance treatment)	15	var(Error) + var(Point)
Year	1	var(Error) + var(Year)
Disturbance treatment*year	2	var(Error) + var(Treatmnt*year)
Census week	8	var(Error) + var(Count)
Disturbance treatment *census week	16	var(Error) + var(Treatmnt*count)
Year*census week	8	var(Error) + var(Year*count)
Disturbance treatment *census week*year	16	var(Error) + var(Treatmnt*count*year)

treatments (i.e. higher frequencies than expected, lower frequencies than expected or no difference between observed and expected frequencies).

Species-Habitat Association Models

I developed species-habitat association models to relate habitat variables to specific species presence, and therefore better understand how disturbance affects bird distribution. I used logistic regression to model the distribution of the most common neotropical-migrant birds (Table 5). For each species model, the null hypothesis was that the slope coefficients for the explanatory variables were zero. In other words, the null hypothesis was that the response variable (species presence or absence) was not correlated with the explanatory habitat variables. I used an alpha level of 0.05 for all variable tests. I overlaid bird territories with vegetation sampling points and classified each point as either having a presence or absence of a specific species. I used spot-mapped territories from 1994 and 1995 for model development. I tested the full models, which contained all habitat variables defined by the factor analysis, and then used a backward selection method to develop the final habitat-association models. I used a significance level of $P = 0.10$ for variables to remain in the model (SAS 1990). I evaluated model performance by using a jackknife test. In addition, I used the Hosmer-Lemeshow statistic (C) to assess the fit of each model to the data (Hosmer and Lemeshow 1989:140-145). I computed the Hosmer-Lemeshow goodness-of-fit statistic using the BMDP statistical software package (BMDP 1992).

Table 5. Neotropical migratory bird species that were observed to have 9 or more total territories in both 1994 and 1995 throughout the two disturbance treatments (clearcut and tornado-disturbed) and undisturbed forest, Oak Ridge Forestry Experiment Station, Oak Ridge, Tennessee.

Species	Number of territories	
	1994	**1995**
Blue-gray gnatcatcher	16.7[A]	21.9
Hooded warbler	18.1	20.3
Indigo bunting	17.4	12.8
Ovenbird	13.3	11.4
Prairie warbler	11.2	9.6
Red-eyed vireo	35.8	31.0
Summer tanager	11.5	9.7
White-eyed vireo	20.0	16.6
Yellow-breasted chat	17.4	16.3

[A] Territories were calculated using procedures outlined by the International Bird Census Committee (1970). Fractions of territories were derived by estimating the fractional proportion of each territory that was within the study plot.

CHAPTER 6

RESULTS

Vegetation Structure

All of the variables initially included in the vegetation analysis and their means are listed (Appendix D; Table D.1). I removed 7 of the 18 variables used to describe habitat conditions prior to factor analysis because they did not have much common variation with the other variables (communalities ≤ 0.3) (Table 6). I used the 11 remaining variables to define the three extracted factors. The three common factors extracted from the habitat variables captured 85% of the variation in the 11 variables (Table 7). The Varimax rotated factor pattern (Table 8) clearly defined the three factors: Factor 1 represented a measure of overstory vegetation, with a negative loading by understory vegetation density; Factor 2 represented herbaceous ground cover; and Factor 3 was a measure of coarse woody debris.

Among the two disturbance treatments and the undisturbed forest, I tested for differences in the 7 individual variables that were removed prior to factor analysis and the three extracted factors. The factor scores and 7 individual variable means differed among the treatments ($F = 98.97$, $P < 0.05$). Factor 1 (overstory and understory vegetation density) differed among treatments (Figure 4; $P < 0.05$), being greatest in undisturbed forest and least in clearcuts (Table 9, $P \leq 0.017$). Factor 2 (herbaceous ground cover) and

Table 6. Final communality estimates of 18 vegetation variables used to characterize habitat conditions in two disturbance treatments and undisturbed forest in 1994 and 1995, Oak Ridge Forestry Experiment Station, Oak Ridge, Tennessee. Underlined variables had low communalities (≤ 0.3) and were excluded from the factor analysis (N = 464).

Variable	Communality estimate
BAACRE[1]	0.947963
BACONF	0.064727
BADECD	0.969691
BASNAG	0.085249
CANPYCOV	0.721212
CANPYHT	0.617412
FORBCOVR	0.378452
GRASCOVR	0.296977
GRNDCOVR	1.00000
LITTER	0.168475
RESIDUAL	0.782238
SAPLDENS	0.285805
SEEDDENS	0.022285
SHRBCOVR	0.141124
VEGDENS	0.411337
VINECOVR	0.747303
WDYDEBR	0.913829
WDYFREQ	0.795855

[1] Variable descriptions are provided in Table 3.

Table 7. The weighted and unweighted variance explained by three factors extracted from 11 vegetation variables in 1994 and 1995, Oak Ridge Forestry Experiment Station, Oak Ridge, Tennessee. The factors were extracted using the maximum-likelihood method.

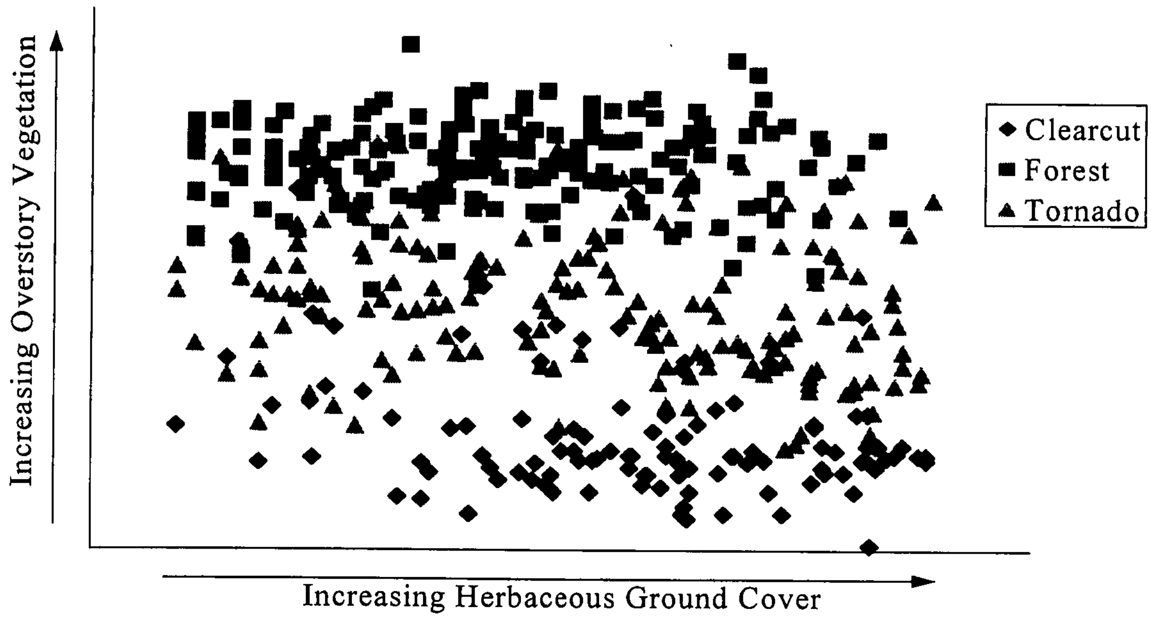
	Factor 1	Factor 2	Factor 3	Total
Weighted	56.41	4.76	16.96	78.14
Unweighted	5.06	2.25	2.04	9.35

Table 8. Correlation coefficients and rotated factor pattern of three factors extracted from habitat variables, 1994 - 1995, Oak Ridge Forestry Experiment Station, Oak Ridge, Tennessee. Factors were derived using the maximum-likelihood method. The shaded areas represent variables with salient loadings on the indicated factor (N = 464).

	Factor 1	**Factor 2**	**Factor 3**
BAACRE[1]	.95365	-.12740	-.20977
BADECD	.94054	-.14461	-.20599
RESIDUAL	.82848	-.13058	-.28072
CANPYCOV	.78641	-.15665	-.27971
CANPYHT	.74018	-.12351	-.23299
VEGDENS	-.55726	.21404	.23449
GRNDCOVR	-.30372	.95154	.04821
VINECOVR	-.30764	.79860	.12207
FORBCOVR	-.01261	.61505	.00103
WDYDEBR	-.19541	.10857	.92944
WDYFREQ	-.19205	.09594	.86589

[1] Variables are described in Table 3.

a.)



b.)

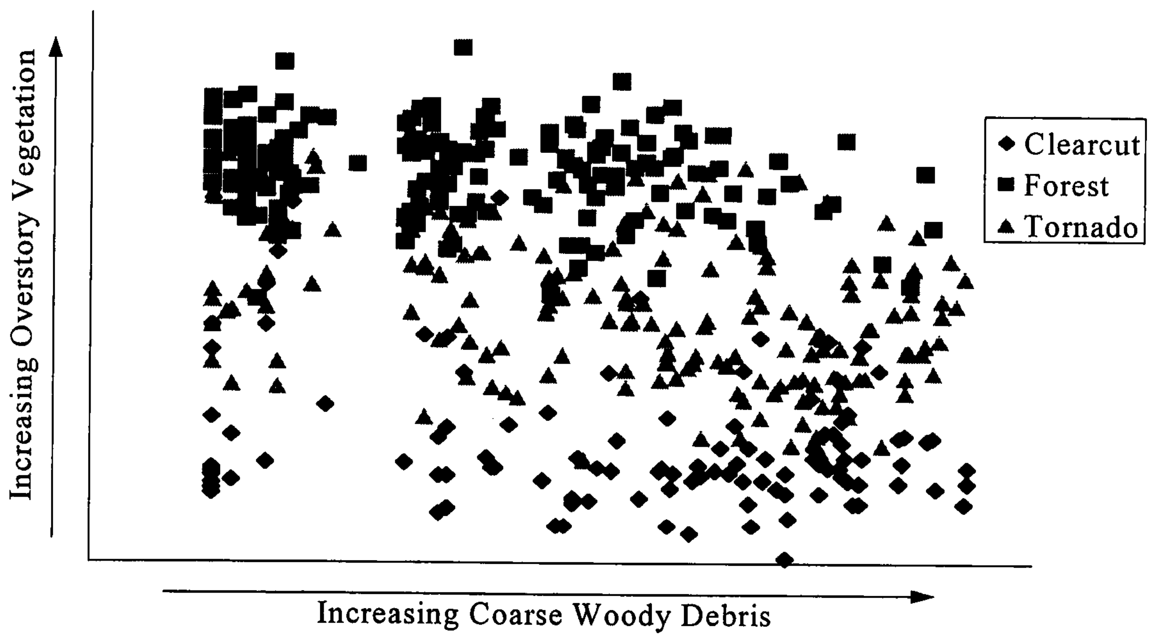


Figure 4. Factor scores of overstory vegetation (Factor 1) and herbaceous ground cover (Factor 2) by treatment (a) and factor scores of overstory vegetation (Factor 1) and coarse woody debris (Factor 3) by treatment (b), Oak Ridge Forestry Experiment Station, Oak Ridge, Tennessee, 1994 and 1995. N = 189 (clearcut n = 54, tornado n = 63, undisturbed forest n = 72).

Table 9. Means and (SE) of 3 factors and 7 variables not represented by the common factors for two disturbed and one undisturbed forest in 1994 and 1995, Oak Ridge Forestry Experiment Station, Oak Ridge, Tennessee (N = 464).

Habitat variables	Clearcut (n = 112)	Forest (n = 180)	Tornado (n = 172)
Overstory vegetation/-understory vegetation density (Factor 1)	-0.861 (0.335) **C**[1]	0.642 (0.018) **A**	-0.111 (0.030) **B**
Herbaceous ground cover (Factor 2)	0.308 (0.074) **A**	-0.291 (0.057) **B**	0.104 (0.069) **A**
Coarse woody debris (Factor 3)	0.289 (0.093) **A**	-0.471 (0.059) **B**	0.305 (0.070) **A**
Shrub cover	48.795 (2.930) **A**	13.972 (1.137) **B**	9.913 (1.042) **C**
Grass cover	24.867 (3.246) **A**	1.083 (0.460) **C**	2.674 (0.495) **B**
Snag basal area	0.000 (0.000) **C**	5.000 (0.737) **A**	2.444 (0.501) **B**
Conifer basal area	0.714 (0.352) **B**	8.889 (1.311) **A**	2.558 (0.672) **B**
Sapling density	2828.57 (76.000) **A**	768.33 (26.373) **B**	702.33 (16.717) **B**
Seedling density	19651.8 (1080.3) **A**	20677.8 (870.8) **A**	19470.9 (721.0) **A**
Litter depth	0.638 (0.032) **B**	0.973 (0.029) **A**	0.568 (0.026) **B**

[1] Means within rows with different letters indicate significant differences across treatments for a Bonferroni-adjusted alpha level of 0.017.

Factor 3 (coarse woody debris) also differed among treatments ($P \leq 0.05$). Mean factor scores for herbaceous ground cover and coarse woody debris were lower in undisturbed forest than in both disturbance treatments ($P \leq 0.017$); Factor 2 and Factor 3 scores for the two disturbance treatments did not differ ($P > 0.017$).

Shrub cover, grass cover, snag basal area, conifer basal area sapling density and litter depth differed among treatments ($P < 0.05$), whereas seedling density did not differ among treatments (0.5867). Shrub cover was greatest in clearcut areas, intermediate in undisturbed forest and lowest in tornado sites (Table 9; $P \leq 0.017$). Grass cover was greatest in clearcuts, intermediate in tornado sites and least in undisturbed forest ($P \leq 0.017$). Snags were most common in undisturbed forest, intermediate in tornado sites and least common in clearcuts ($P \leq 0.017$). Conifer basal area was greatest in undisturbed forest ($P \leq 0.017$) but did not differ between disturbance treatments ($P = 0.1627$). Sapling density was lowest in undisturbed forest ($P < 0.017$) but did not differ between disturbance treatments ($P = 0.0702$). Seedling density did not differ among treatments ($P = 0.5867$). Litter depth was greatest in undisturbed forest ($P < 0.017$), but did not differ between clearcut and tornado areas ($P = 0.0620$).

Avian Characteristics

Overview

I mapped breeding territories of 37 and 38 bird species in 1994 and 1995, respectively (Appendix C; Table C.1). In 1994, I recorded 42 species on 50-m radius point counts (Appendix C; Table C.2). I counted 48 species on 50-m radius point counts in 1995. During point counts, I observed both species recorded as territory holders and transients that did not appear to occupy territories; thus the number of species observed during point counts exceeded the number observed with territories during the spot mapping.

Avian community

Total abundance, richness and diversity

Based on Horn's Index of Community Similarity, clearcut and tornado areas had the greatest amount of community overlap both 1994 and 1995; tornado and undisturbed forests had an intermediate amount of overlap; and clearcut and undisturbed forests had little overlap (Table 10). Within treatments, there was little difference between replicates (Table 11) or years (Table 12).

Based on point counts, species richness, total abundance and diversity differed among treatments (Figure 5; $F = 5.72$, $P < 0.05$), but not across replicate study areas ($F = 1.28$, $P = 0.3070$). Species richness was lower in undisturbed forest than in both clearcut and tornado-disturbed areas ($P \leq 0.017$). Species richness did not differ between clearcut and tornado areas ($P = 0.8703$). Total abundance was lower in undisturbed forest than in clearcut and tornado areas ($P < 0.017$), but did not differ between clearcut and tornado sites ($P = 0.1606$). Diversity (H') did not differ between clearcut and tornado areas ($P = 0.9163$), but was lower on undisturbed forest sites ($P < 0.017$). Equitability (J') did not differ among treatments ($P = 0.1213$) or between years (Figure 5; $P = 0.1980$). Species richness, total abundance and diversity were greater in 1995 than in 1994 ($P \leq 0.05$).

Table 10. Horn's Index of Community Similarity (R_o) for two disturbance treatments and an undisturbed forest in 1994 and 1995, Oak Ridge Forestry Experiment Station, Oak Ridge, Tennessee.

	Clearcut	Forest	Tornado
		1994	
Clearcut	----		
Forest	0.290[A]	----	
Tornado	0.726	0.579	----
		1995	
Clearcut	----		
Forest	0.263	----	
Tornado	0.742	0.619	----

[A] $R_o = 0$ means no species in common between two treatments;
$R_o = 1$ means all species occurred in equal abundances in both treatments.

Table 11. Horn's Index of Community Similarity (R_o) between two replicates of two disturbance treatments and an undisturbed forest in 1994 and 1995, Oak Ridge Forestry Experiment Station, Oak Ridge, Tennessee.

	Clearcut	Forest	Tornado
		1994	
Clearcut	0.881[A]		
Forest		0.828	
Tornado			0.889
		1995	
Clearcut	0.869		
Forest		0.844	
Tornado			0.881

[A] $R_o = 0$ means no species in common between two treatments;
$R_o = 1$ means all species occurred in equal abundances in both treatments.

Table 12. Horn's Index of Community Similarity (R_o) for two disturbance treatments and an undisturbed forest comparing 1994 and 1995, Oak Ridge Forestry Experiment Station, Oak Ridge, Tennessee.

	Clearcut	Forest	Tornado
Clearcut	0.928[A]		
Forest		0.878	
Tornado			0.923

[A] $R_o = 0$ means no species in common between two treatments;
$R_o = 1$ means all species occurred in equal abundances in both treatments.

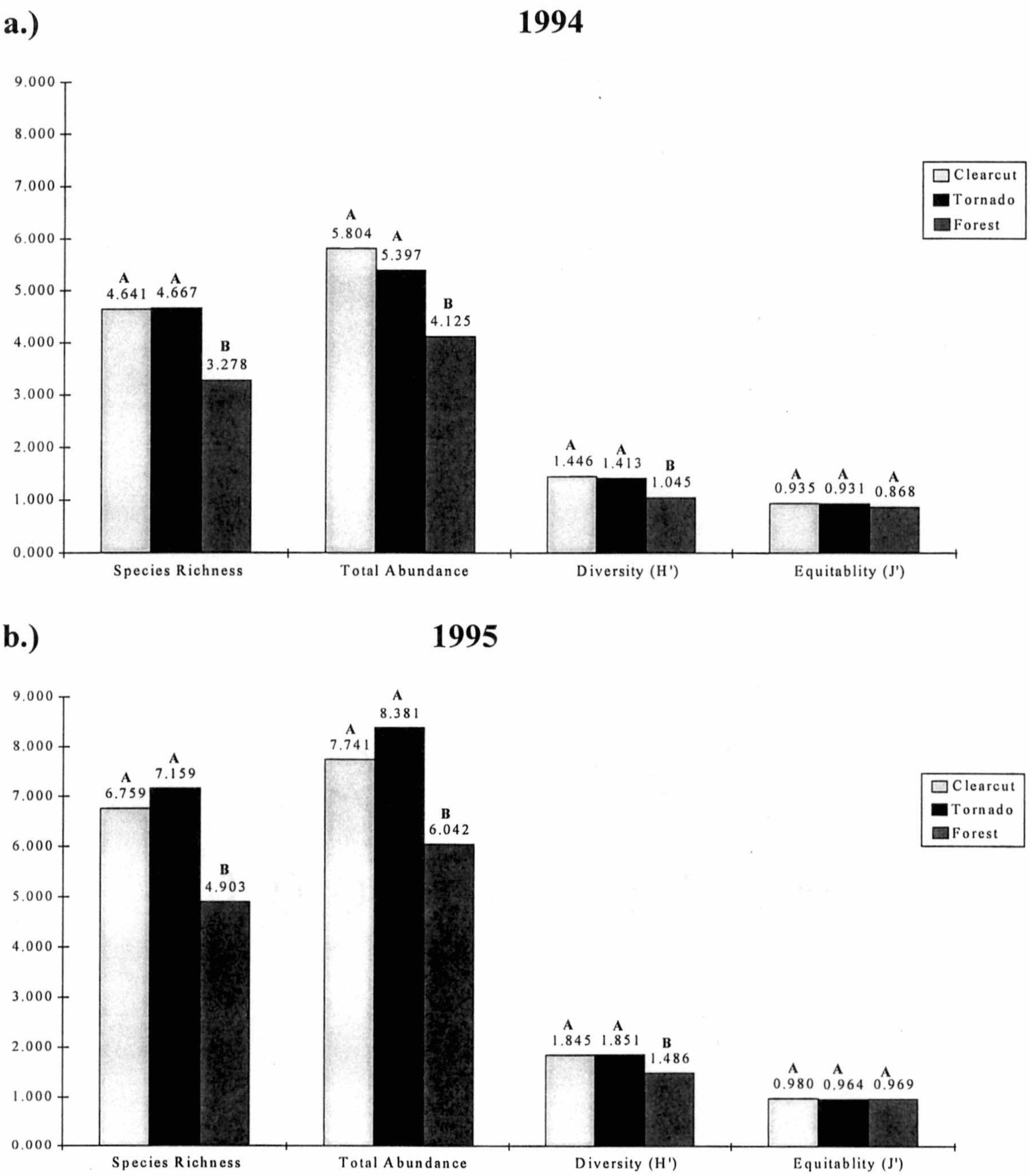


Figure 5. Mean species richness, abundance, diversity and equitablity per point count in 1994 (a) and 1995 (b) of breeding birds in two disturbance treatments (clearcut and tornado-disturbed) and undisturbed forest, Oak Ridge Forestry Experiment Station, Oak Ridge, Tennessee. Estimates with different letters differ based on a Bonferroni-adjusted alpha level ($P \leq 0.017$). N = 189 (clearcut n = 54, tornado n = 63, undisturbed forest n = 72).

Guild abundances

Nesting guilds. Based on point counts, all four nesting guild abundances differed among treatments (Figure 6; $P \leq 0.05$). In both years, cavity nesters were most abundant in tornado areas, intermediate in undisturbed areas and least abundant in clearcuts ($P \leq 0.017$). In 1994, canopy nesters were less abundant in clearcuts than in undisturbed or tornado-disturbed forests ($P \leq 0.017$). In 1995, canopy nesters were most abundant in undisturbed forest, intermediate in tornado areas and least abundant in clearcuts ($P \leq 0.017$). In 1994 and 1995, shrub nesters were most abundant in clearcuts, intermediate in tornado areas and least abundant in undisturbed sites ($P \leq 0.017$). In 1994, ground nesters were less abundant in clearcuts than in undisturbed and tornado-disturbed sites ($P \leq 0.017$). In 1995, ground nesters were more abundant in tornado areas than in undisturbed forest ($P < 0.017$).

Foraging guilds. Based on point counts, canopy, shrub and ground forager abundances differed among the two disturbance treatments and undisturbed forest (Figure 7; $P \leq 0.05$). In 1994, canopy foragers were less abundant in clearcuts than in either the undisturbed or tornado-disturbed areas ($P \leq 0.017$). In 1995, canopy foragers were most abundant in undisturbed forests, intermediate in tornado sites and least abundant in clearcuts ($P \leq 0.017$). In 1994 and 1995, shrub foragers were most abundant in clearcuts, intermediate in tornado sites and least abundant in undisturbed forests ($P \leq 0.017$). In 1994, ground forager abundance did not differ among treatments ($P \geq 0.017$). In 1995, ground foragers were less abundant in undisturbed forests than in clearcuts and tornado sites ($P \leq 0.017$).

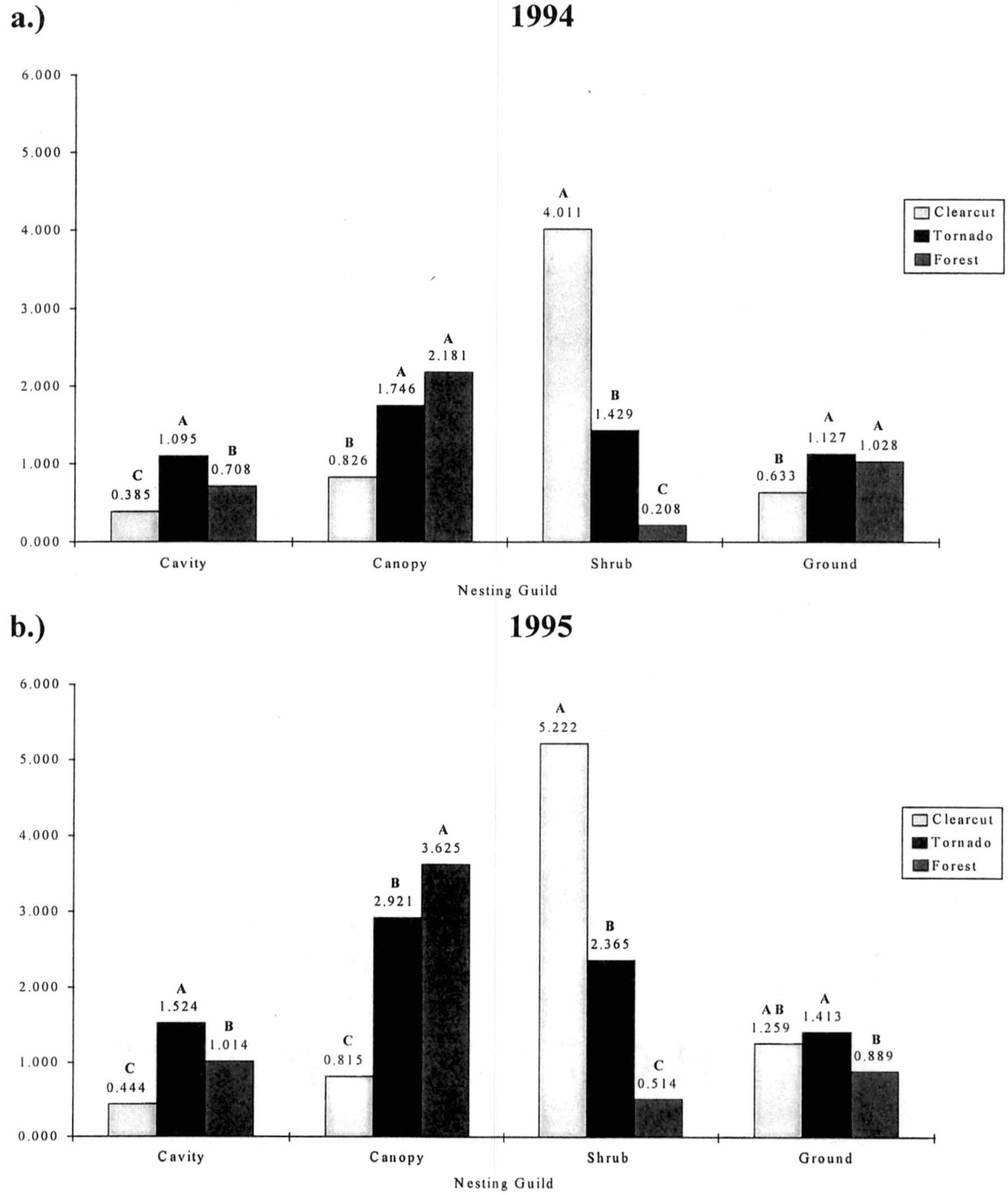


Figure 6. Mean abundance per point count of 4 nesting guilds in 1994 (a) and 1995 (b) of breeding birds in two disturbance treatments (clearcut and tornado-disturbed) and undisturbed forest, Oak Ridge Forestry Experiment Station, Oak Ridge, Tennessee. Estimates with different letters differ based on a Bonferroni-adjusted alpha level ($P \leq 0.017$). N = 189 (clearcut n = 54, tornado n = 63, undisturbed forest n = 72).

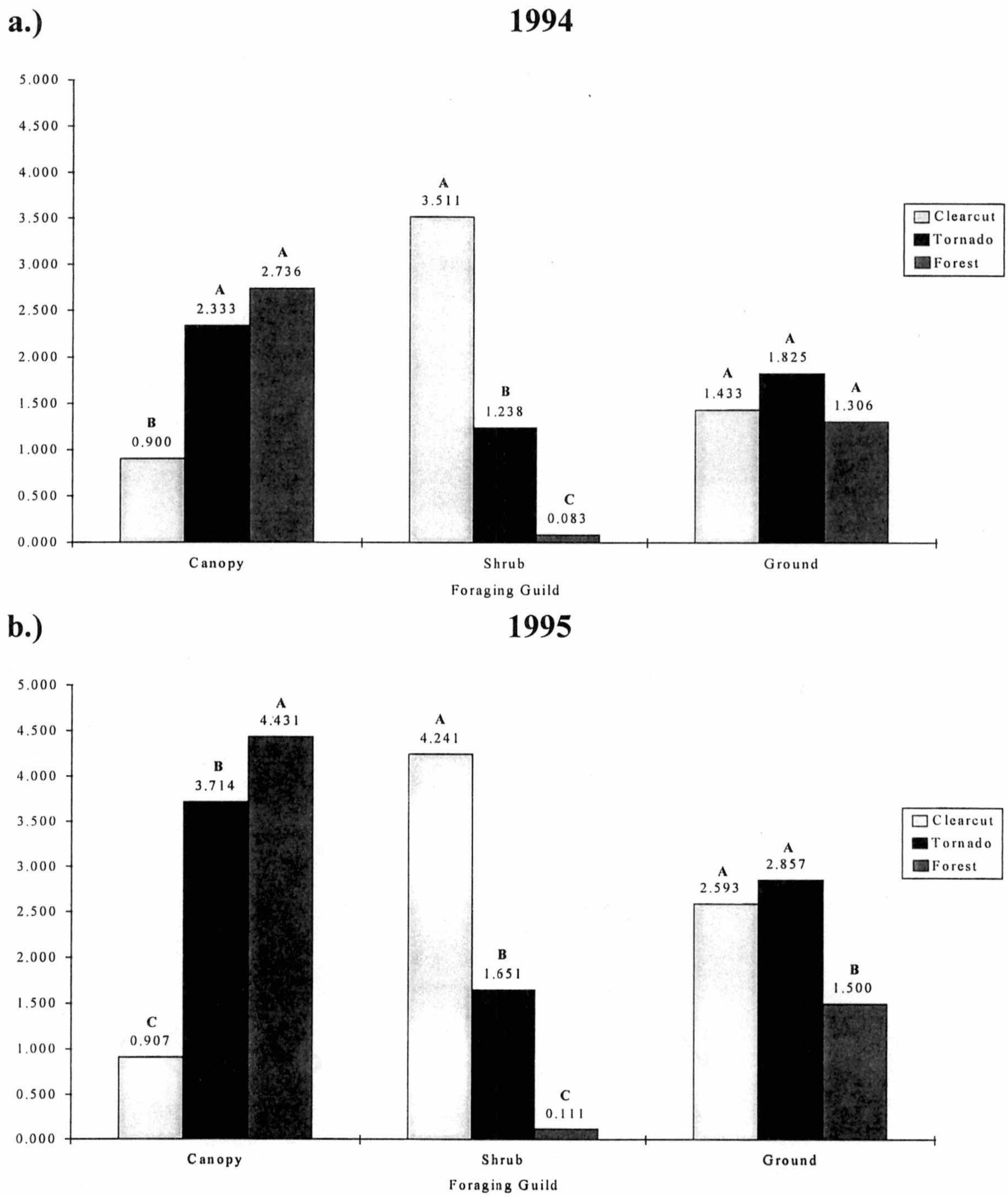


Figure 7. Mean abundance per point count of 3 foraging guilds in 1994 (a) and 1995 (b) of breeding birds in two disturbance treatments (clearcut and tornado-disturbed) and undisturbed forest, Oak Ridge Forestry Experiment Station, Oak Ridge, Tennessee. Estimates with different letters differ based on a Bonferroni-adjusted alpha level ($P \leq 0.017$). N = 189 (clearcut n = 54, tornado n = 63, undisturbed forest n = 72).

Species composition

Avian community composition in the two disturbance treatments and the undisturbed forest differed (Table 13). In both 1994 and 1995, the model that omitted the species and treatment interaction term did not fit ($P \leq 0.05$), indicating that treatment does affect the relationship between species and presence/absence (Table 13). In each treatment, several species had observed frequencies that were different from expected (Table 14).

Species-Habitat Associations

Blue-gray gnatcatcher

Full model

Blue-gray gnatcatchers were present at 136 points and absent at 328 points. Wald chi-square values indicated that only one parameter estimate, percent shrub cover, was significantly different from zero (Table 15; $P \leq 0.1$). The full model resulted in a correct classification rate of 68.3% for the unbiased jackknife test. The Hosmer-Lemeshow goodness-of-fit statistic indicated that the full model did not fit the data ($P = 0.0000$).

Reduced model

The stepwise procedure selected 2 variables (Factor 1 and percent shrub cover) as the best predictors of blue-gray gnatcatcher presence and absence in the Oak Ridge Experimental Forest (Table 15; $P \leq 0.1$). Overstory vegetation/understory vegetation density was positively correlated and percent shrub cover was negatively correlated with blue-gray gnatcatcher presence (Table 15). The reduced model had a correct classification

Table 13. Analysis of variance table for logit model testing the treatment and species interaction term, 1994 - 1995, Oak Ridge Forestry Experiment Station, Oak Ridge, Tennessee.

Year	Source	D.F.	Chi-square	$Pr \geq \chi^2$
1994	Intercept	1	115.27	0.0000
	Disturbance treatment	2	17.13	0.0002
	Species	41	169.40	0.0000
	Disturbance treatement*Species	82	274.37	0.0000
1995	Intercept	1	120.19	0.0000
	Disturbance treatment	2	31.24	0.0000
	Species	47	203.61	0.0000
	Disturbance treatement*Species	94	341.27	0.0000

Table 14. Bird species observed in two disturbance treatments and undisturbed forest in 1994 and 1995, Oak Ridge Forestry Experiment Station, Oak Ridge, Tennessee. Numbers are the frequency of points within each area where the species was observed. The letter in the parenthesis indicates whether the observed frequency was higher (H), lower (L) or did not differ (N) from the expected frequencies calculated from a logit model that omitted the treatment and species interaction.

	1994			1995		
Species	Clearcut (n = 6)	Forest (n = 8)	Tornado (n = 7)	Clearcut (n = 6)	Forest (n = 8)	Tornado (n = 7)
ACFL[1]	0 (L)	5 (H)	0 (L)	0 (L)	5 (H)	0 (L)
AMCR	*	*	*	0 (L)	1 (H)	1 (N)
AMGO	*	*	*	1 (H)	0 (L)	1 (N)
AMRE	*	*	*	0 (L)	1 (H)	0 (L)
BAOW	*	*	*	0 (L)	0 (N)	1 (N)
BGGN	1 (L)	5 (N)	7 (H)	2 (L)	6 (H)	7 (H)
BHCO	4 (N)	3 (L)	7 (H)	3 (L)	5 (N)	6 (N)
BLJA	2 (N)	4 (H)	1 (L)	0 (L)	2 (N)	4 (H)
BRTH	1 (H)	0 (N)	0 (L)	1 (H)	0 (N)	0 (L)
BWWA	*	*	*	1 (H)	0 (N)	0 (L)
CACH	4 (L)	6 (N)	7 (H)	5 (L)	7 (N)	7 (H)
CAWR	1 (L)	1 (L)	7 (H)	3 (L)	4 (N)	7 (H)
COFL	1 (H)	0 (N)	0 (L)	1 (H)	0 (L)	1 (N)
COGR	0 (L)	1 (H)	0 (L)	0 (L)	1 (N)	2 (N)
COYE	1 (H)	0 (N)	0 (L)	3 (H)	0 (L)	0 (L)
DOWO	0 (L)	0 (N)	1 (H)	0 (L)	0 (L)	3 (H)
EABL	0 (L)	0 (N)	1 (H)	*	*	*
EAKI	*	*	*	1 (H)	0 (N)	0 (L)
EAPH	*	*	*	0 (L)	0 (N)	1 (N)
EWPE	0 (L)	1 (N)	2 (N)	0 (L)	0 (L)	4 (N)
FISP	5 (H)	0 (L)	0 (L)	3 (H)	0 (L)	0 (L)
GCFL	0 (L)	0 (N)	1 (H)	0 (L)	1 (H)	1 (N)
GRCA	*	*	*	2 (H)	0 (L)	2 (N)

Table 14. (Continued).

	1994			1995		
Species	Clearcut (n = 6)	Forest (n = 8)	Tornado (n = 7)	Clearcut (n = 6)	Forest (n = 8)	Tornado (n = 7)
HAWO	2 (N)	4 (H)	2 (L)	0 (L)	7 (H)	5 (N)
HOFI	1 (H)	0 (N)	0 (L)	*	*	*
HOWA	3 (L)	4 (N)	7 (H)	5 (H)	2 (L)	7 (H)
INBU	6 (H)	0 (L)	6 (H)	6 (H)	0 (L)	6 (H)
KEWA	3 (N)	0 (L)	5 (H)	3 (H)	0 (L)	5 (H)
MODO	1 (N)	0 (L)	1 (N)	3 (H)	0 (L)	5 (H)
NOCA	4 (H)	2 (L)	5 (N)	6 (H)	3 (L)	7 (H)
NOOR	*	*	*	1 (H)	0 (N)	0 (L)
OVEN	1 (L)	8 (H)	1 (L)	0 (L)	8 (H)	0 (L)
PIWA	0 (L)	1 (H)	0 (L)	0 (L)	3 (H)	0 (L)
PIWO	0 (L)	0 (N)	1 (H)	0 (L)	1 (N)	2 (N)
PRWA	5 (H)	0 (L)	0 (L)	6 (H)	0 (L)	3 (L)
RBWO	1 (L)	3 (N)	5 (H)	0 (L)	2 (N)	5 (H)
REVI	3 (L)	8 (H)	6 (N)	2 (L)	8 (H)	7 (H)
RSTO	6 (H)	0 (L)	4 (N)	6 (H)	0 (L)	3 (L)
RTHA	0 (L)	0 (N)	1 (H)	*	*	*
RTHU	1 (N)	0 (L)	1 (N)	0 (L)	0 (N)	1 (N)
SCTA	1 (L)	6 (H)	1 (L)	0 (L)	7 (H)	5 (N)
SUTA	4 (L)	5 (N)	7 (H)	4 (N)	3 (L)	7 (H)
TUTI	2 (L)	3 (N)	5 (H)	2 (N)	4 (H)	2 (L)
WBNU	0 (L)	4 (H)	4 (N)	0 (L)	3 (H)	5 (H)
WEVI	6 (H)	0 (L)	3 (N)	6 (H)	0 (L)	5 (N)
WEWA	0 (L)	1 (H)	0 (L)	1 (H)	0 (N)	0 (L)
WITU	*	*	*	0 (L)	1 (H)	0 (L)
WOTH	0 (L)	2 (H)	1 (N)	2 (N)	4 (H)	1 (L)
YBCH	6 (H)	0 (L)	4 (N)	6 (H)	0 (L)	4 (N)
YBCU	3 (N)	4 (H)	2 (L)	1 (L)	4 (H)	3 (N)
YTVI	2 (H)	0 (L)	2 (N)	1 (N)	2 (N)	3 (N)
YTWA	0 (L)	0 (N)	1 (H)	*	*	*

[1] = Common and scientific names of species are given in Appendix A.

* = No observations of this species where made during the year.

Table 15. Full and backward stepwise selection results of logistic regression for response variable - blue-gray gnatcatcher presence/absence. Explanatory habitat variables were collected in 1994 and 1995, Oak Ridge Forestry Experiment Station, Oak Ridge, Tennessee (N = 464).

Variable	Parameter estimate	Wald chi-square $P > \chi^2$	Test of Model Predictive Power Classification Table (Jackknife test)	Goodness-of-Fit Hosmer/Lemeshow Statistic
Full model				
Intercept	0..3080	0.6258	68.3%	C = 38.576 P = 0.000
Overstory vegetation/ -understory vegetation (Factor 1)	0.3668	0.1272		
Herbaceous ground vegetation (Factor 2)	0.1112	0.4235		
Coarse woody debris (Factor 3)	-0.0630	0.6211		
Sapling density	-0.00067	0.4774		
Percent shrub cover	-0.00258	0.0040		
Basal area of conifers	-0.00052	0.6855		
Seedling density	0.000202	0.8016		
Basal area of snags	0.000664	0.6132		
Percent grass cover	-0.00138	0.2649		
Litter depth	-0.00115	0.2095		
Final backward stepwise model				
Intercept	-0.2925	0.1634	70.5%	C = 11.763 P = 0.162
Overstory vegetation/ -understory vegetation (Factor 1)	0.4210	0.0141		
Percent shrub cover	-0.00279	0.0011		

rate of 70.5%. The reduced model fit the data adequately (Table 15; C = 11.763, P = 0.162).

Hooded warbler

Full model

I observed hooded warblers at 132 points; they were absent from 332 points. Four variables (Factor 1, Factor 2, Factor 3 and shrub cover) had Wald chi-square scores ($P \leq 0.1$) that indicated they were related to the presence/absence of hooded warblers (Table 16). The jackknife test predicted 72.8% of the observations correctly. The Hosmer-Lemeshow statistic indicated that the full model fit the data well (P = 0.506).

Reduced model

The stepwise procedure selected Factors 1-3 and shrub cover as the best set of predictors (Table 16). Factors 1-2 and shrub cover were negatively correlated with hooded warbler presence whereas Factor 3 was positively correlated with hooded warbler presence. The reduced model resulted in a correct classification rate of 73.1% and the Hosmer-Lemeshow goodness-of-fit statistic indicated a good fit to the data (P = 0.278).

Indigo bunting

Full model

I observed indigo buntings at 80 of 464 points. Factor 1 and litter depth had significant Wald chi-square scores ($P \leq 0.1$) in the full model, indicating these variables were related to indigo bunting presence and absence (Table 17). The full model correctly classified 80.0% of the observations (Table 17). The Hosmer-Lemeshow statistic indicated the full model did not fit the data (P = 0.024).

Table 16. Full and backward stepwise selection results of logistic regression for response variable - hooded warbler presence/absence. Explanatory habitat variables were collected in 1994 and 1995, Oak Ridge Forestry Experiment Station, Oak Ridge, Tennessee (N = 464).

Variable	Parameter estimate	Wald chi-square $P > \chi^2$	Test of Model Predictive Power: Classification Table (Jackknife test)	Goodness-of-Fit: Hosmer/Lemeshow Statistic
Full model				
Intercept	0.2647	0.7137	72.8%	C = 7.287 P = 0.506
Overstory vegetation/ -understory vegetation (Factor 1)	-1.2667	0.0001		
Herbaceous ground vegetation (Factor 2)	-0.4448	0.0033		
Coarse woody debris (Factor 3)	0.2494	0.0610		
Sapling density	0.000587	0.5711		
Percent shrub cover	-0.00336	0.0006		
Basal area of conifers	-0.00206	0.2166		
Seedling density	0.000685	0.4250		
Basal area of snags	0.000361	0.8248		
Percent grass cover	-0.00121	0.3245		
Litter depth	-0.00091	0.3447		
Final backward stepwise model				
Intercept	-0.2919	0.2012	73.1%	C = 9.822 P = 0.278
Overstory vegetation/ -understory vegetation (Factor 1)	-1.3439	0.0001		
Herbaceous ground vegeatation (Factor 2)	-0.4869	0.0006		
Coarse woody debris (Factor 3)	0.2762	0.0340		
Percent shrub cover	-0.00347	0.0002		

Table 17. Full and backward stepwise selection results of logistic regression for response variable - indigo bunting presence/absence. Explanatory habitat variables were collected in 1994 and , Oak Ridge Forestry Experiment Station, Oak Ridge, Tennessee (N = 464).

Variable	Parameter estimate	Wald chi-square $P > \chi^2$	Test of Model Predictive Power: Classification Table (Jackknife test)	Goodness-of-Fit: Hosmer/Lemeshow Statistic
Full model				
Intercept	1.0661	0.4097	80.0%	C = 17.618 P = 0.024
Overstory vegetation/ -understory vegetation (Factor 1)	-1.5028	0.0001		
Herbaceous ground vegetation (Factor 2)	-0.00899	0.9624		
Coarse woody debris (Factor 3)	0.2473	0.1305		
Sapling density	0.00103	0.4735		
Percent shrub cover	-0.00035	0.7844		
Basal area of conifers	-0.00368	0.1963		
Seedling density	0.000845	0.4423		
Basal area of snags	-0.00663	0.1449		
Percent grass cover	-0.00153	0.2972		
Litter depth	-0.00445	0.0005		
Final backward stepwise model				
Intercept	-1.2623	0.0001	82.1%	C = 7.105 P = 0.525
Overstory vegetation/ -understory vegetation (Factor 1)	-1.6126	0.0001		
Coarse woody debris (Factor 3)	0.2739	0.0753		
Litter depth	-0.00406	0.0007		

Reduced model

The stepwise procedure selected a three variable model (Factor 1, Factor 3 and litter depth) to best explain the variation in indigo bunting presence and absence (Table 17). Factor 1 and litter depth were negatively correlated with indigo bunting presence ($P < 0.1$). Factor 3 was positively related to indigo bunting presence (Table 17; $P \leq 0.1$). The three variable model resulted in a correct classification rate of 82.1% and fit the data well ($C = 7.105$, $P = 0.525$).

Ovenbird

Full model

I observed ovenbirds at 105 points, thus oven birds were absent at 359 points. Factor 1 was the only significant variable ($P \leq 0.1$) in the full model (Table 18). The full model correctly predicted ovenbird presence and absence 80.0% of the time. The full model fit the data adequately ($P = 0.233$).

Reduced model

Factor 1 was the only variable needed to predict ovenbird presence (Table 18; $P \leq 0.1$). Ovenbird presence had a strong positive correlation with Factor 1. The reduced model resulted in a correct classification rate of 82.1% (Table 18). The reduced model marginally fit the data ($P = 0.104$).

Prairie warbler

Full model

I observed prairie warblers at 54 points and failed to observe them at 410 points. Factor 1, shrub cover and grass cover were significant ($P \leq 0.1$) variables in the full model

Table 18. Full and backward stepwise selection results of logistic regression for response variable - ovenbird presence/absence. Explanatory habitat variables were collected in 1994 and , Oak Ridge Forestry Experiment Station, Oak Ridge, Tennessee (N = 464).

Variable	Parameter estimate	Wald chi-square $P > \chi^2$	Test of Model Predictive Power: Classification Table (Jackknife test)	Goodness-of-Fit: Hosmer/Lemeshow Statistic
Full model				
Intercept	-3.8032	0.0001	80.0%	C = 10.481 P = 0.233
Overstory vegetation/ -understory vegetation (Factor 1)	4.2877	0.0001		
Herbaceous ground vegetation (Factor 2)	0.1200	0.5512		
Coarse woody debris (Factor 3)	-0.0113	0.9516		
Sapling density	0.00112	0.4007		
Percent shrub cover	0.00141	0.3196		
Basal area of conifers	0.000766	0.6169		
Seedling density	0.000032	0.9770		
Basal area of snags	-0.00049	0.7514		
Percent grass cover	-0.00071	0.7240		
Litter depth	0.00199	0.1312		
Final backward stepwise model				
Intercept	-2.9084	0.0001	82.1%	C = 13.226 P = 0.104
Overstory vegetation/ -understory vegetation (Factor 1)	4.4179	0.0001		

(Table 19). The full model correctly predicted 100.0% of the observations. The goodness-of-fit statistic indicated the model fit the data very well ($P = 0.748$).

Reduced model

The stepwise procedure selected a three variable model, with Factor 1, shrub cover and grass cover, as best at predicting prairie warbler distribution (Table 19; $P \leq 0.1$). Factor 1 was negatively correlated, whereas shrub and grass cover were positively correlated with prairie warbler presence (Table 19). This three variable model classified 90.7% of the observations correctly. The reduced model fit the data well ($P = 0.724$).

Red-eyed vireo

Full model

I observed red-eyed vireos at 205 points and failed to observe them at 259 points. Factor 1, shrub cover and grass cover were significant in the full model (Table 20; $P \leq 0.1$). The full model resulted in a correct classification rate of 68.3%. The full model fit the data well (Table 20; $P = 0.680$).

Reduced model

The stepwise procedure selected a three variable model to best predict red-eyed vireo distribution. Factor 1, shrub cover and grass cover all had significant Wald chi-square scores ($P \leq 0.1$; Table 20). Factor 1 was positively correlated with red-eyed vireo presence, whereas shrub and grass cover were negatively correlated with red-eyed vireo presence (Table 20). The reduced model classified 69.4% of the observations correctly. The reduced model fit the data extremely well ($P = 0.832$).

Table 19. Full and backward stepwise selection results of logistic regression for response variable - prairie warbler presence/absence. Explanatory habitat variables were collected in 1994 and 1995, Oak Ridge Forestry Experiment Station, Oak Ridge, Tennessee (N = 464).

Variable	Parameter estimate	Wald chi-square $P > \chi^2$	Test of Model Predictive Power: Classification Table (Jackknife test)	Goodness-of-Fit: Hosmer/Lemeshow Statistic
Full model				
Intercept	18.4644	0.0001	100.0%	C = 5.088 P = 0.748
Overstory vegetation/ -understory vegetation (Factor 1)	-1.5722	0.0074		
Herbaceous ground vegetation (Factor 2)	0.0678	0.8040		
Coarse woody debris (Factor 3)	-0.0424	0.8348		
Sapling density	0.00236	0.2788		
Percent shrub cover	0.00432	0.0297		
Basal area of conifers	-0.00694	0.1730		
Seedling density	-0.0006	0.6788		
Basal area of snags	-0.1096	0.9970		
Percent grass cover	0.00310	0.0864		
Litter depth	-0.00076	0.6424		
Final backward stepwise model				
Intercept	-5.2563	0.0001	90.7%	C = 5.310 P = 0.724
Overstory vegetation/ -understory vegetation (Factor 1)	-2.2473	0.0001		
Percent shrub cover	0.00488	0.0086		
Percent grass cover	0.00289	0.0766		

Table 20. Full and backward stepwise selection results of logistic regression for response variable - red-eyed vireo presence/absence. Explanatory habitat variables were collected in 1994 and 1995, Oak Ridge Forestry Experiment Station, Oak Ridge, Tennessee (N = 464).

Variable	Parameter estimate	Wald chi-square $P > \chi^2$	Test of Model Predictive Power: Classification Table (Jackknife test)	Goodness-of-Fit: Hosmer/Lemeshow Statistic
Full model				
Intercept	0.8105	0.2010	68.3%	C = 5.710, P = 0.680
Overstory vegetation/ -understory vegetation (Factor 1)	1.3005	0.0001		
Herbaceous ground vegetation (Factor 2)	0.0348	0.8017		
Coarse woody debris (Factor 3)	-0.1774	0.1660		
Sapling density	0.000916	0.3313		
Percent shrub cover	-0.00270	0.0030		
Basal area of conifers	-0.00088	0.4784		
Seedling density	0.000718	0.3785		
Basal area of snags	0.000364	0.7832		
Percent grass cover	-0.00297	0.0178		
Litter depth	-0.00052	0.5739		
Final backward stepwise model				
Intercept	0.8041	0.0145	69.4%	C = 4.269, P = 0.832
Overstory vegetation/ -understory vegetation (Factor 1)	1.2914	0.0001		
Percent shrub cover	-0.00235	0.0066		
Percent grass cover	-0.00272	0.0240		

Summer tanager

Full model

I observed summer tanagers at 126 points and failed to observe them at 338 points. The parameter estimates for Factor 1, Factor 2, sapling density, shrub cover, snag basal area and litter depth were all significantly different from zero (Table 21; $P \leq 0.1$). The full model resulted in a correct classification rate of 74.8% (Table 21). The full model provided a very good fit to the data ($P = 0.840$).

Reduced model

The stepwise procedure selected 6 variables as the best predictors of summer tanager presence and absence ($P \leq 0.1$). Factor 1, Factor 2, sapling density, shrub cover, snag basal area and litter depth were all negatively correlated with summer tanager presence (Table 21). This six variable model resulted in a correct classification rate of 75.0% (Table 21). The Hosmer-Lemeshow statistic indicated that the reduced model fit the data extremely well ($P = 0.986$).

White-eyed vireo

Full model

I observed white-eyed vireos at 92 points and failed to observe them at 372 points. The estimated slope coefficients of Factor 1, sapling density, shrub cover and seedling density were all different ($P \leq 0.1$) from zero (Table 22). The full model resulted in a correct classification rate of 79.1% (Table 22). The full model marginally fit the data ($P =$ 0.053).

Table 21. Full and backward stepwise selection results of logistic regression for response variable - summer tanager presence/absence. Explanatory habitat variables were collected in 1994 and 1995, Oak Ridge Forestry Experiment Station, Oak Ridge, Tennessee (N = 464).

Variable	Parameter estimate	Wald chi-square $P > \chi^2$	Test of Model Predictive Power: Classification Table (Jackknife test)	Goodness-of-Fit: Hosmer/Lemeshow Statistic
Full model				
Intercept	2.8123	0.0003	74.8%	C = 4.186, P = 0.840
Overstory vegetation/ -understory vegetation (Factor 1)	-0.9428	0.0007		
Herbaceous ground vegetation (Factor 2)	-0.3105	0.0418		
Coarse woody debris (Factor 3)	-0.0468	0.7321		
Sapling density	-0.00343	0.0012		
Percent shrub cover	-0.00476	0.0001		
Basal area of conifers	-0.00145	0.3601		
Seedling density	0.000515	0.5569		
Basal area of snags	-0.00446	0.0232		
Percent grass cover	0.000183	0.8849		
Litter depth	-0.00388	0.0001		
Final backward stepwise model				
Intercept	2.6187	0.0001	75.0%	C = 1.824, P = 0.986
Overstory vegetation/ -understory vegetation (Factor 1)	-0.9474	0.0001		
Herbaceous ground vegetation (Factor 2)	-0.3261	0.0237		
Sapling density	-0.00336	0.0014		
Percent shrub cover	-0.00468	0.0001		
Basal area of snags	-0.00442	0.0236		
Litter depth	-0.00398	0.0001		

Table 22. Full and backward stepwise selection results of logistic regression for response variable - white-eyed vireo presence/absence. Explanatory habitat variables were collected in 1994 and 1995, Oak Ridge Forestry Experiment Station, Oak Ridge, Tennessee (N = 464).

Variable	Parameter estimate	Wald chi-square $P > \chi^2$	Test of Model Predictive Power Classification Table (Jackknife test)	Goodness-of-Fit Hosmer/Lemeshow Statistic
Full model				
Intercept	0.1750	0.8927		
Overstory vegetation/ -understory vegetation (Factor 1)	-1.8474	0.0001		
Herbaceous ground vegetation (Factor 2)	0.0702	0.7128		
Coarse woody debris (Factor 3)	0.2061	0.1979	79.1%	C = 15.346 P = 0.053
Sapling density	0.00265	0.0594		
Percent shrub cover	-0.00229	0.0712		
Basal area of conifers	-0.00459	0.1099		
Seedling density	0.00187	0.0847		
Basal area of snags	-0.00695	0.1268		
Percent grass cover	-0.00056	0.6982		
Litter depth	-0.00049	0.6891		
Final backward stepwise model				
Intercept	-1.9302	0.0001		
Overstory vegetation/ -understory vegetation (Factor 1)	-2.1874	0.0001		
Sapling density	0.00246	0.0577	78.2%	C = 15.903 P = 0.044
Percent shrub cover	-0.00294	0.0122		

Reduced model

The best fitting reduced model contained three explanatory variables; Factor 1, shrub cover and sapling density (Table 22). Factor 1 and shrub cover were negatively correlated with white-eyed vireo presence, whereas sapling density was positively correlated with white-eyed vireo presence ($P \leq 0.1$). The correct classification rate of the reduced model was 78.2%. However, the three variable model did not fit the data ($P = 0.044$).

Yellow-breasted chat

Full model

I recorded yellow-breasted chats at 109 points and failed to observe them at 355 points. The Wald chi-square scores indicated that Factor 1 and Factor 2 had significant correlations with yellow-breasted chat presence (Table 23; $P \leq 0.1$). The full model correctly classified 80.8% of the observations (Table 23). The full model fit the data adequately ($P = 0.180$).

Reduced model

The stepwise procedure selected Factor 1, Factor 2 and grass cover as the best predictors of yellow-breasted chat presence (Table 23; $P \leq 0.1$). Factor 1 was negatively correlated with yellow-breasted chat presence, whereas Factor 2 and grass cover were positively correlated with yellow-breasted chat presence (Table 23). The reduced model resulted in a correct classification rate of 81.2% (Table 23). The reduced model provided an adequate fit to the data ($P = 0.228$).

Table 23. Full and backward stepwise selection results of logistic regression for response variable - yellow-breasted chat presence/absence. Explanatory habitat variables were collected in 1994 and 1995, Oak Ridge Experimental Forest, Tennessee (N = 464).

Variable	Parameter estimate	Wald chi-square $P > \chi^2$	Test of Model Predictive Power: Classification Table (Jackknife test)	Goodness-of-Fit: Hosmer/Lemeshow Statistic
Full model				
Intercept	-2.6345	0.0060	80.8%	C = 11.394 P = 0.180
Overstory vegetation/ -understory vegetation (Factor 1)	-2.1668	0.0001		
Herbaceous ground vegetation (Factor 2)	0.5771	0.0029		
Coarse woody debris (Factor 3)	-0.1315	0.4149		
Sapling density	-0.00012	0.9310		
Percent shrub cover	0.000345	0.7771		
Basal area of conifers	-0.0005	0.8148		
Seedling density	0.000726	0.4998		
Basal area of snags	0.000024	0.9921		
Percent grass cover	0.00208	0.1245		
Litter depth	0.000871	0.4755		
Final backward stepwise model				
Intercept	-2.3601	0.0001	81.2%	C = 10.565 P = 0.228
Overstory vegetation/ -understory vegetation (Factor 1)	-2.1060	0.0001		
Herbaceous ground vegetation (Factor 2)	0.5077	0.0051		
Percent grass cover	0.00219	0.0860		

CHAPTER 7

DISCUSSION

Vegetation Structure

One of the immediate and most obvious effects of the tornado disturbance on the UTFES forests was a reduction of overstory vegetation (Figure 4; Table 9). A tornado created similar patterns in a southeastern Texas forest (Glitzenstein and Harcombe 1988). The primary, short-term effect of the Texas tornado was to select strongly against dominants in the pre-tornado forest. Snags in the pre-tornado forest did not withstand the strong winds and were also quite susceptible to tornado damage (Glitzenstein and Harcombe 1988). Therefore, I expected overstory vegetation (Factor 1) to separate clearcut and tornado sites from undisturbed sites. I did not expect, however, that this factor would separate clearcut and tornado sites (Figure 4). Although the storm removed dominant trees and snags, a significant amount of overstory vegetation remained on sites disturbed by the tornado (Tables 9 and D.1). I estimated canopy coverage in the tornado-disturbed sites as 59.95%, around 35% less than the canopy cover in the undisturbed forest (Table D.1). The tornado reduced basal area to 5.94 $m^2/0.4$ ha, about 50% of the basal area in the undisturbed forest. Unlike the tornado, the clearcuts removed virtually all overstory vegetation; clearcut sites had canopy coverage of 6.39%, approximately 90% less than the canopy cover in the undisturbed forest (Table D.1). Clearcutting reduced basal area to 1.25 m^2/0.4 ha (SE = 0.22), about 10% of the basal area of undisturbed forest.

Coarse woody debris (Factor 3) did not differ among the three treatments as much as overstory vegetation differed among the treatments (Figure 4). However, coarse woody debris did separate undisturbed forest from the two disturbance treatments; Factor 3 did not differ between clearcuts and tornado sites (Table 9). The tornado increased the volume of woody debris about three-fold, from 2.61 m^3/0.4 ha in undisturbed forest to 9.41 m^3/0.4 ha (Table D.1). Similar to the tornado-disturbed areas, clearcuts had a woody debris volume of 10.74 m^3/0.4 ha, an increase of 8.14 m^3/0.4 ha from the undisturbed forest (Table D.1). Clearcuts had high amounts of coarse woody debris because of the site preparation treatments. Three of the site preparation treatments involved slashing down all standing trees after the removal of commercially valuable trees. Therefore, the clearcuts probably had higher amounts of coarse woody debris than clearcuts that do not receive slash down site preparations.

The removal of overstory vegetation by the tornado and clearcut disturbances resulted in a substantial amount of mid- and understory vegetation development. Herbaceous vegetation (Factor 2), grass cover and understory vegetation density were greater in the two disturbance treatments than in the undisturbed forest (Table 9). Shrub cover and sapling density were greatest on clearcuts. This pattern probably occurred because the clearcuts had virtually no overstory vegetation, therefore releasing the shrub and sapling mid-story from competition of overstory trees (Smith 1986). The tornado-disturbed sites had a residual overstory that probably prevented the complete release of the mid-story shrubs and saplings. In addition, mid-story vegetation in the tornado-disturbed areas may not have had enough time to be completely released. I collected vegetation data in the tornado-disturbed sites in the summer of 1994. Therefore, only two growing seasons had occurred between the tornado event and when I measured the vegetation structure. In Wisconsin, a forest had a mid-story density two years after a wind disturbance that did not differ from the pre-disturbance density (Dunn et. al 1983). In contrast, I sampled the two clearcuts areas 4 years after the timber harvests. In a few years, the shrubs and saplings in tornado sites may exhibit greater response to their release. In northern Kentucky, a tornado-disturbed forest exhibited a large increase in mid-story density eleven years after the storm (Held and Bryant 1989).

Snag basal area, conifer basal area and litter depth were greater in undisturbed forests than in the two disturbed treatments (Table 9). Snag basal area was greatest in undisturbed forests, intermediate in tornado sites and lowest in clearcuts. I expected clearcuts to have the lowest snag and conifer basal area because the timber harvests removed all overstory trees, including snags and conifers. However, I did not expect undisturbed forests to have greater snag basal area than tornado sites. Undisturbed forests had greater snag basal area than tornado sites because the storm removed all dead and weak trees that occurred in the pre-tornado forest. Although the storm damaged many of the residual trees in tornado sites, most were not killed. Conversely, the tornado did not remove any trees or snags from undisturbed forests. Therefore, undisturbed forests had greater snag basal area than tornado sites. Conifer basal area was greater in undisturbed forests than in tornado sites because conifers are susceptible to wind damage (Smith 1986) and were removed by the tornado. Litter depth was greater in undisturbed forests because timber removal and site preparation (e.g., burning) activities in the clearcuts (Smith 1986:389-393) and wind disturbance in the tornado sites removed some of the litter layer.

The clearcut and tornado-disturbed sites exhibited more variability in Factors 1 - 3 (i. e. greater spread of points) than did undisturbed forest (Figure 4). In clearcuts, variability might be attributed to the four distinct site preparation treatments used. Areas that received burning as a site preparation treatment tended to have greater herbaceous ground cover, and less coarse woody debris and overstory vegetation. Conversely, non-burned, slash-downed and control treatment areas had higher amounts of woody debris and residual overstory vegetation, and less ground cover than burned areas. In tornado-disturbed sites, the high variability may reflect the heterogeneous nature of the tornado event. The tornado did not remove overstory vegetation uniformly. Instead, the tornado removed virtually all of the overstory in some areas, and little in other areas. This pattern resulted in patchy overstory vegetation, herbaceous vegetation and coarse woody debris.

Avian Community Response and Habitat Characteristics

Overview

My results support the research hypothesis that avian community response to natural disturbance (tornadic wind) differs from avian community response to anthropogenic disturbance (clearcutting). The avian abundance, species richness, diversity and equitability estimates generated from point count data suggest that the bird communities in the two disturbed sites do not differ markedly. However, these estimates only provide information dealing with the overall structure of the communities (i. e., how many individuals in the community, how many species are present in the community, and how evenly distributed are those species through the community). Because large differences in species composition may be accompanied by only small differences in total abundance (Pimm 1991:321-328), comparisons of community similarity should be based on species compositions. Although Horn's Index of Community Similarity illustrated that both disturbance treatments had bird communities more similar to one another than to the undisturbed forest, the avian communities were not identical. In both 1994 and 1995, community overlap within treatments between years and replicates was greater than community overlap among treatments (Tables 10, 11 and 12). The guild analyses and logit model analyses suggest that the tornado and clearcut communities differ based on species distributions.

Avian community

Community-wide estimates

The UTFES had significantly greater avian abundance, species richness, and diversity in clearcut and tornado-disturbed sites than in undisturbed forests (Figure 5). In eastern hardwood forests, other studies of bird communities have also reported greater avian abundance, species richness, and diversity in clearcuts than in undisturbed forests (Ambrose 1975:70-122, Conner and Adkisson 1975, Webb et al. 1977, Titterington et al. 1979, Crawford et al. 1981, Horn 1984, Yahner 1986, Yahner 1987a, Derleth et al. 1989, Probst et al. 1992, Dickson et al. 1993, Thompson et al. 1993). Regenerating stands may have greater avian abundance, species richness, and diversity because birds are attracted to the dense foliage of seedlings/saplings and patchiness of the stand (Thompson et al. 1993).

Many vegetation variables (Table 9) showed greater variability in disturbed areas than in undisturbed forest.

In the clearcuts, the four site preparation treatments may have influenced the species richness and diversity estimates. The four site preparation treatments used in the clearcuts resulted in a variety of vegetation characteristics that would not have occurred in clearcuts that had only one treatment. For example, burned areas had high components of grass, forb and shrub vegetation, but low sapling density. Unburned areas had small amounts of grass, forb and shrub vegetation, but high sapling density. Clearcuts that receive only one site preparation treatment would probably have lower avian species richness and diversity because they would provide fewer habitats than the clearcuts that received four distinct treatments.

Guild abundances

The abundances of each nesting and foraging guild provide greater insight into how bird communities differ among treatments. Cavity nesting birds were most abundant in tornado-disturbed sites. These birds require dead or damaged trees for nesting habitat. The tornado did not create an abundance of snags immediately, but it did cause extensive tree damage. Damaged trees may provide nesting habitat for cavity nesting birds, such as Carolina chickadees, tufted titmice and woodpeckers. Damaged and dying trees may have also provided foraging sites for cavity nesting birds by attracting insects. In Virginia, woodpeckers fed heavily on insects that occurred in woody debris created by clearcutting (Conner and Crawford 1974). Undisturbed forest had a greater number of snags than either disturbance treatments, but was intermediate in abundance of cavity nesters.

Apparently nesting and/or foraging opportunities in damaged, live trees and snags in tornado sites exceeded nesting and/or foraging opportunities in snags for cavity nesters in undisturbed forest. Cavity nesters were less abundant in clearcuts than in the either undisturbed or tornado-disturbed sites (Figure 6). Clearcut sites had virtually no standing snags or damaged trees. Cavity nesters probably avoided clearcuts because these sites had limited nesting and/or foraging opportunities (Conner and Crawford 1974, Dickson et al. 1983, Yahner 1986; Probst et al. 1992).

Canopy nesters and foragers were most abundant in undisturbed forests, intermediate in abundance in tornado sites and least abundant in clearcuts (Figures 6 and 7). Many canopy nesters and foragers require substantial overstory vegetation to provide adequate nesting and foraging habitat. The differences in avian abundance coincided with the differences in canopy cover among treatments. Undisturbed forests provided the most overstory vegetation and, thus, the most habitat for these species (Table 9). Similarly, in northern hardwood forests, canopy foraging birds were positively correlated with overstory vegetation and were most abundant in undisturbed forests (Yahner 1986, Thompson and Capen 1988, Probst et al. 1992). Tornado sites were intermediate in canopy cover and canopy nesters and foragers. Clearcuts had virtually no overstory vegetation and thus provided little suitable habitat for canopy nesting and foraging birds. These results are consistent with other studies that compared avian response in undisturbed and clearcut-disturbed forests (Conner and Adkisson 1975, Conner et al. 1979, Yahner 1986, Thompson and Capen 1988, Probst et al. 1992, Thompson et al. 1992).

Shrub nesting and foraging birds had greater abundances in clearcut and tornado-disturbed sites than in undisturbed forest. Large amounts of woody and herbaceous growth characterized both disturbance treatments, and probably provided suitable habitat for shrub nesting and foraging birds. Presence of shrub nesting and foraging birds has been shown to be positively correlated with clearcuts and dense understory vegetation (Yahner 1986, Thompson and Capen 1988, Probst et al. 1992). Shrub nesters and foragers were more abundant in disturbed sites than in undisturbed forests. Similar results have been reported in studies that have compared undisturbed and clearcut-disturbed forests (Conner and Adkisson 1975, Conner et al. 1979, Yahner 1986, Thompson and Capen 1988, Probst et al. 1992, Thompson et al. 1992). Shrub nesting and foraging birds, however, were much more abundant in clearcuts than in tornado-disturbed stands. Shrub specialists apparently responded to the greater shrub cover, grass cover, sapling density and understory vegetation density found in clearcuts. Therefore, clearcuts may have provided more suitable habitat for shrub nesters and foragers than did tornado-disturbed areas.

In 1994, the abundance of ground nesting and foraging birds did not differ between undisturbed and tornado-disturbed sites. In 1995, ground nesters and foragers were less abundant in undisturbed forests than in tornado-disturbed sites. Many ground nesting and foraging bird distributions have been positively correlated with dense understory vegetation (Yahner 1986, Probst et al. 1992). Tornado-disturbed sites had a substantial amount of coarse woody debris and herbaceous cover that provided habitat for ground nesting and foraging birds. Tornado sites also contained many pits and mounds created by uprooted trees that may have provided additional breeding sites for ground nesting birds such as Carolina wrens and Kentucky warblers. Clearcuts did not have pits and mounds created by uprooted trees, but did have coarse woody debris and herbaceous cover that provided adequate vegetative structure for ground nesting and foraging birds. Although undisturbed forests lacked coarse woody debris and herbaceous cover, the abundance of ground nesting and foraging birds did not differ between this treatment and tornado sites in 1994 (Figures 6 and 7). In 1994, ovenbirds were the only ground nesting and foraging bird that commonly occurred in undisturbed forests (Table 14). This species typically occurs in mature forests with sparse understories (Ehrlich et al. 1988:542, Hamel 1992:281). Therefore, in 1994 the abundance of ground nesters and foragers did not differ between undisturbed forests and tornado sites because ovenbirds were common in the undisturbed forest. In 1995, ovenbirds were less abundant than in 1994 (Appendix C, Table C.2) and, consequently, ground nester and forager abundances were lower in undisturbed forests than in tornado sites.

Species composition

Species composition differed among study areas. In both years, clearcuts had many early successional species, such as common yellowthroats, field sparrows, indigo buntings, prairie warblers, rufous-sided towhees and white-eyed vireos, with observed frequencies greater than expected (Table 14). Conversely, many late successional species, such as acadian flycatchers, ovenbirds, red-eyed vireos, red-bellied woodpeckers and scarlet tanagers, had lower than expected frequencies in clearcuts. In undisturbed forests, late successional species, such as ovenbirds, red-eyed vireos, scarlet tanagers, hairy woodpeckers, wood thrushes and acadian flycatchers, had greater than expected frequencies in both 1994 and 1995 (Table 14). In contrast, prairie warblers, indigo buntings, white-eyed vireos, northern cardinals, rufous-sided towhees and other early successional species generally had lower than expected frequencies in undisturbed forests. In summary, species composition in clearcuts favored early successional species and species composition in undisturbed forests favored late successional species, as expected (Conner and Adkisson 1975, Webb et al. 1977, Conner et al. 1979, Crawford et al. 1981, Yahner 1986, Thompson and Capen 1988, Thompson and Fritzell 1990, Thompson et al. 1992, Probst et al. 1992, Welsh and Healy 1993).

I observed a more complex pattern of avian community composition in tornado-disturbed areas. Some early successional species, such as Carolina wrens, indigo buntings, mourning doves and northern cardinals, had greater than expected frequencies in tornado-disturbed sites (Table 14). The tornado sites had very dense understories and high amounts of coarse woody debris that provided suitable nesting and foraging habitats for these species. However, other early successional species, such as brown thrashers, common yellowthroats, field sparrows, prairie warblers, yellow-breasted chats and rufous-sided towhees, had lower than expected frequencies in tornado sites. The presence of residual canopy apparently discouraged these early successional species from colonizing tornado sites. These observations suggest that clearcuts provide more suitable habitat for some species than do tornado-disturbed sites. A few mature forest species, such as blue-gray gnatcatchers, hooded warblers, Kentucky warblers, and red-eyed vireos, had greater than expected frequencies in tornado sites. These species may have persisted in tornado sites because of high site fidelity (Greenwood and Harvey 1982, Holmes and Sherry 1992). The residual canopy apparently provided enough suitable nesting and/or foraging habitat structure for these late successional birds to establish breeding territories. Late successional species may also exhibit site fidelity in clearcuts, but the absence of residual overstory may preclude the establishment of breeding territories. Other late successional species, such as acadian flycatchers, ovenbirds, pine warblers and scarlet tanagers, had lower than expected frequencies in tornado areas. The lack of a continuous canopy may have discouraged these species from remaining in tornado sites. In summary, the observed species composition in tornado-disturbed sites was unique. The occurrence of a dense understory, high amounts of coarse woody debris and residual overstory may have contributed to the observed, unique combination of early and late successional species in tornado-disturbed areas.

Species-Habitat Associations

The combination of late and early successional species in tornado sites and the species-habitat association models suggests that early and late successional classifications of species may be an over-simplification of their habitat selection. My species-habitat association models suggest that birds select habitat based on specific vegetative characteristics, such as overstory canopy and understory vegetation, rather than on generalized late or early successional conditions. Other studies have also suggested that birds base habitat selection on specific vegetation characteristics (MacAuthur et al. 1962, Cody 1981, Cody 1985, Wiens 1989a:283-296). Habitat selection based on specific vegetation characteristics may have contributed to the observed combination of early and late successional species in the tornado-disturbed sites.

The tornado disturbance altered late-successional forest structure uniquely and bird species responded to these changes differently than in clearcuts. Late successional species were present in both undisturbed and tornado sites, but were rare in clearcuts (Table 14). Three species (i. e., blue-gray gnatcatchers, hooded warblers and red-eyed vireos) that were common in the tornado areas are described as late successional species because they typically breed in mature forests and avoid clearcuts (DeGraaf and Rudis 1986:279, 300 and 329; Ehrlich et al. 1988:450, 496 and 540; Hamel 1992:234, 254 and 287). My habitat-association models, however, suggested that these species were actually sensitive to specific vegetative characteristics (Tables 15, 16 and 20). Hence, in the tornado-disturbed sites these species may have selected a specific habitat characteristic that typically occurs in late successional forests (i. e., overstory vegetation), rather than simply late successional habitats.

Early successional species were common in clearcuts and tornado-disturbed sites, but were rare in undisturbed forest (Table 14). Four species (i. e., indigo buntings, prairie warblers, white-eyed vireos and yellow-breasted chats) that were present in the tornado sites are described as early successional species because they breed in clearcuts and avoid mature forests (DeGraaf and Rudis 1986:295, 315 and 332; Ehrlich et al. 1988:488, 528 and 548; Hamel 1992:249, 273 and 290). My habitat-association models suggested these species were specifically selecting against overstory vegetation (Tables 17, 19, 22 and 23).

Thus, these species may have selected a specific habitat characteristic (i. e., absence of overstory vegetation), rather than simply early successional habitats.

Avian Response To Disturbance And Future Research

The avian communities differed between clearcut and tornado-disturbed areas. Avian response to habitat structure explained, in part, community differences between disturbance treatments. However, other factors may have contributed to avian community response to the two disturbances. One of these factors may be site fidelity (Greenwood and Harvey 1982, Holmes and Sherry 1992). The occurrence of late successional species in tornado sites could have been a result of site fidelity rather than habitat selection. Because tornado areas were recently disturbed (completed 1 growing season by 1994), some late successional birds may be returning to the same breeding site they occupied in the pre-disturbed forest. In contrast, site fidelity may not have occurred in clearcuts because they were not disturbed as recently as tornado areas (completed 3 growing seasons by 1994). Also, the virtual absence of residual overstory in clearcuts may have excluded late-successional birds that bred in the pre-disturbance forest from establishing territories.

Although late successional birds may establish breeding territories in tornado-disturbed areas, they may suffer low breeding success. I was unable to address the question of breeding success with my productivity data because of limited sample sizes (Table C.3). Future research could determine avian breeding success in disturbed areas and better clarify the effects of site fidelity.

Another factor that may influence avian community response to clearcut and tornado disturbance is the opportunity for local species colonizations and extinctions. Species compositions are determined by the successful invasion of species and loss of species through local extinctions (Wiens 1989:73-101, Pimm 1991:173-270). Because tornado-disturbed and clearcuts were adjacent, their colonization sources were the same. Based on their distance from source populations, both disturbed treatments had an equal probability of colonization by species. However, clearcutting greatly changed forest habitat structure by removing virtually all overstory canopy and releasing an abundance of understory vegetation. This set the stage for rapid colonization by early successional species and local extinction of some late successional species. Tornado disturbance also changed forest habitat structure, but not as drastically as clearcutting. Some of the niches in tornado sites probably remained occupied by late successional species. Opportunities for colonization by early successional species, therefore, may have been more limited than in clearcuts.

The ages of the two disturbance treatments may also have affected the differences observed in the bird communities. In 1994 the clearcut areas had completed 3 growing seasons, whereas the tornado-disturbed sites had completed only 1 growing season. Although the clearcut sites were older than the tornado-disturbed sites, the vertical vegetation development was similar in the two disturbance treatments. The clearcut sites had virtually all mid-story and advanced regeneration removed by the harvesting and site preparation treatments. Therefore, the clearcuts required a few growing seasons to re-develop the vertical vegetation structure that the harvesting and site preparation treatments removed. Hardwood clearcut succession typically consists of a herbaceous and shrub vegetation stage (1-3 years of age) followed by a sapling stage (4-12 years of age) (Smith, 1986:367-395, DeGraaf et al. 1992). In hardwood clearcuts of the Southeast, avian community diversity and abundance are initially low in the herbaceous/shrub stage, but increase as the vegetation develops into the sapling stage. (Conner and Adkisson 1975, Horn 1984, Kerpez and Stauffer 1989). In contrast to the clearcut sites, the tornado did not remove mid-story and advanced regeneration vegetation in tornado-disturbed areas. Hence, vertical vegetation structure did not have to develop in the tornado-disturbed sites. Because vertical vegetation structure was present, avian community diversity and abundance may initially be high in the tornado-disturbed sites.

The scale on which avian communities were viewed and the landscape context they occurred within could have also influenced observed patterns. The small study plots that I used may have affected species diversity. Many studies have documented that larger habitat patches have higher avian species richness and diversity than smaller habitat patches (Galli et al. 1976, Ambuel and Temple 1983, Rafe et al. 1985, Opdam et al. 1985, Wiens 1989b:200-247). The areas adjacent to my study plots may have also influenced the observed bird communities. For example, the tornado and clearcut sites were adjacent to undisturbed forests. Some late successional species may have occurred in the clearcut and tornado areas because they moved into the disturbance treatments from their territories in adjacent mature forests. Adjacent habitats may have also affected the distribution of prairie warblers. Prairie warblers are area-sensitive species that prefer large contiguous areas of early successional habitat with little overstory vegetation (Ehrlich et al. 1988:528, Robbins et al. 1989, Hamel 1992:273). Although this species was rare in tornado-disturbed sites, it was common in the clearcuts. The residual overstory vegetation in the tornado areas probably precluded prairie warblers from establishing territories. This species was probably common in clearcuts because virtually no overstory vegetation remained and the clearcut study areas were adjacent to salvaged, tornado-disturbed forests. The salvage operations that were conducted adjacent to the clearcuts removed all marketable trees from approximately 150 ha and resulted in a large area that closely resembled the clearcut treatments. Hence, prairie warblers were abundant in clearcuts probably because the study plots and adjacent salvaged forest created a large, contiguous patch of early successional habitat that attracted this species. These observations suggest that clearcuts provide more suitable habitat than tornado-disturbed sites for some species and large clearcuts may be more suitable for some species than small clearcuts.

Future research may also address the key question of whether or not the bird communities in the regenerating clearcut- and tornado-disturbed forests will converge to communities with similar species compositions? My research has examined the initial avian response to disturbance. Two possible recovery pathways may be followed by these sites. First, clearcut and tornado-disturbed areas may progress into different mature forests as they regenerate. These sites may support two distinct avian communities as birds respond to differences in forest structure and composition. Secondly, the two disturbance treatments may regenerate into similar forests and the two bird communities may similarly converge.

Because tornado-disturbed sites had greater overstory vegetation than clearcuts, the two areas will probably regenerate into different mature forests and support two distinct avian communities. First, overstory vegetation differences between the clearcut and tornado-disturbed sites will affect species composition (Smith 1986:191-212). By influencing micro-site factors (i. e., light, temperature and moisture), the residual overstory vegetation in the tornado sites will probably promote the development of shade-tolerant and semi-tolerant species (Sanders 1980, Johnson and Jacobs, 1981, Horsley 1982, Childs and Flint 1987, Kelty, 1987, Beck 1988). Species that existed in the pre-tornado forest as suppressed mid-story and advanced regeneration, such as red maple, American beech, blackgum and some species of oak, will probably become the overstory canopy species in the regenerated, mature forest. Conversely, clearcuts had virtually no overstory, mid-story or advanced regeneration and probably will promote the development of intolerant species, such as yellow poplar, pines and some oak and hickory species (Sanders 1980, Johnson and Jacobs 1981, Horsley 1982, Lees 1987, Beck 1988). Secondly, the differences in overstory vegetation between clearcut and tornado-disturbed areas will probably affect vegetation structure. The residual overstory vegetation in tornado sites will be present in mature forest as large trees and snags (Franklin 1989, Smith et al. 1989). However, since no overstory vegetation remains in the clearcuts, no residual large trees or snags will occur in the regenerated, mature stand.

In summary, the two regenerating disturbance treatments currently have different overstory vegetation structures, and will probably develop into two distinct forests with different species compositions and structures. Avian communities have been found to be closely linked to vegetation structure (MacAuthur and MacAuthur 1961, MacAuthur et al. 1962, Cody 1981). Therefore, the clearcut and tornado-disturbed sites will probably regenerate into different mature forests and support two distinct avian communities. However, a long term study that follows the regeneration of these disturbance treatments, and the assembly of their respective bird communities, is needed to provide a definitive answer to whether or not the bird communities will converge.

CHAPTER 8

MANAGEMENT IMPLICATIONS

My research has documented the short term differences in avian response to a managed and natural disturbance. Avian community structure has been found to be closely linked to vegetation structure (MacAuthur and MacAuthur 1961, MacAuthur et al. 1962). Therefore, control of vegetation structure in managed disturbances may define avian communities in those areas. My research suggests that overstory vegetation and coarse woody debris were most affected by the tornado disturbance. Forest managers may be better able to mimic natural disturbance by managing these two variables during timber harvests.

Forest managers can manage overstory vegetation by controlling the amount of residual basal area after a timber harvest. The tornado-disturbed sites had a mean basal area of 5.944 m^2/0.4 ha. This amount of basal area is similar to the residual basal area that a shelterwood timber harvest may maintain (Smith 1986:396-426). In fact, a shelterwood method that has been suggested for regenerating commercially important oaks in the Southern Appalachians maintains residual basal area at levels similar to the tornado-disturbed sites (Loftis 1990).

Although shelterwood harvests may better mimic a wind disturbance than clearcuts, an important distinction does occur between these natural and managed disturbances. In most shelterwood harvests, residual trees are spaced at uniform distances and a uniform overstory canopy is often maintained (Smith 1986:403-404). In tornado-disturbed sites, however, the residual trees and the overstory canopy were not uniformly spaced; overstory vegetation was variable and stands were heterogeneous. An examination of the basal area and canopy cover estimate variabilities illustrates these patterns (Table D.1). The tornado-disturbed sites had much higher variances in their basal area and canopy cover estimates than the other two treatments, indicating that the overstory vegetation was not uniform. Therefore, to mimic natural wind disturbances, a shelterwood harvest needs to create a heterogeneous overstory by maintaining non-uniform spacing of residual trees. An irregular group-shelterwood method may be able to mimic tornado disturbance. A group-shelterwood technique (Smith 1986:413-415) removes trees from expanding patches and creates a stand with heterogeneous overstory. An irregular shelterwood method (Smith 1986:413-415) can be managed to maintain scattered trees in the stand throughout the entire rotation. Therefore, an irregular group-shelterwood method could create a heterogeneous overstory by removing trees from patches and could provide large, residual trees in the succeeding stand by maintaining residual overstory (Smith 1986:414, Smith et al. 1992).

A second action that managers can do to imitate natural disturbance through their managed disturbances is to provide coarse woody debris. The tornado-disturbed sites had high amounts of woody debris that increased vegetation structure. After timber harvests, slash left in the stand could provide some of this vegetation structure at the ground level. Slash is often burned after timber harvests for silvicultural reasons (Smith 1986:223-234).

However the maintenance of slash will provide structural habitat for many species of birds, small mammals (Andreadis 1995), and other species of wildlife (Hunter 1990:175-180).

By managing overstory vegetation and coarse woody debris, forest managers can control most other vegetation characteristics. For example, removal of some overstory canopy will result in the release of mid- and understory vegetation. Therefore, forest managers may be able to better mimic natural wind disturbance through managed disturbances by maintaining non-uniform overstory vegetation and downed coarse woody debris.

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APPENDICES

Appendix A.

Common and scientific names of bird species recorded in the Oak Ridge Forestry Experiment Station, Oak Ridge, Tennessee, 1994 and 1995.

Table A.1. Common names, scientific names and species codes used to identify bird species mentioned in the text.

Common name	Scientific name	Species code
Acadian flycatcher	*Empidonax virescens*	ACFL
American crow	*Corvus brachyrhynchos*	AMCR
American goldfinch	*Carduelis tristis*	AMGO
American redstart	*Setophaga ruticilla*	AMRE
American robin	*Turdus migratorius*	AMRO
Barred owl	*Strix varia*	BAOW
Black-and-white warbler	*Mniotilta varia*	BWWA
Blue jay	*Cyanocitta cristata*	BLJA
Blue-gray gnatcatcher	*Polioptila caerulea*	BGGN
Brown thrasher	*Toxostoma rufum*	BRTH
Brown-headed cowbird	*Molothrus ater*	BHCO
Carolina chickadee	*Parus carolinensis*	CACH
Carolina wren	*Thryothorus ludovicianus*	CAWR
Chestnut-sided warbler	*Dendroica pensylvanica*	CSWA
Chimney swift	*Chaetura pelagica*	CHSW
Common flicker	*Colaptes auratus*	COFL
Common grackle	*Quiscalus quiscula*	COGR
Common yellowthroat	*Geothlypis trichas*	COYE
Downy woodpecker	*Picoides pubescens*	DOWO
Eastern bluebird	*Sialia sialis*	EABL
Eastern kingbird	*Tyrannus tyrannus*	EAKI
Eastern phoebe	*Sayornis phoebe*	EAPH
Eastern wood-pewee	*Contopus virens*	EWPE
Field sparrow	*Spizella pusilla*	FISP
Gray catbird	*Dumetella carolinensis*	GRCA
Great crested flycatcher	*Myiarchus crinitus*	GCFL
Hairy woodpecker	*Picoides villosus*	HAWO
Hooded warbler	*Wilsonia citrina*	HOWA
House finch	*Carpodacus mexicanus*	HOFI
House sparrow	*Passer domesticus*	HOSP
House wren	*Troglodytes aedon*	HOWR
Indigo bunting	*Passerina cyanea*	INBU
Kentucky warbler	*Oporornis formosus*	KEWA
Louisiana waterthrush	*Seiurus motacilla*	LOWA
Mourning dove	*Zenaida macroura*	MODO
Northern cardinal	*Cardinalis cardinalis*	NOCA
Northern oriole	*Icterus galbula*	NOOR
Ovenbird	*Seiurus aurocapillus*	OVEN
Pileated woodpecker	*Dryocopus pileatus*	PIWO
Pine warbler	*Dendroica pinus*	PIWA
Prairie warbler	*Dendroica discolor*	PRWA
Red-bellied woodpecker	*Melanerpes carolinus*	RBWO
Red-eyed vireo	*Vireo olivaceus*	REVI
Red-headed woodpecker	*Melanerpes erthrocephalus*	RHWO

Table A.1. (Continued).

Common name	Scientific name	Species code
Red-shouldered hawk	*Buteo lineatus*	RSHA
Red-tailed hawk	*Buteo jamaicensis*	RTHA
Rock dove	*Columba livia*	RODO
Rose-breasted grosbeak	*Pheucticus ludovicianus*	RBGR
Ruby-throated hummingbird	*Archilochus colubris*	RTHU
Rufous-sided towhee	*Pipilo erthrophthalmus*	RSTO
Scarlet tanager	*Piranga olivacea*	SCTA
Summer tanager	*Piranga rubra*	SUTA
Tufted titmouse	*Parus bicolor*	TUTI
Turkey vulture	*Cathartes aura*	TUVU
Whip-poor-will	*Caprimulgus vociferus*	WHIP
White-breasted nuthatch	*Sitta carolinensis*	WBNU
White-eyed vireo	*Vireo griseus*	WEVI
Wild turkey	*Meleagris gallopavo*	WITU
Wood thrush	*Hylocichla mustelina*	WOTH
Worm-eating warbler	*Helmitheros vermivorus*	WEWA
Yellow-billed cuckoo	*Coccyzus americanus*	YBCU
Yellow-breasted chat	*Icteria virens*	YBCH
Yellow-throated vireo	*Vireo flavifrons*	YTVI
Yellow-throated warbler	*Dendroica dominica*	YTWA

Appendix B.

Common and scientific names of plant species recorded in the Oak Ridge Forestry Experiment Station, Oak Ridge, Tennessee, 1994 and 1995.

Table B.1. Common and Scientific names of the shrub and tree species observed on the Oak Ridge Forestry Experiment Station, Oak Ridge, Tennessee, 1994 and 1995.

Common Name	Scientific Name	Common Name	Scientific Name
American basswood	*Tilia heterophylla*	Strawberry bush	*Euonymus americanus*
American beech	*Fagus grandifolia*	Sugar maple	*Acer saccharum*
American chestnut	*Castanea dentata*	Sweet gum	*Liquidambar styraciflua*
American elm	*Ulmus americana*	Sycamore	*Platanus occidentalis*
American hornbeam	*Carpinus caroliniana*	Virginia pine	*Pinus virginiana*
Azela	*Rododendrum nudiflorum*	White ash	*Fraxinus americana*
Big leaf magnolia	*Magnolia tripetala*	White oak	*Quercus alba*
Bitternut hickory	*Carya cordiformis*	White pine	*Pinus strobus*
Black cherry	*Prunus serotina*	Winged elm	*Ulmus alata*
Black gum	*Nyssa sylvatica*	Winged sumac	*Rhus scopallina*
Black oak	*Quercus velutina*	Yellow poplular	*Lirodendron tulipifera*
Black walnut	*Juglans nigra*		
Blackjack oak	*Quercus marilandica*		
Blueberry sp.	*Vaccinium* sp.		
Carolina buckthorn	*Rhamnus caroliniana*		
Carolina silverbell	*Halesia carolina*		
Chestnut oak	*Quercus prinus*		
Eastern hemlock	*Tsuga canadensis*		
Flowering dogwood	*Cornus florida*		
Green ash	*Fraxinus pennsylvanica*		
Hackberry	*Celtis laevigata*		
Loblolly pine	*Pinus taeda*		
Mimosa	*Albiza julibrissin*		
Mockernut hickory	*Carya tomentosa*		
Musclewood	*Ostrya virginiana*		
Northern red oak	*Quercus rubra*		
Pawpaw	*Asimina triloba*		
Pignut hickory	*Carya glabra*		
Princess tree	*Paulownia tomentosa*		
Privet	*Ligustrum sinense*		
Red cedar	*Juniperus virginiana*		
Red maple	*Acer rubrum*		
Red mulberry	*Morus rubra*		
Redbud	*Cercis canadensis*		
Sassafras	*Sassafras albidum*		
Scarlet oak	*Quercus coccinea*		
Serviceberry	*Amelachier arborea*		
Shagbark hickory	*Carya ovata*		
Short leaf pine	*Pinus echinata*		
Slippery elm	*Ulmus rubra*		
Smooth sumac	*Rhus glabra*		
Sourwood	*Oxydendrum arboreum*		
Southern red oak	*Quercus falcata*		
Sparkleberry	*Vaccinium arboreum*		

Table B.2. Scientific names of the grass, forb and woody vine species observed on the Oak Ridge Forestry Experiment Station, Oak Ridge, Tennessee, 1994 and 1995.

Sceintific name	Sceintific name
Ambrosia arcmisifolia	*Scleria* sp.
Ambrosia trifida	*Setaria glauca*
Andropogon virginiana	*Smilacina* sp.
Asarum canadense	*Smilax* sp.
Aureolaria scropluloram	*Solanum carolinense*
Bidens bipinnata	*Solidago* sp.
Carduus nutans	*Sorghum vulgare*
Cassia nictitans	*Trifolium repens*
Chimaphila maculata	*Verbascum thapsus*
Coreopsis angustifolia	*Verbesina occidentalis*
Dactylis glomerata	*Vernonia glauca*
Desmodium sp.	*Viola* sp.
Dioscorea villosa	*Vitis* sp.
Erechtites hieracifolia	
Erigeron annuus	
Erigeron canadensis	
Eupatorium perfoliatum	
Eupatorium pupureum	
Eupatorium rugosum	
Festuca elatior	
Fragaria virginiana	
Galium aparine	
Galium pilosum	
Gnaphalium obtusifolium	
Hedeoma pulegioides	
Hepatica americana	
Ipomoea purpurea	
Lespedeza cuneata	
Lespedeza hirta	
Lespedeza striata	
Lobelia inflata	
Lonicera japonica	
Lycopodium distatum	
Microstegium vimineum	
Oxalis stricta	
Panicum sp.	
Parthenocissus quinquefolia	
Perilla frutescens	
Phytolacca americana	
Podophyllum pelatum	
Polystichum acrostichoides	
Pteridium aquilinum	
Rhus radicans	
Rubus sp.	

Appendix C.

Avian species abundances estimated from spot maps and 50 m radius point counts and avian productivity, Oak Ridge Forestry Experiment Station, Oak Ridge, Tennessee, 1994 and 1995.

Table C.1. Mean density (number of territories per 40 ha) and (SE) of breeding bird species encountered on two disturbance treatments and an undisturbed forest, Oak Ridge Forestry Experiment Station, Oak Ridge, Tennessee, 1994 and 1995. Densities were calculated from spot maps (N = 6).

	1994			1995		
Species	Clearcut (n = 2)	Forest (n = 2)	Tornado (n = 2)	Clearcut (n = 2)	Forest (n = 2)	Tornado (n = 2)
ACFL	0.000 (0.000)	5.250 (0.750)	0.000 (0.000)	0.000 (0.000)	7.300 (2.300)	0.000 (0.000)
AMGO	8.333 (8.333)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)
BGGN	9.556 (1.556)	8.700 (3.700)	21.952 (7.215)	11.778 (6.222)	18.500 (7.500)	24.901 (6.151)
BHCO[1]	3.5	6	9	4	4	3
BLJA	0.000 (0.000)	10.950 (0.550)	3.399 (0.768)	1.111 (1.111)	4.000 (0.000)	3.048 (2.215)
BRTH	4.000 (4.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)
CACH	19.444 (5.556)	12.200 (7.800)	30.241 (3.925)	17.833 (1.167)	13.550 (3.950)	12.971 (2.445)
CAWR	5.444 (1.556)	0.000 (0.000)	28.575 (2.259)	14.778 (9.222)	3.750 (0.250)	27.029 (2.445)
COFL	5.000 (5.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)
COYE	12.778 (5.000)	0.000 (0.000)	0.000 (0.000)	10.556 (0.556)	0.000 (0.000)	0.000 (0.000)
DOWO	0.000 (0.000)	0.000 (0.000)	3.421 (3.421)	0.000 (0.000)	0.000 (0.000)	6.316 (6.316)
EABL	0.000 (0.000)	0.000 (0.000)	1.053 (1.053)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)
EAPH	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	1.042 (1.042)
EWPE	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	5.340 (0.077)
FISP	21.667 (11.667)	0.000 (0.000)	0.000 (0.000)	8.334 (8.334)	0.000 (0.000)	0.000 (0.000)
GCFL	0.000 (0.000)	0.000 (0.000)	2.083 (2.083)	0.000 (0.000)	1.500 (1.500)	2.084 (2.084)
HAWO	0.000 (0.000)	4.750 (0.750)	4.167 (4.167)	0.000 (0.000)	7.500 (0.500)	4.792 (4.792)
HOFI	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)
HOWA	26.778 (6.222)	4.250 (4.250)	21.776 (0.724)	31.000 (6.000)	4.650 (1.850)	23.289 (1.711)
INBU	41.278 (5.722)	0.000 (0.000)	14.770 (1.020)	25.722 (1.278)	0.000 (0.000)	13.246 (0.088)
KEWA	13.333 (6.667)	0.000 (0.000)	14.145 (1.645)	10.278 (4.722)	0.000 (0.000)	13.936 (1.853)
MODO	0.000 (0.000)	0.000 (0.000)	0.526 (0.526)	8.334 (8.334)	0.000 (0.000)	12.281 (4.386)
NOCA	22.500 (12.500)	0.000 (0.000)	17.007 (1.743)	25.167 (6.833)	4.500 (0.500)	19.463 (2.621)
OVEN	0.000 (0.000)	28.500 (9.500)	0.000 (0.000)	0.000 (0.000)	25.050 (2.550)	0.000 (0.000)
PIWA	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	2.750 (2.750)	0.000 (0.000)

Table C.1. (Continued).

	1994			1995		
Species	Clearcut (n = 2)	Forest (n = 2)	Tornado (n = 2)	Clearcut (n = 2)	Forest (n = 2)	Tornado (n = 2)
PIWO	0.000 (0.000)	1.000 (1.000)	0.833 (0.833)	0.000 (0.000)	0.000 (0.000)	0.833 (0.833)
PRWA	36.667 (3.333)	0.000 (0.000)	2.884 (0.800)	30.167 (1.833)	0.000 (0.000)	3.037 (0.121)
RBWO	1.944 (1.944)	2.800 (2.800)	9.945 (0.471)	0.000 (0.000)	3.500 (0.500)	5.197 (2.697)
REVI	9.944 (3.944)	41.500 (5.500)	32.807 (3.860)	3.056 (3.056)	36.050 (10.450)	31.776 (10.724)
RSTO	32.056 (4.055)	0.000 (0.000)	14.650 (7.982)	41.333 (4.667)	0.000 (0.000)	8.081 (3.498)
RSHA	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.500 (0.500)	0.000 (0.000)	0.000 (0.000)
RTHU	0.000 (0.000)	0.000 (0.000)	2.084 (2.084)	0.000 (0.000)	0.000 (0.000)	2.084 (2.084)
SCTA	0.000 (0.000)	7.500 (2.500)	3.180 (2.654)	0.000 (0.000)	18.600 (0.600)	4.825 (1.491)
SUTA	8.222 (1.222)	4.000 (0.000)	16.524 (3.893)	6.333 (4.667)	1.750 (1.750)	17.697 (0.197)
TUTI	6.389 (3.611)	8.150 (0.650)	7.829 (4.671)	2.222 (2.222)	3.400 (3.400)	2.083 (2.083)
TUVU	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.209 (0.209)
WBNU	0.000 (0.000)	6.500 (1.500)	14.145 (1.645)	0.000 (0.000)	4.000 (4.000)	6.590 (1.327)
WEVI	59.444 (20.556)	0.000 (0.000)	12.610 (8.443)	38.889 (1.111)	0.000 (0.000)	13.454 (0.296)
WEWA	0.000 (0.000)	2.000 (2.000)	0.000 (0.000)	1.500 (1.500)	0.000 (0.000)	0.000 (0.000)
WITU	0.000 (0.000)	0.000 (0.000)	0.209 (0.209)	0.000 (0.000)	0.000 (0.000)	0.417 (0.417)
WOTH	0.000 (0.000)	10.000 (0.000)	0.000 (0.000)	0.000 (0.000)	11.600 (11.600)	0.789 (0.789)
YBCH	42.222 (2.222)	0.000 (0.000)	13.443 (7.610)	39.722 (4.722)	0.000 (0.000)	11.645 (4.145)
YBCU	2.778 (2.778)	6.500 (1.500)	3.607 (0.976)	0.000 (0.000)	4.500 (0.500)	3.125 (3.125)
YTVI	1.833 (0.167)	0.000 (0.000)	4.090 (1.173)	0.000 (0.000)	2.250 (2.250)	1.623 (0.044)

[1] No territories were determined for brown headed cowbirds, instead the mean number of observed females are reported.

Table C.2. Mean abundance (number per point count) and (SE) of breeding bird species observed on 50-m radius point counts in two disturbance treatments and an undisturbed forest, Oak Ridge Forestry Experiment Station, Oak Ridge, Tennessee, 1994 and 1995. (N = 189).

	1994			1995		
Species	Clearcut (n = 54)	Forest (n = 72)	Tornado (n = 63)	Clearcut (n = 54)	Forest (n = 72)	Tornado (n = 63)
ACFL	0.0000 (0.0000)	0.1528 (0.0427)	0.0000 (0.0000)	0.0000 (0.0000)	0.3056 (0.0547)	0.0000 (0.0000)
AMCR	0.0000 (0.0000)	0.0000 (0.0000)	0.0000 (0.0000)	0.0000 (0.0000)	0.0139 (0.0139)	0.0159 (0.0159)
AMGO	0.0000 (0.0000)	0.0000 (0.0000)	0.0000 (0.0000)	0.0370 (0.0259)	0.0000 (0.0000)	0.0159 (0.0159)
AMRE	0.0000 (0.0000)	0.0000 (0.0000)	0.0000 (0.0000)	0.0000 (0.0000)	0.0139 (0.0139)	0.0000 (0.0000)
BAOW	0.0000 (0.0000)	0.0000 (0.0000)	0.0000 (0.0000)	0.0000 (0.0000)	0.0000 (0.0000)	0.0317 (0.0317)
BGGN	0.0185 (0.0185)	0.2500 (0.0585)	0.3968 (0.0833)	0.0741 (0.0446)	0.6250 (0.0958)	0.5873 (0.0866)
BHCO	0.2407 (0.0874)	0.1388 (0.5346)	0.4444 (0.1103)	0.1667 (0.1667)	0.1806 (0.0535)	0.3492 (0.0851)
BLJA	0.0370 (0.0259)	0.1111 (0.0422)	0.0159 (0.0159)	0.0000 (0.0000)	0.0556 (0.0336)	0.0635 (0.0310)
BRTH	0.0185 (0.0185)	0.0000 (0.0000)	0.0000 (0.0000)	0.0185 (0.0185)	0.0000 (0.0000)	0.0000 (0.0000)
BWWA	0.0000 (0.0000)	0.0000 (0.0000)	0.0000 (0.0000)	0.0185 (0.0185)	0.0000 (0.0000)	0.0000 (0.0000)
CACH	0.2222 (0.0778)	0.3750 (0.1194)	0.4444 (0.0809)	0.3518 (0.1095)	0.4444 (0.1151)	0.5714 (0.1102)
CAWR	0.0185 (0.0185)	0.0139 (0.0139)	0.5556 (0.0809)	0.2407 (0.0644)	0.1389 (0.0456)	0.8095 (0.0842)
COFL	0.0185 (0.0185)	0.0000 (0.0000)	0.0000 (0.0000)	0.0185 (0.0185)	0.0000 (0.0000)	0.0159 (0.0159)
COGR	0.0000 (0.0000)	0.0139 (0.0139)	0.0000 (0.0000)	0.0000 (0.0000)	0.0139 (0.0139)	0.0317 (0.0223)
COYE	0.0741 (0.0360)	0.0000 (0.0000)	0.0000 (0.0000)	0.2222 (0.0571)	0.0000 (0.0000)	0.0000 (0.0000)
DOWO	0.0000 (0.0000)	0.0000 (0.0000)	0.0159 (0.0159)	0.0000 (0.0000)	0.0000 (0.0000)	0.1587 (0.0516)
EABL	0.0000 (0.0000)	0.0000 (0.0000)	0.0159 (0.0159)	0.0000 (0.0000)	0.0000 (0.0000)	0.0000 (0.0000)
EAKI	0.0000 (0.0000)	0.0000 (0.0000)	0.0000 (0.0000)	0.0185 (0.0185)	0.0000 (0.0000)	0.0000 (0.0000)
EAPH	0.0000 (0.0000)	0.0000 (0.0000)	0.0000 (0.0000)	0.0000 (0.0000)	0.0000 (0.0000)	0.0159 (0.0159)
EWPE	0.0000 (0.0000)	0.0278 (0.0195)	0.0317 (0.0223)	0.0000 (0.0000)	0.0000 (0.0000)	0.0000 (0.0000)
FISP	0.3333 (0.0699)	0.0000 (0.0000)	0.0000 (0.0000)	0.3333 (0.0648)	0.0000 (0.0000)	0.0000 (0.0000)
GCFL	0.0000 (0.0000)	0.0000 (0.0000)	0.0159 (0.0159)	0.0000 (0.0000)	0.0278 (0.0195)	0.0159 (0.0159)
GRCA	0.0000 (0.0000)	0.0000 (0.0000)	0.0000 (0.0000)	0.0370 (0.0259)	0.0000 (0.0000)	0.0317 (0.0223)
HAWO	0.0370 (0.0259)	0.0833 (0.0328)	0.0476 (0.0270)	0.0000 (0.0000)	0.2500 (0.0551)	0.2540 (0.0678)
HOFI	0.0185 (0.0185)	0.0000 (0.0000)	0.0000 (0.0000)	0.0000 (0.0000)	0.0000 (0.0000)	0.0000 (0.0000)

Table C.2. (Continued).

	1994			1995		
Species	Clearcut (n = 54)	Forest (n = 72)	Tornado (n = 63)	Clearcut (n = 54)	Forest (n = 72)	Tornado (n = 63)
HOWA	0.1481 (0.0555)	0.0694 (0.0302)	0.4921 (0.0746)	0.5556 (0.1012)	0.1111 (0.0373)	0.6190 (0.0798)
INBU	0.4814 (0.0782)	0.0000 (0.0000)	0.2540 (0.0783)	0.6852 (0.0983)	0.0000 (0.0000)	0.3651 (0.0611)
KEWA	0.0740 (0.0360)	0.0000 (0.0000)	0.3015 (0.0665)	0.1296 (0.0464)	0.0000 (0.0000)	0.4762 (0.0872)
MODO	0.0185 (0.0185)	0.0000 (0.0000)	0.0159 (0.0159)	0.2037 (0.0613)	0.0000 (0.0000)	0.2857 (0.0657)
NOCA	0.1111 (0.0506)	0.0556 (0.0272)	0.1905 (0.0673)	0.5741 (0.0900)	0.1944 (0.0614)	0.6984 (0.0866)
NOOR	0.0000 (0.0000)	0.0000 (0.0000)	0.0000 (0.0000)	0.0185 (0.0185)	0.0000 (0.0000)	0.0000 (0.0000)
OVEN	0.0185 (0.0185)	1.0000 (0.0987)	0.0159 (0.0159)	0.0000 (0.0000)	0.7361 (0.0685)	0.0000 (0.0000)
PIWA	0.0000 (0.0000)	0.0139 (0.0139)	0.0000 (0.0000)	0.0000 (0.0000)	0.0972 (0.0352)	0.0000 (0.0000)
PIWO	0.0000 (0.0000)	0.0000 (0.0000)	0.0159 (0.0159)	0.0000 (0.0000)	0.0139 (0.0139)	0.0317 (0.0223)
PRWA	0.8704 (0.1449)	0.0000 (0.0000)	0.0000 (0.0000)	0.8704 (0.0750)	0.0000 (0.0000)	0.0476 (0.0270)
RBGR	0.0000 (0.0000)	0.0000 (0.0000)	0.0000 (0.0000)	0.0185 (0.0185)	0.0000 (0.0000)	0.0000 (0.0000)
RBWO	0.0370 (0.0259)	0.0556 (0.0272)	0.2222 (0.0528)	0.0000 (0.0000)	0.0417 (0.0237)	0.1429 (0.0444)
REVI	0.1851 (0.0652)	1.0556 (0.0987)	0.5238 (0.0779)	0.0741 (0.0360)	1.4167 (0.0810)	0.7778 (0.0889)
RSTO	0.4815 (0.0825)	0.0000 (0.0000)	0.2540 (0.0639)	0.8519 (0.0931)	0.0000 (0.0000)	0.1270 (0.0423)
RTHA	0.0000 (0.0000)	0.0000 (0.0000)	0.0159 (0.0159)	0.0000 (0.0000)	0.0000 (0.0000)	0.0000 (0.0000)
RTHU	0.0185 (0.0185)	0.0000 (0.0000)	0.0159 (0.0159)	0.0000 (0.0000)	0.0000 (0.0000)	0.0317 (0.0223)
SCTA	0.0185 (0.0185)	0.2222 (0.0493)	0.0159 (0.0159)	0.0000 (0.0000)	0.5972 (0.0675)	0.9520 (0.0373)
SUTA	0.1296 (0.0461)	0.1111 (0.0373)	0.1905 (0.0499)	0.2222 (0.0629)	0.0695 (0.0302)	0.5079 (0.0843)
TUTI	0.0370 (0.0259)	0.0833 (0.0328)	0.2222 (0.0695)	0.0741 (0.0360)	0.0695 (0.0302)	0.0794 (0.0343)
WBNU	0.0000 (0.0000)	0.1111 (0.0373)	0.0952 (0.0373)	0.0000 (0.0000)	0.1667 (0.0485)	0.2222 (0.0617)
WEVI	0.7222 (0.0968)	0.0000 (0.0000)	0.1270 (0.0423)	0.8704 (0.0879)	0.0000 (0.0000)	0.1905 (0.0499)
WEWA	0.0000 (0.0000)	0.0139 (0.0139)	0.0000 (0.0000)	0.0185 (0.0185)	0.0000 (0.0000)	0.0000 (0.0000)
WITU	0.0000 (0.0000)	0.0000 (0.0000)	0.0000 (0.0000)	0.0000 (0.0000)	0.0139 (0.0139)	0.0000 (0.0000)
WOTH	0.0000 (0.0000)	0.0833 (0.0383)	0.0159 (0.0159)	0.0556 (0.0315)	0.2083 (0.0591)	0.0476 (0.0270)
YBCH	0.8889 (0.1142)	0.0000 (0.0000)	0.3492 (0.0756)	0.9444 (0.0670)	0.0000 (0.0000)	0.3492 (0.0756)
YBCU	0.0741 (0.0446)	0.0833 (0.0328)	0.0317 (0.0223)	0.0185 (0.0185)	0.1111 (0.0373)	0.0952 (0.0373)
YTVI	0.0370 (0.0259)	0.0000 (0.0000)	0.0317 (0.0223)	0.0185 (0.0185)	0.1250 (0.0392)	0.0635 (0.0310)
YTWA	0.0000 (0.0000)	0.0000 (0.0000)	0.0159 (0.0159)	0.0000 (0.0000)	0.0000 (0.0000)	0.0000 (0.0000)

Table C.3. Species with active nests in two disturbance treatments and undisturbed forest in 1994 and 1995, Oak Ridge Forestry Experiment Station, Oak Ridge, Tennessee. Years were combined because sample sizes were small (n = 28 in 1994 and n = 11 in 1995) and no nests were found in the undisturbed forest in 1995.

Disturbance treatment	Species	Total number of active nests	Number of successful nests[1]	Number of nests that were parasitized[2]	Number of nests that failed due to predation	Number of nests that failed due to sources other than predation[3]
Clearcut	Common-yellowthroat	1	0	0	1	0
Clearcut	Field sparrow	2	2	0	0	0
Clearcut	Indigo bunting	2	2	1	0	0
Clearcut	Mourning dove	1	1	0	0	0
Clearcut	Northern cardinal	1	1	0	0	0
Clearcut	Prairie warbler	2	1	0	1	0
Clearcut	White-eyed vireo	1	1	0	0	0
Clearcut	Yellow-breasted chat	7	4	0	1	2
Clearcut	Yellow-billed cuckoo	1	0	0	0	1
Forest	Red-eyed vireo	1	1	0	0	0
Forest	Wood thrush	6	3	2	3	0
Tornado	Carolina wren	1	1	0	0	0
Tornado	Indigo bunting	1	1	1	0	0
Tornado	Mourning dove	3	2	0	0	1
Tornado	Northern cardinal	2	1	0	0	1
Tornado	Turkey vulture	1	0	0	0	1
Tornado	Whip-poor-will	4	NA[4]	0	NA	NA
Tornado	Yellow-breasted chat	2	2	1	0	0

[1] nests fledging at least one host young were considered successful
[2] nests with one brown-headed cowbird egg were considered parasitized
[3] nests that were destroyed or lost due to other factors besides predation (storms, abandonment, etc.)
[4] the fate of the whip-poor-will nests were unknown, due to the fact the young are semi-precocial and able to move from the nest after hatching

Appendix D.

Estimated means and standard errors of eighteen vegetation variables used to summarize habitat conditions in the Oak Ridge Forestry Experiment Station, Oak Ridge, Tennessee, 1994 and 1995.

Table D.1. Means and (SE) of eighteen habitat variables used to describe two disturbance treatments and an undisturbed forest, Oak Ridge Forestry Experiment Station, Oak Ridge, Tennessee, 1994 and 1995. (N = 464).

Variable [1]	Clearcut (n = 112)	Forest (n = 180)	Tornado (n = 172)
BAACRE	1.254 (0.220)	11.740 (0.240)	5.944 (0.260)
BACONF	0.0.64 (0.032)	0.800 (0.118)	0.230 (0.060)
BADECD	1.189 (0.221)	10.460 (0.258)	5.494 (0.245)
BASNAG	0.000 (0.000)	0.450 (0.066)	0.220 (0.045)
CANPYCOV	6.393 (1.368)	96.428 (0.578)	59.948 (2.379)
CANPYHT	2.967 (0.466)	18.744 (0.202)	11.806 (1.825)
FORBCOVR	23.705 (2.625)	21.500 (1.424)	31.337 (2.047)
GRASCOVR	24.867 (3.246)	1.083 (0.460)	2.674 (0.495)
GRNDCOVR	71.964 (2.518)	44.694 (2.037)	55.349 (2.252)
LITTER	1.621 (0.081)	2.471 (0.737)	1.443 (0.066)
RESIDUAL	3.884 (0.878)	99.706 (0.152)	34.884 (2.375)
SAPLDENS	2828.570 (76.000)	768.333 (26.373)	702.326 (16.717)
SEEDDENS	19651.79 (1080.33)	20677.78 (870.820)	19470.93 (721.030)
SHRBCOVR	48.795 (2.930)	13.972 (1.137)	9.913 (1.042)
VEGDENS	66.473 (2.322)	20.778 (1.479)	47.820 (2.406)
VINECOVR	64.911 (2.896)	31.722 (2.019)	49.273 (2.717)
WDYDEBR	10.744 (1.377)	2.612 (0.469)	9.406 (0.863)
WDYFREQ	2.518 (0.219)	1.111 (0.0877)	2.558 (0.174)

[1] Variable description provided in text (Table 4).

VITA

Chris Newbold was born in Harrisburg, Illinois, in 1972 and was raised in a small town in southern Illinois. Chris developed a love of outdoors and natural resources at a young age through activities such as camping, hiking, fishing and hunting with his parents and grandparents. In 1990 Chris graduated from Zeigler-Royalton High School, Zeigler, Illinois. He attended the University of Missouri, Columbia, and graduated with a Bachelor of Science degree in Fisheries and Wildlife in May 1994.

Chris' work and educational experience with universities and various public agencies has reinforced his conservation ethic, but has also developed his understanding of combining resource conservation with resource utilization. Chris received his Master of Science degree in Wildlife and Fisheries Science from the University of Tennessee, Knoxville, in May 1996. Chris' primary interest is management of non-game wildlife and he is committed to conserving all natural resources for the enjoyment of people today and for future generations.